Effects of aberrant visuo-vestibular information on higher cognition

Corcoran, J.P.

Effects of aberrant visuo-vestibular information on higher cognition

Jeremy Peter Corcoran

A thesis submitted in partial fulfilment of the
requirements of the University of Westminster
for the degree of Doctor of Philosophy

April 2019

Abstract

The ‘balance system’ comprises the peripheral and central components of the vestibular and visual systems. The peripheral structures code information pertaining to the spatial relationships and motion of the whole body. The central networks modulate and integrate this ‘space-motion information’. Coding or modulatory disturbances, due to pathology or incongruous environmental conditions, can lead to a syndromic ‘balance disorder’. This is because such disturbances result in the execution of balance system functions based on aberrant space-motion information.

The cardinal manifestations of balance disorders include instability and dizziness. Higher cognitive dysfunction is also a possible sequela, but the mechanisms that give rise to it are unclear. Prevailing theory implies that disruption of higher cognition is an indirect, mediated consequence of balance disorders. The specific objective of this research programme was to determine if aberrant space-motion information can affect higher cognition directly.

To fulfil this objective, the effects of experimentally-induced balance disorders on spatial cognitions were examined using tasks that call upon space-motion information to different extents. The results of the first study did not reveal a differential disruption of performance variables because the spatial perspective-taking (SPT) task did not reliably evoke mental self-translocation (MS-TL). Therefore, it did not call upon space-motion information any more than the control task. This led to the creation and validation of new experimental and control tasks in the second study. There was a monotonic response time function on the new SPT task, the ‘SASS task’, but not on the new control task (interaction effect: $F(1, 29) = 16.58, p < .001, \eta_p^2 = .364$). This was the first study to show empirically that performance monotonicity on a SPT task is not accounted for by graded spatial compatibility effects.

In studies 3 and 4, participants completed the new tasks while exposed to two forms of aberrant stimulation. In study 3, disruption of performance caused by optokinetic stimulation was not found to be selective to the SASS task. However, in study 4, responses

on that task after impulse stimulation were characterised by smaller boundary separations (simple effect: $t(14) = 2.89$, $p = .014$, $r = .612$). This effect was selective to the SASS task according to a significant task by cue congruity interaction ($F(2, 40) = 4.07$, $p = .025$, $\eta_p^2 = .169$), and was not due to the effects of anxiety according to mediation analyses. In the absence of concurrent inordinate disturbances of the physiological states of the participants in the SASS task group, the selective effect implied that aberrant space-motion information can have a direct effect on higher cognition.

This was the first empirical study to show the direct effect. Erroneous self-motion velocity information caused by impulse stimulation may have disrupted the temporal integration of covert body movements during MS-TL. The direct effect of aberrant space-motion information, specifically on MS-TL, has clinical implications. This cognitive function and its dependent cognitions, including ‘theory of mind’, may be particularly vulnerable. According to the results of this project, further research is warranted to explore the integrity of social functioning in persons contending with balance disorders.

Contents

Chapter 7. Study 4: The effect of impulse stimulation on spatial perspective-taking and comparison tasks with 3-D task stimuli.....203

Declaration

I declare that all the material contained in this thesis is my own work.

Jeremy P Corcoran, April 2019

Acknowledgements

First and foremost, I would like to thank my supervisors for their guidance and support over the past seven years. I am sincerely grateful to my Director of Studies, Dr Mark Gardner, whose logic and careful consideration were instrumental to the formulation of both the research and this thesis. I extend my gratitude to Professor John Golding who enabled the research to progress smoothly, not least by re-establishing the laboratories and helping devise solutions for technical issues. I thank Professor Tony Towell for being so approachable and for projecting calm.

I wish to thank members of the physiotherapy leadership team at Guy’s and St Thomas’ Hospitals, namely Dr Jacky Jones and Mr Gareth Jones. I appreciate their encouragement and collaboration. I thank the Guy’s and St Thomas’ Charity for funding my sabbatical in 2018.

I am also grateful to Dr David Barron; the undisputed ‘go-to guy’ in the Psychology Department at the University of Westminster.

Thank you to Dr Barry Seemungal and Professor Juha Silvanto for examining this work.

This thesis is dedicated to my family. I am indebted (financially as well as formatively!) to my parents, Geraldine and John. Thank you mum, for your unwavering belief in me, and dad, for your perpetual selflessness (as well as your Excel wizardry!). Finally, I would not have been able to complete this work without the love, patience and understanding of my fiancé, Bex.

List of figures

List of tables

List of presentations

Corcoran, J. P., Gardner, M. R., Towell, A., & Golding, J. F. (2017). Domain-specific cognitive function disrupted by visuo-vestibular incongruity. *11th Meeting of the British Society of Neuro-Otology*. St Thomas' Hospital, London, UK.

Corcoran, J. P., Golding, J. F., Towell, A., & Gardner, M. R. (2015). Visual-vestibular discord differentially disrupts embodied mental transformations. *British Psychological Society, Cognitive Psychology Section Annual Conference*. University of Kent, Canterbury, UK.

Corcoran, J. P., Golding, J. F., Towell, A., & Gardner, M. R. (2018). Body-based spatial reasoning selectively disrupted by vertigo after a decelerating velocity step. *30th Bárány Society Meeting*. Uppsala, Sweden.

List of abbreviations

2-D	2-dimensional
3-D	3-dimensional
a	boundary separation
ANOVA	analysis of variance
CCS	cross-coupled stimulation
COP	centre of pressure
CVPA	cortical vestibular processing area
CVS	caloric vestibular stimulation
DASS task	Double Avatar Stimulus Set task
DS cells	direction-selective ganglion cells
DV(s)	dependent variable(s)
GVS	galvanic vestibular stimulation
HRV	heart rate variability
IV(s)	independent variable(s)
LF/HF ratio	ratio of low frequency to high frequency components of a series of heartbeats
LF projector	large field projector
m	metre(s)
M	mean
M_i	a mediator variable
ms	millisecond(s)
MBPR	mental body part rotation
MOR	mental object rotation
MSTd	dorsal portion of medial superior temporal cortex
MS-TL	mental self-translocation
NDT	non-decision time
OBT task	Own Body Transformation task
OKS	optokinetic stimulation
P_e	error proportion
PIVC	parieto-insular vestibular cortex
RT(s)	response time(s)
s	second(s)
SASS task	Single Avatar Stimulus Set task

SD	standard deviation
SF projector	small field projector
SOSS task	Single Object Stimulus Set task
SPT	spatial perspective taking
T_{er}	non-decision time
TPJ	temporo-parietal junction
v	drift rate
V5/MT	visual area 5, synonymous with middle temporal visual area
VNC	vestibular nuclear complex
VO neurons	vestibular-only neurons of the vestibular nuclear complex
VOR	vestibulo-ocular reflex

Preface. Scope of this programme of research

i. Motivation for this programme of research

Balance, orientation, motion and other fundamental human functions rely upon a multimodal system (Brandt, 2000; Luxon & Bamiou, 2007), sometimes referred to as the “balance system” (Elzière, Devèze, Bartoli, & Levy, 2017, p. 171; Luxon, 2004, p. iv45). It comprises the peripheral and central components of the vestibular and visual systems. The peripheral structures code information pertaining to the spatial relationships and motion of the whole body. The central networks modulate and integrate this ‘space-motion information’. Coding or modulatory disturbances, due to pathology or incongruous environmental conditions associated with experimentation and other unnatural circumstances, can lead to a syndromic ‘balance disorder’ (Lin & Bhattacharyya, 2012; Luxon, 2004; Luxon & Bamiou, 2007). This is because such disturbances result in the execution of balance system functions based on aberrant space-motion information. This reductive account of balance disorders is based on the computer metaphor, or the idea that organisms and their systems are processors of information (Mayer, 2013).

The cardinal, often co-occurring consequences or manifestations of pathological balance disorders include postural instability, disordered eye movements, anxiety, nausea and the perceptual disturbance that is dizziness (Brandt, 2000; Ehrenfried, Guerraz, Thilo, Yardley, & Gresty, 2003; Gresty, Golding, Le, & Nightingale, 2008; Kennedy & Fowlkes, 1992; Kennedy, Lane, Lilienthal, Berbaum, & Hettinger, 1992; Luxon, 2004; Luxon & Bamiou, 2007; Smith & Zheng, 2013). Higher cognitive dysfunction is also recognised as a possible sequela of pathological balance disorders (Brandt, Strupp, & Dieterich, 2014; Ellis, Schone, Vibert, Caversaccio, & Mast, 2018; Seemungal, 2014; Smith & Zheng, 2013; Smith, Zheng, Horii, & Darlington, 2005; Walther, 2017). The mechanisms that give rise to disturbed cognition[1] are poorly understood relative to those underpinning most of the cardinal manifestations (Cousins et al., 2013; Ellis et al., 2018; Smith & Zheng, 2013). Improving the mechanistic explanations for the cognitive disruption associated with

---

[1] In this thesis, ‘cognition’ or ‘cognitive function’ will typically refer to higher, goal-driven or purposive mental processes, which are contingent on brain-body-environment interactions such that they are ‘embodied’ (Engel, Maye, Kurthen, & König, 2013; Frith & Dolan, 1996; Montello & Raubal, 2013; Pezzulo, Donnarumma, Iodice, Maisto, & Stoianov, 2017)

pathological balance disorders could lead to more responsive care for patients (Ellis et al., 2018), who often have significant functional limitations (Elzière et al., 2017; Lin & Bhattacharyya, 2012; Luxon, 2004). This prospect was the motivation for the programme of research documented in this thesis.

ii. Context of this programme of research

The contemporary mechanistic explanations for cognitive disruption affecting patients with balance-disorders can be understood in terms of mediation models of analysis. Such models describe the relationship between a causal agent or 'predictor variable' X and an 'outcome variable' Y (Hayes, 2013) . The predictor variable may have a direct effect on the outcome variable. Additionally, or alternatively, it may exert an indirect effect through one or more intervening 'mediator variables' M_i. Those variables may be arranged in parallel and/or in series. The direct and indirect effects of the predictor variable are conceptualised diagrammatically in Figure i.

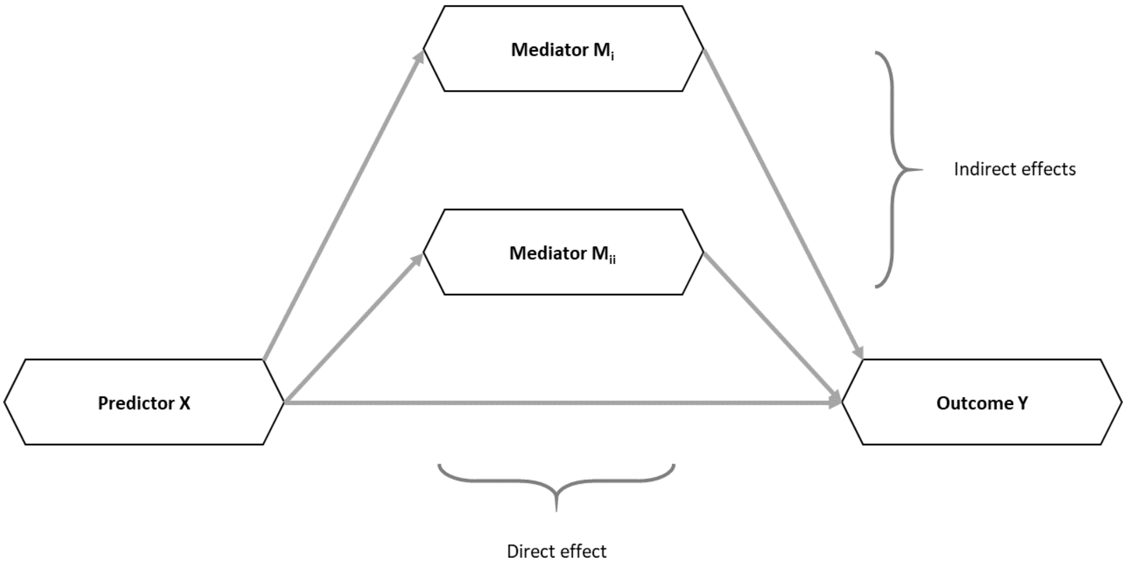


Figure i: A conceptual diagram of a parallel multiple mediator model.

Here, there are three pathways or mechanisms by which the predictor variable X can influence the outcome variable Y. One of these passes directly from X to Y, and represents the potential for X to exert a direct effect. The other two pathways lead from X to mediator variables (M_i and M_{ii}) and then to Y. These pathways represent the indirect effects that X may have on Y (Field, 2013; Hayes, 2013).

According to this scheme, (aberrant) space-motion information[2] can be conceived as the predictor variable, and higher cognitive function as the outcome variable. The cardinal manifestations of balance disorders can be modelled as potential mediator variables. Distraction or attentional diversion[3] might also be treated as a mediator variable, and be placed in series, rather than in parallel, with the cardinal manifestations, based on the mechanistic explanations that follow.

Due to their potential simultaneity, it can be difficult to distinguish the effects of these predictor and mediator variables, as acknowledged in two narrative reviews of relevant research (Smith & Zheng, 2013; Smith et al., 2005). The authors of the reviews focused mainly on discerning whether vestibular lesions can directly impair human cognition in isolation of the potential mediating effects of the lesions' cardinal manifestations. The reviews cite the results of Redfern et al. (2004) as evidence for a separable, direct effect of peripheral vestibular dysfunction. Fifteen patients with unilateral vestibular loss, but no ongoing problems with dizziness or imbalance, and 15 age- and gender-matched controls were submitted to a series of cognitive tasks, including an inhibitory reaction time (RT) task. Notably, the patients were slower to respond than the controls when the tasks were performed sitting down. The main interpretation of the results was that asymptomatic patients with vestibular lesions have disrupted attention to cognitive tasks, even when there is no postural imperative (Redfern et al., 2004; Smith & Zheng, 2013; Smith et al., 2005). Rather than promoting a direct effect of vestibular pathology and the resultant aberrance of space-motion information on higher cognition, this interpretation appears to imply there is mediation by attentional diversion.

Other studies have investigated the contribution of one of the most overt manifestations of balance disorders - deranged postural control (Smith & Zheng, 2013) - to their cognitive sequelae. Yardley et al. (2001) gauged balance-disordered and healthy participants' performance on cognitive tasks requiring both low and high levels of attention while they stood with eyes closed on stable and unstable platforms. Across the sample, the increase in balance challenge on the unstable surface led to longer RTs on the low load spatial and non-spatial tasks plus greater error on the high load cognitive tasks. Such findings have

---

[2] The focus herein is on aberrant space-motion information due to relatively acute pathology or incongruous space-motion (sensory) cues, rather than due to chronic balance system compromise (e.g. established bilateral vestibular failure) or prolonged sensory impoverishment (e.g. long-term exposure to microgravity).

[3] Attention is conceptualised as a 'fundamental cognitive function' rather than a higher cognitive function after Frith and Dolan (1996), Ardid et al. (2007), Squire et al. (2013) and Northoff (2016).

led to the proposition of a ‘posture-first principle’ (see Gresty & Golding, 2009), which asserts that maintaining or regaining balance draws on attentional resources to the detriment of higher cognitions. Hence, this principle implies a serial multiple mediator model whereby aberrant space-motion information impairs postural control which disrupts attention which, in turn, affects cognition.

In acute balance disorders, unstable visual fixation, due to nystagmus from aberrant vestibulo-ocular reflex (VOR) activation, may affect cognition or confound the assessment of it (Smith & Zheng, 2013). Smith et al. (2005) and Smith and Zheng (2013) argue that visual fixation may compete for attentional resources and, in doing so, provide further support for a serial multiple mediator model wherein attention is the pivotal mediator variable. Similarly, the psychological manifestations of balance disorders, principally anxiety, may also distract patients and, thereby, impair their performance on cognitive tasks (Smith & Zheng, 2013; Smith et al., 2005). These authors based this proposal largely on the study by Gizzi et al. (2003) which evaluated the cognitive complaints of a large sample of patients with non-traumatic balance disorders. Smith and Zheng (2013) also suggest that the intense dizziness experienced by patients with balance disorders such as Meniere’s disease might lead to cognitive disruption via attentional diversion.

Based on the reviews by Smith et al. (2005) and Smith and Zheng (2013), a combined parallel-sequential multiple mediator model accounts for the cognitive consequences of balance disorders. This model is depicted in Figure ii. The reviews provide little evidence or support for several effects, most notably for the direct, unmediated effect of aberrant space-motion information on higher cognition.

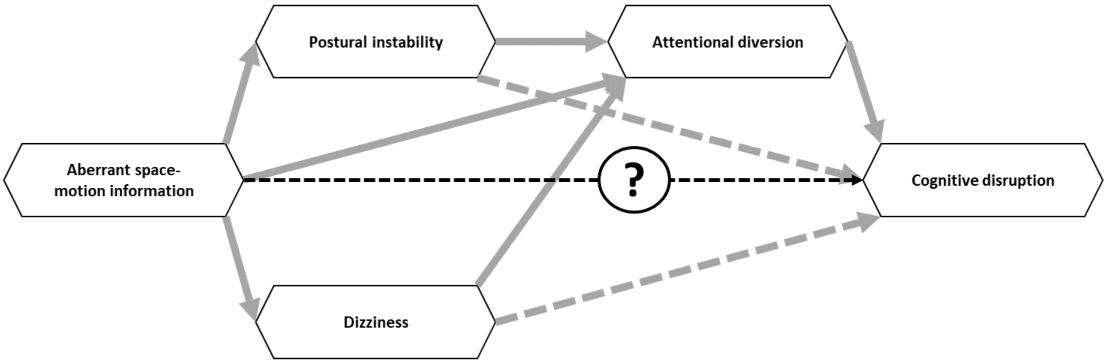


Figure ii: The combined parallel-sequential multiple mediator model of the higher cognitive sequelae of balance disorders, based on the reviews of Smith et al. (2005) and Smith and Zheng (2013).

For clarity, only two cardinal manifestations (dizziness and postural instability) are shown in parallel. Solid and dashed lines depict those effects which are strongly and weakly implied, respectively. The question mark indicates the effect which the present research programme sought to evaluate. It is possible that this direct pathway is relevant for some but not all higher cognitions. Hence, it is represented by a narrower dashed line.

The mediator model presented in Figure ii may be most applicable to controlled, experimental conditions. Moreover, a direct effect of aberrant space-motion information may be best determined by studying cognitive performance in participants with experimentally-induced balance disorders. This paradigm limits potentially confounding interactions between the cardinal manifestations. Patients with balance disorders may, for example, have anxiety which causes or compounds dizziness rather than just acting on cognitive function in parallel with it (Smith & Zheng, 2013). Many studies have adopted the paradigm, exposing healthy participants to incongruous vestibular or visual cues while submitting them to higher cognitive tasks (e.g. Gardner, Stent, Mohr, & Golding, 2017; Gresty et al., 2008; Preuss, Harris, & Mast, 2013). However, as explained in Chapter 2, there is scope for further research to ascertain the direct, unmediated effect of aberrant space-motion information, associated with incongruous visuo-vestibular cues, on cognition. Cognitive task selection may be important; tasks that evoke the cognitive function of mental self-translocation (MS-TL) may be especially well-suited to the investigation of the direct effect. MS-TL entails manipulations of a mental representation of one’s body position; that is, of self-location (Blanke et al., 2005). It may have a particular dependence on space-motion information.

iii. Goals of this programme of research

The overarching aim of this research programme was to advance the mechanistic explanations for the higher cognitive sequelae of balance disorders. The specific objective was to determine if aberrant space-motion information can directly affect higher cognition together with, or even in isolation of, the cardinal manifestations and attentional diversion caused by such misinformation.

Chapter 1. General introduction: Theoretical perspectives on visuo-vestibular cues and mental self-translocation

1.1 Overview

The visual and vestibular systems can be thought of as ‘space-motion systems’; they encode information relating to the whole body’s spatial relationships and its motion. Evidence suggests that this space-motion information is processed by the sensorimotor circuitry which controls whole-body movement. Forward models in the circuitry predict the visuo-vestibular signals that voluntary body movements should yield. The predicted space-motion information is deducted from the actual information provided by the space-motion systems. The difference serves to update the brain’s representation of body position. The updating process may involve temporal integration of space-motion information. Research has indicated that this computation benefits from an accurate, initial sensory context or starting point.

Mental self-translocation is the main higher cognitive function of interest throughout this thesis. It entails imaginary changes of the position of the body, and allows for sophisticated mental insights about other people’s surroundings and states of mind. Mental self-translocation is hypothesised to use the sensorimotor circuitry for overt body movement. Accordingly, motor commands are produced by the circuitry, but these are prevented from reaching the effector systems of the body so no movement occurs. The commands pass to forward models which predict the space-motion information that would have been coded had the body moved. This information is integrated over time such that there is a progressive transformation of the imaginary position of the body. Mental self-translocation may be particularly vulnerable to aberrant space-motion information because of the way temporal integration seems to rely on accurate visuo-vestibular cues in order to get started. Studying mental self-translocation during exposures to incongruous sensory cues may provide insight into whether aberrant space-motion information can affect cognition directly.

1.2 Introduction

The Preface introduced the term ‘space-motion information’, which stems from Indovina et al. (2014). Theory relating to the coding and modulation of this information warrants further attention. Similarly, the higher cognitive function of mental self-translocation (MS-TL) requires further explanation in order to provide a theoretical basis for the remainder of this thesis.

The specific aims of this chapter are:

- To detail the two main sensory systems that provide space-motion information,
- To review the computations which comprise the higher-level processing of space-motion information,
- To precis the two forms of aberrant sensory stimulation employed in this programme of research,
- To outline the theoretical basis of MS-TL, and,
- To develop the rationale for comparing the effects of aberrant sensory stimulation on tasks that evoke MS-TL and on control tasks that do not.

1.3 Basic visuo-vestibular sciences

1.3.1 Framing the vestibular and visual systems as ‘space-motion systems’

In this thesis, ‘space-motion information’ refers to encoded temporo-spatial activity, specifically of the whole body. It includes modal and amodal data regarding the body’s acceleration, velocity, and position with respect to time. For the sake of clarity, the term has an inconstant meaning throughout this thesis; sometimes it may refer to a specific temporo-spatial parameter derived from a particular sensory system e.g. head velocity encoded by the vestibular system, but, at other times, ‘space-motion information’ may have a less discrete meaning.

The most pertinent peripheral receptors that code space-motion information, secondary to self-generated and/or externally imposed temporo-spatial activity of the body, are the “proprioceptors” (Sherrington, 1907, p. 477). Sherrington (1907, p. 469) maintained that the key proprioceptors lay both in “a deep field constituted by the tissues of the organism beneath the surface” and in the vestibular labyrinth of the inner ear. To this day, proprioceptors are largely identified as being mechanoreceptors in muscles and joints (Lackner & DiZio, 2005; Purves et al., 2012), which probably account for Sherrington’s receptors ‘of the deep field’. Muscle proprioceptors are crucial in detecting the relative configuration of the body segments (Lackner & DiZio, 2005). While they also sense the orientation and motion of the body as a whole (Lackner & DiZio, 2005), the vestibular proprioceptors are more potent in this regard (Gu, DeAngelis, & Angelaki, 2007; Valko, Lewis, Priesol, & Merfeld, 2012; Walsh, 1961) .

Sherrington (1907) specified that receptor systems should be classified either as those which are informative about the activity of the body (i.e. as proprioceptors), or as those which signal the state of the environment; be that the internal environment enveloped by the alimentary canal, or the external environment to which the surface of the body is exposed. The latter subdivision of receptors Sherrington (1907, p. 476) termed “extero-ceptors”, and he labelled the photoreceptors of the eye as such. J. J. Gibson (1966) subsequently debated this strict delineation of receptor systems, and Sherrington’s categorisation of the photoreceptors in particular. He argued that visual afference is also informative about the position and movements of the body. Hence, vision should be considered proprioceptive as well as exteroceptive. Some modern textbooks (e.g. Carpenter, 2003; Schmidt & Lee, 2011) emphasise this point, no matter that photoreceptors are not mechanoreceptors like the classical proprioceptors are. Indeed, research has shown that vision can convey potent proprioceptive information pertaining to the whole body (Jürgens & Becker, 2011; Lee & Aronson, 1974).

Separate reviews have suggested that visual and vestibular signals constitute the most sensitive information about whole-body-related activity (Britten, 2008; DeAngelis & Angelaki, 2012; Roberts, Bronstein, & Seemungal, 2013) . In keeping with this suggestion, much recent research into self-motion perception and related higher cognitions has focused solely on understanding the interactions between vestibular and visual cues (Acerbi, Dokka, Angelaki, & Ma, 2017; Butler, Campos, & Bülthoff, 2015; De Winkel, Katliar, & Bülthoff, 2015; De Winkel, Katliar, Diers, & Bülthoff, 2018; Fetsch, Pouget, Deangelis, & Angelaki, 2012; Fetsch, Turner, DeAngelis, & Angelaki, 2009). The programme of research documented in this thesis followed suit. Accordingly, descriptions of the functional anatomy of both the vestibular and visual systems are given next, accompanied by synopses of the intricacies of temporo-spatial coding by these systems. It is important to appreciate the workings of these systems in the quest to determine if aberrant space-motion information can directly affect cognitive function. They will be referred to as ‘space-motion systems’ in order to distinguish them from other systems that extract velocity and other temporo-spatial data that are not specific to the whole body.

1.3.2 The vestibular system

1.3.2.1 Relevant functional anatomy of the vestibular system

An in-depth account of the anatomy and physiology of the peripheral vestibular system was recently authored by Kingma and van de Berg (2016). Unless otherwise stated, their account underpins the detail given below on the morphology and dynamics of the peripheral apparatus. Later in this subsection, the focus is primarily on the components of the central vestibular system which are probably involved in higher-level, as opposed to reflexive, processing of space-motion information.

1.3.2.1.1 Morphology of the vestibular labyrinth

On each side of the head, the postero-lateral part of the labyrinthine inner ear constitutes the vestibular organ. The organ itself is anatomically divisible into duct-like structures - the semicircular canals - and pouch-like structures - the otolith organs. The semicircular canals are three in number, with a roughly orthogonal relationship to each other, and contain endolymphatic fluid. One end of each canal is enlarged, and this substructure is known as the ampulla. Within a distinct area of the ampullary epithelium, hair cells are embedded. At their basal aspects, toward the non-luminal surface of the epithelium, the hair cells synapse with both afferent and efferent nerve branches. The afferent fibres have resting discharge rates due to leakage of neurotransmitter into the synaptic clefts i.e. due to synaptic noise (Lowenstein, 1975). Tufts of cilia emanate from the apical surface of each hair cell, forming a crest of cilia in the ampullary lumen. More accurately, the crest permeates a gelatinous mass - a cupula - housed within the ampulla. The cupula has the same density as the surrounding endolymphatic fluid, and it is apically anchored as well as basally fixed around the ciliary crest. Therefore, the cupula hydraulically seals the ampulla (Goldberg & Fernandez, 1984; Rabbitt et al., 2009) and does not get deflected by gravity. Instead, its form is distorted when angular acceleration of the head causes movement of the skull-fixed semicircular canal relative to the encapsulated fluid due to inertia of the latter. Cupular distortion by the fluid is analogous to the billowing of a ship's sail in the wind. The distortion deflects the cilia, affecting mechano-sensitive transduction channels in the apical portions of the hair cells and, therefore, the cells' membrane potentials. Ciliary deflection in a specific direction depolarises the hair cells, leading to increased neurotransmitter release at their basal synapses, and a net increase in afferent discharge compared to the resting rate. Ciliary deflection in the opposite direction leads to hyperpolarisation and a reduction in afferent discharge.

There are two otolith organs, the utricle and saccule, which also contain endolymph and have a delimited area of sensory epithelium comprising hair cells. As per the histological arrangement in the semicircular canals, cilia project from the hair cells into a gelatinous mass which covers the luminal surface of the sensory epithelium. However, in the otolith organs, the gelatinous mass is flattened and impregnated on its free surface with calcareous crystalline matter. Linear acceleration of the head causes movement of the skull-fixed sensory epithelium relative to the weighted gelatinous layer due to inertia of the latter. Ciliary deflection occurs, and this ultimately affects the action potential frequency in afferent fibres with which the hair cells synapse.

1.3.2.1.2 Hindbrain components of the vestibular system

The afferent vestibular neurons are bipolar cells, and their cell bodies are aggregated in the vestibular (Scarpa's) ganglion at the lateral end of the internal auditory canal (Furness, 2016). Axons pass medially from the ganglion through the canal and into the brainstem to synapse with second-order neurons in the ipsilateral vestibular nuclear complex (VNC), although some project directly to the cerebellum (Barmack, 2003; Carpenter, 2003; Cullen, 2016; Hitier, Besnard, & Smith, 2014). Several classes of second-order neurons in the VNCs have been described, including position-vestibular-pause (PVP) neurons, floccular target neurons (FTN) and vestibular-only (VO) neurons (Cullen, 2016; Cullen & Taube, 2017; Goldberg et al., 2012). The PVP and FTN neurons are sometimes classed as vestibulo-ocular reflex (VOR) neurons (Cullen & Taube, 2017). Currently, the VO neurons (not the VOR neurons) are considered to have the most prominent role in relaying vestibular signals to the thalamus and cerebral cortex (Cullen, 2016; Cullen & Taube, 2017; Goldberg et al., 2012); the higher centres which presumably mediate cognitive functions that may utilise space-motion information (Blanke, Thut, Landis, & Seeck, 2000;

Brandt, Bartenstein, Janek, & Dieterich, 1998; Cousins et al., 2013; Lopez & Blanke, 2011). However, other classes of VNC neurons might also be implicated given that there are multiple anatomical connections between the VNC, thalamus and cortex (Cullen, 2016; Dieterich & Brandt, 2015; Klingner, Axer, Brodoehl, & Witte, 2016). Furthermore, vestibular-sensitive regions of the cerebellum, which communicate with the VNCs, also project to the thalamus (Cullen, 2016; Hitier et al., 2014). The cerebellum may mediate vestibular-perceptual processing in cortical regions, as well as vestibular-reflexive processing in the brainstem (Nigmatullina, Hellyer, Nachev, Sharp, & Seemungal, 2015). Moreover, cerebellar vermal activity has been shown to correspond with the important transformation of head-centred vestibular signals into earth-referenced self-orientation and -motion cues (Yakusheva et al., 2007).

1.3.2.1.3 Tracts and decussations of the vestibular system

Ascending projections from each VNC are said to arise predominantly from their rostral aspects and pass mainly to the ventrobasal portions of the thalami (Barmack, 2003). With a relatively high degree of consistency in the literature, two discrete tracts are specified in these ascending projections: ipsilateral and contralateral vestibulothalamic tracts (Dieterich & Brandt, 2015; Kirsch et al., 2016; Lopez & Blanke, 2011). In addition, there may be an ipsilateral vestibulothalamic tract in the vicinity of the medial lemniscus tract and a contralateral tract within the medial longitudinal fasciculus or MLF (Lopez & Blanke, 2011). The latter may account for disruptions of verticality perception in patients with MLF lesions (Hitier et al., 2014). Direct connections between the VNCs and the insular cortices have been proposed (Dieterich & Brandt, 2015; Kirsch et al., 2016).

Cullen and Taube (2017) refer to two main functional pathways from the VNCs via the thalamus to the cortex: the anterior and posterior thalamocortical pathways. The former comprises direct projections from the anterior dorsal thalamus to the retrosplenial cortex and indirect, polysynaptic projections to the entorhinal cortex. This pathway is hypothesised to comprise the head direction network, which is thought to be important for navigation. The posterior pathway passes from the VNCs to parietal and temporoparietal cortices via the ventrolateral and posterolateral thalamus. This has been less extensively studied but may contribute to the coordination of space-motion perceptions (see section 1.5.3) and other higher cognitions less dependent on spatial memory (Cullen & Taube, 2017).

There are robust, decussating or commissural connections between the VNCs, and between higher centres sensitive to vestibular stimulation. Three crossings between the VNCs on opposing sides of the brainstem have been identified (Dieterich & Brandt, 2015; Kirsch et al., 2016). The splenium of the corpus callosum is proposed to be the main route of inter-hemispheric transmission between vestibular areas of the cortex (Dieterich & Brandt, 2015; Kirsch et al., 2016). The robust commissural system may enable coherent perceptual and cognitive processing of vestibular information in the posterior thalamocortical pathway. It remains unclear if and how that pathway may merge with its anterior counterpart (Cullen & Taube, 2017).

1.3.2.1.4 Forebrain components of the vestibular system

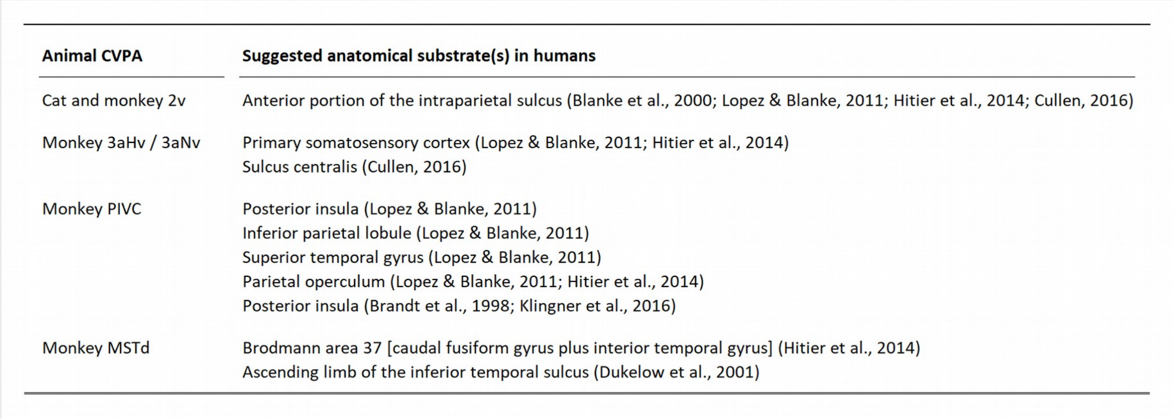
Vestibular stimulation activates a wider dispersion of thalamic regions than other forms of sensory stimulation (Hitier et al., 2014). Similarly, a wide array of cortical areas is modulated by vestibular stimulation. These areas are clustered at the temporoparietal junction (TPJ), or perisylvian region (Blanke et al., 2000; Dieterich & Brandt, 2015), and have been described as forming a parietotemporal network (Dieterich & Brandt, 2015). However, areas beyond those lobes adapt with vestibular stimulation, hence, ‘cortical vestibular processing areas’ (CVPAs) may be a more apt term (adapted from Hitier et al., 2014).

1.3.2.1.5 Distributivity of the cortical vestibular system

The whereabouts of the CVPAs is well-established in some lower animals due to anatomical tracer studies and single unit recordings (Dieterich & Brandt, 2015; Kaski et al., 2016). Human homologues of these CVPAs have been sought through largely non-functional, unilateral stimulations of the peripheral vestibular system (e.g. by galvanic or caloric vestibular stimulation, or by sound stimulation i.e. vestibular-evoked myogenic potentials) while participants have been relatively immobile in scanners or electrophysiological recording apparatus (Dieterich & Brandt, 2015; Klingner et al., 2016). Therefore, the exact locations of some, if not all, of the human CVPAs are still unclear (Lopez & Blanke, 2011). Table 1.1 lists some of the key animal CVPAs and possible human homologues of these.

Table 1.1: Possible human correlates of animal cortical vestibular processing areas (CVPAs)

2v - posterior border of Brodmann area 2; 3aHv - 3a-hand-vestibular area; 3aNV - 3a-neck-vestibular area; PIVC - parieto-insular vestibular cortex; MSTd - dorsal portion of medial superior temporal area



Animal CVPA	Suggested anatomical substrate(s) in humans
Cat and monkey 2v	Anterior portion of the intraparietal sulcus (Blanke et al., 2000; Lopez & Blanke, 2011; Hitier et al., 2014; Cullen, 2016)
Monkey 3aHv / 3aNv	Primary somatosensory cortex (Lopez & Blanke, 2011; Hitier et al., 2014) Sulcus centralis (Cullen, 2016)
Monkey PIVC	Posterior insula (Lopez & Blanke, 2011) Inferior parietal lobule (Lopez & Blanke, 2011) Superior temporal gyrus (Lopez & Blanke, 2011) Parietal operculum (Lopez & Blanke, 2011; Hitier et al., 2014) Posterior insula (Brandt et al., 1998; Klingner et al., 2016)
Monkey MSTd	Brodmann area 37 [caudal fusiform gyrus plus interior temporal gyrus] (Hitier et al., 2014) Ascending limb of the inferior temporal sulcus (Dukelow et al., 2001)

The engagement of other areas of the human cortex, not necessarily so strongly linked with animal CVPAs, has been reported during vestibular stimulation. These areas include the superior parietal lobule (Klingner et al., 2016), premotor and primary motor cortices (Klingner et al., 2016; Lopez & Blanke, 2011), regions of the inferior, middle and superior frontal gyri (Klingner et al., 2016; Lopez & Blanke, 2011), and hippocampus and parahippocampal areas (Hitier et al., 2014; Klingner et al., 2016; Lopez & Blanke, 2011).

1.3.2.1.6 Bilaterality of the cortical vestibular system

The exact whereabouts of the human CVPAs may be unclear, but the duplication of all of the areas between the hemispheres is much less so (Dieterich & Brandt, 2015; Mast, Preuss, Hartmann, & Grabherr, 2014). Some intricacies of this bilateral arrangement include: the dominance of CVPAs in the non-dominant hemisphere (Dieterich & Brandt, 2015; Nigmatullina et al., 2015), and the greater engagement of CVPAs ipsilateral to the vestibular end organ most strongly stimulated (Dieterich & Brandt, 2015; Lopez & Blanke, 2011). The lack of case reports of perceptual deficits following focal cortical lesions attests to the notion that self-motion perception is processed bilaterally in the cortex (Kaski et al., 2016).

1.3.2.1.7 Hierarchism versus parallelism in the cortical vestibular system

Table 1.1 indicates that the whereabouts of the human homologue of the parieto-insular vestibular cortex (PIVC) is particularly controversial. The functional role of this region has also been the topic of considerable attention and debate. Several research groups have postulated that the human PIVC has a dominant role in encoding self-orientation and -motion perceptions (Brandt et al., 1998; Cullen, 2016; Hitier et al., 2014; Klingner et al., 2016; Zu Eulenburg, Caspers, Roski, & Eickhoff, 2012). The human PIVC is certainly well-connected to the other CVPAs (Cullen, 2016), which may confer its dominance. Dieterich and Brandt (2015) suggest that a vestibular cortical hierarchy arises from the network of connections between the CVPAs, and that the human PIVC is likely to be at the lowest level in that hierarchy, and the human MSTd at the highest. However, Kaski et al. (2016) propose that the TPJ, which probably contains the human PIVC[4], functions like a cortical temporal integrator, enabling self-location perception by summing velocity and/or acceleration signals over time (see section 1.4.3 for further details). This proposal is supported by the work of Ionta et al. (2011), who found brain damage localised to the TPJ in patients with discrete disorders of self-location awareness. Accordingly, the human PIVC would be toward the pinnacle of a vestibular cortical hierarchy. It is unclear if and how the head direction network, comprising the anterior thalamocortical pathway, might feature in such a hierarchy (Cullen & Taube, 2017).

Lopez and Blanke (2011) conclude that there is still insufficient evidence that the human PIVC is preeminent, due to the poor temporal resolution of the functional neuroimaging techniques used in studies that have suggested it is. Studies using techniques with higher temporal resolution, e.g. electroencephalography (EEG), have indicated that there is parallel processing of vestibular information and not such a clear hierarchy (Lopez & Blanke, 2011).

1.3.2.1.8 Multimodality of the cortical vestibular system

Even if the human PIVC were the hub of higher vestibular processing, there would still be no substrate for a 'primary vestibular cortex'. After all, the PIVC and all of the other CVPAs are sensitive not only to peripheral vestibular stimulation, but also to afferent signals from other sensory systems (Brandt et al., 1998; Cullen, 2016). More specifically,

---

[4] The specific area of the TPJ suggested by Kaski et al. (2016) to be the temporal integrator was the (right) angular gyrus.

all CVPAs are modulated by signals that stem from the retina and/or muscle proprioceptors, meaning that these areas are intrinsically multimodal (Brandt, Kugler, Schniepp, Wuehr, & Huppert, 2015; Cullen, 2016; Dieterich & Brandt, 2015). This multimodality in several regions of the cortex is said to be vital for perceptual and cognitive processing (Cullen, 2016). Given that the CVPAs are, in fact, a collection of areas which process all manner of sensory signals about head/body attitude and movement, some researchers have suggested a move away from considering these as the components of a "vestibular network" (Klingner et al., 2016, p. 379). Instead, they appear to constitute a 'space-motion network'.

1.3.2.2 Aspects of temporo-spatial coding by the vestibular system

1.3.2.2.1 Temporo-spatial coding by the semicircular canals

The semicircular canals and otolith organs of the vestibular apparatus are functionally, as well as anatomically, distinguishable. Since the roughly orthogonal semicircular canals in one ear are mirror symmetric with the canals of the contralateral ear, co-planar pairs of canals exist between the two ears. Mutually antagonistic afferent signals are transmitted from the opposing lateral semicircular canals, and from the superior canals and contraposed posterior canals, to the vestibular nuclear complexes and cerebellum (Carpenter, 2003). Although deflections of the cupula and cilia are reactions to angular head accelerations, duct-cupula-endolymph dynamics mean that discharge in the vestibular afferents encodes rotational velocity of the head. Those dynamics are disrupted during low frequency (<0.1 Hz) head movements which results in our underestimation or complete imperception of such head movements based on vestibular signals alone (Mergner & Rosemeier, 1998). Humans typically demonstrate higher perceptual than vestibulo-ocular reflex (VOR) thresholds (Seemungal, Gunaratne, Fleming, Gresty, & Bronstein, 2004). In the yaw plane, the perceptual thresholds for angular velocity and acceleration are approximately 1°/s (Bermúdez Rey et al., 2016) and $1°/s^2$ (Seemungal et al., 2004), respectively.

The semicircular canals can be conceptualised as instantaneous head angular velocity detectors (Carpenter, 2003; Mergner & Rosemeier, 1998) because their outputs have a short time constant of approximately 3 to 5 s. Yet related neural activity in the VNC has a longer time constant of 15 to 25 s (Yakushin, Raphan, & Cohen, 2017). A central integrative network, referred to as the velocity storage integrator (Laurens & Angelaki, 2011; Yakushin et al., 2017), lengthens the processing of the afferent vestibular signal. Typically, the conversion from the shorter to the longer time constant has a corresponding influence on vestibular-reflexive and vestibular-perceptual activity. This was clearly demonstrated in a group of healthy participants whose perception of angular velocity, following impulse decelerations in a motorised rotatory chair, decayed at a rate commensurate with the decrease in slow phase velocity of their nystagmus (Okada, Grunfeld, Shallo-Hoffmann, & Bronstein, 1999). Perceptual and reflexive activity can, however, be uncoupled by certain fates of ontogenetic development (Nigmatullina et al., 2015). Despite the action of the velocity storage mechanism, the central processing of semicircular canal signals does adapt to constant velocity rotation of the head in one direction. A consequence of this adaptation is that a person who has been set spinning at a fixed speed will have a gradual reduction of his or her perception of the ongoing turning motion (Carpenter, 2003; Laurens & Angelaki, 2011).

1.3.2.2.2 Temporo-spatial coding by the otolith organs

The functional distinction of the otolith organs is that they are biological linear accelerometers rather than instantaneous head angular velocity detectors. As referred to in the anatomy subsection above (see section 1.3.2.1.1), earth-horizontal accelerations of the head cause a relative displacement of the weighted gelatinous otolithic membrane due to its inertia. Displacement of the membrane also occurs during static head tilts i.e. head position changes relative to gravity; the membrane shifts to a more dependent position with the same shearing effect on the cilia which permeate it. The otolith organs are, therefore, said to give rise to “vestibular graviception” (Barra et al., 2010, p. 3552). As this suggests, and as Einstein’s equivalence principle asserts (Einstein, 1907), the discharge from the otolith organs does not distinguish linear accelerations that are due to head tilts from those that are the result of translational self-motion (Cullen, 2016; Merfeld, Park, Gianna-Poulin, Black, & Wood, 2005). However, the central integration of otolith signals with semicircular canal signals enables tilt-translation disambiguation (Cullen, 2016; Merfeld et al., 2005). There is much less adaptation of signalling in the otolith subsystem than in the semicircular canal subsystem (Carpenter, 2003; Walsh, 1961).

1.3.3 The visual system

1.3.3.1 Relevant functional anatomy of the visual system

The components of the visual system that transmit space-motion information match those of the vestibular system for complexity and, in some regards, elusiveness. In humans, as with most other vertebrates, signals spread in visual pathways from the retina - the photosensitive layer inside the eye - mainly to forebrain areas. The retina comprises ten strata (Douglas & Lawnenson, 2016; Rokszin et al., 2010), but three cell types straddling those strata warrant particular attention herein. The descriptions of these cell types will be based on the reputable medical textbook 'Gray's Anatomy' (Douglas & Lawnenson, 2016), unless otherwise specified.

1.3.3.1.1 Histology of the retina

The first of the retinal cell types of interest lies basally and constitutes the photoreceptors - rod and cone cells. There is a homogeneous population of rod cells in the retina, but three classes of cone cells - S, M and L cones. S cones are fewest in number and are distributed evenly throughout the retina, although they are absent from the fovea - the pitted part of the retina that contains tightly-packed M and L cones and provides sharp central vision. The M and L cones are unevenly distributed throughout the rest of the retina, and are vastly outnumbered by the rod cells beyond the fovea. The rod cells are most densely distributed around the peripheries of the fovea and the optic disc. Rods and cones are both long, radially-oriented cell types. They both have a stack of membranous discs at their basal extremities. Embedded in these discs are visual pigments - rhodopsins - bound to a light-absorbing substance - retinal.

Bipolar cells comprise the second cell type of interest. These nerve cells are also radially-oriented, lying in series with the photoreceptors; that is, beyond the photoreceptors' apices. The dendritic branches of the bipolar cells synapse with either rod or cone cells beneath. Cone bipolar cells have fewer connections with cone cells than rod bipolar cells have with rod cells.

The axons of the bipolar cells synapse with ganglion cells which comprise the third cell type of interest. These are the output neurons of the retina and lie near its free surface. Ganglion cells have been identified in lower mammals which respond to visual stimuli in a direction-selective (DS) manner (Barmack, 2003; Borst & Euler, 2011). That is, these DS ganglion cells extract motion information from image sequences, even though the output of the photoreceptors does not vary with the direction of a moving stimulus (Borst & Euler, 2011). Although the existence of DS cells in the retinae of primates has yet to be confirmed, it is thought that the extraction of motion direction is a conserved function of the retina (Borst & Euler, 2011).

1.3.3.1.2 Forebrain and midbrain projections from the retina

Three main types of DS ganglion cells have been identified to date in lower mammals - ON/OFF, ON and OFF DS cells - so-called because of the different ways they respond to the onset (i.e. leading edge) and/or offset (i.e. trailing edge) of a moving stimulus (Borst & Euler, 2011). The majority of the ON/OFF DS cells, and all of the OFF DS cells, project with the bulk of the other non-DS ganglion cells to the lateral geniculate nucleus (LGN) of the metathalamus in the diencephalon. Projections also pass from these ganglion cells to the superior colliculus (SC) of the mesencephalon (Borst & Euler, 2011; Rokszin et al., 2010). The so-called ON DS cells, comprising the third DS cell type, respond preferentially to large field motion across the retina, and their direction-sensitivities correspond to those of the three semicircular canal pairings (Borst & Euler, 2011). Unlike the other DS cell types, the ON DS cells project predominantly to the series of mesencephalic nuclei which form the accessory optic system (AOS)[5] (Borst & Euler, 2011). These nuclei of the AOS project to second-order vestibular neurons in brainstem structures, including the nucleus prepositus hypoglossi (NPH) and vestibular nuclei[6] (Barmack, 2003). The response properties and connectivity of the ON DS cells would suggest that they are good candidates for mediating space-motion perceptions, particularly the perception of self-motion. However, the weight of opinion is that signals transmitted by these ganglion cells via the AOS mediate the reflexive, gaze-stabilising component of optokinetic nystagmus (OKN), and contribute to the velocity storage mechanism which prolongs the processing of afferent vestibular signals (Borst & Euler, 2011; Cullen, 2016).

---

[5] This is one of several accounts given in the literature about the major source of input to the accessory optic system (AOS). Other accounts emphasise that visual signals are transmitted to the AOS from select ganglion cells functionally connected with S cone cells (Douglas & Lawnenson, 2016) or, in primates, from the various regions of the visual cortex (Barmack, 2003).

[6] The brainstem targets of the AOS are less controversial than the inputs to the AOS. However, the brainstem structures, which the AOS projects to, are probably still best understood in lower mammals (Barmack, 2003).

1.3.3.1.3 Lower visual motion processing areas of the cortex

In comparison to the role of the ON DS cells, the function of projections from the ON/OFF and OFF DS ganglion cells via the LGN and SC is less clear. However, these and other ganglion cell projections might serve higher perceptual and/or cognitive functions (Borst & Euler, 2011) and, therefore, warrant further consideration. In humans, axons from the LGN curve dorso-medially as the optic radiation to the primary visual cortex (also referred to as the striate cortex or V1) located in and around the calcarine sulcus of the occipital lobe (Douglas & Lawnenson, 2016). Certain layers of V1, including 4B and 6, are described as being particularly direction-selective (Rokszin et al., 2010). Motion information propagates from these layers along the dorsal visual pathway, formed by a hierarchy of extrastriate cortical regions implicated in processing the spatial locations of visual stimuli (i.e. the ‘where’ of those stimuli) as opposed to the identity of visual stimuli (i.e. the ‘what’ of those stimuli) (Britten, 2008; Goodale & Milner, 1992; Rokszin et al., 2010). The classical dorsal pathway in primates includes visual areas V2, V3 and V5/MT (Rokszin et al., 2010). The latter has an integral role in processing the direction and speed of visual stimuli. Furthermore, it contributes to the perception of three-dimensional shape from motion signals i.e. to the so-called ‘structure-from-motion perception’ (Rokszin et al., 2010).

Some scholars have recently highlighted the fact that V5/MT receives direct input from V1, as well as indirect input via V2 and V3 (Britten, 2008; Gilaie-Dotan, 2016; Rokszin et al., 2010). Moreover, human studies have shown a tract connecting the LGN with the ipsilateral V5/MT, bypassing V1 (Gilaie-Dotan, 2016; Rees, 2008). This casts some doubt on whether V5/MT should even be considered part of the dorsal pathway’s hierarchy, let alone a high-up centre in that pathway (de Haan & Cowey, 2011; Gilaie-Dotan, 2016). In effect, the direct communication between the LGN and V5/MT places the latter at the same or earlier processing stage as V1, which may attest to the importance and ubiquity of visual motion processing in all manner of visual functions (Gilaie-Dotan, 2016) .

1.3.3.1.4 Higher visual motion processing areas of the cortex

Visual motion processing does not cease within V5/MT. This area projects to numerous, ‘upper’ regions beyond the occipital cortex (Britten, 2008). Of note, V5/MT has substantial connections with the medial superior temporal area in primates (Rokszin et al., 2010). Cells in this area tend to have larger receptive fields than cells in V5/MT, which make it better suited to the analysis of coherent motion across large regions of the visual field (Angelaki, Gu, & DeAngelis, 2011; Britten, 2008; Gilaie-Dotan, 2016). In natural settings, as discussed further in the sub-section below (1.3.3.2.3), large-field visual motion is often caused by self-motion (Carpenter, 2003). Studies have, indeed, shown that the dorsal part of the medial superior temporal area (MSTd) in macaque monkeys processes large flows of visual information (Angelaki et al., 2011; Dukelow et al., 2001; Rokszin et al., 2010).

Interestingly, the monkey MSTd is also recognised as a ‘cortical vestibular processing area’ (CVPA), as discussed in section 1.3.2.1. Indeed, neurons in this area are sensitive not only to large-field visual motion (i.e. to motion of the primates in the light), but also to motion in darkness, indicating that these neurons receive vestibular as well as visual inputs (Angelaki et al., 2011). There is overlap of visual-vestibular sensitivities in other CVPAs, including in the macaque parieto-insular vestibular cortex, where neurons have been found to respond both to body acceleration in one direction and optokinetic stimulation in the opposite direction (Brandt et al., 1998; Grusser, Pause, & Schreiter, 1990).

1.3.3.1.5 Discrete cortical integration of space-motion information

This review of the functional anatomy of the visual system has further highlighted that visual and vestibular signals converge on discrete neuronal clusters at two levels of the neuraxis at least: on brainstem structures inclusive of the vestibular nuclei, and on forebrain regions inclusive of important CVPAs. This implies that there is separate visuo-vestibular integration for the purpose of reflexive functions versus higher perceptual and cognitive functions (Fetsch, DeAngelis, & Angelaki, 2010). This hypothesis is supported by the fact that the activity of vestibular-only (VO) neurons, those second-order vestibular neurons most implicated in the conveyance of vestibular signals from the brainstem to higher centres (see section 1.3.2.1.2), are not reliably modulated by large-field visual stimulation in mouse or primates (Cullen, 2016; Goldberg et al., 2012). Also, discrete cerebellar circuits appear to process the VOR and the perception of angular velocity (Shaikh et al., 2013).

1.3.3.2 Aspects of temporo-spatial coding by the visual system

1.3.3.2.1 Physiology of the retina

Light that reaches a photoreceptor in the retina is absorbed by the retinal contained within the stacked discs at the basal extremities of the cell. The configuration of the retinal is changed as a result, and this separates the substance from the attached rhodopsin proteins. In turn, an enzyme cascade is activated that, ultimately, leads to the closure of ion channels in the discs' membranes. The photoreceptor becomes hyperpolarised, reducing the quantal release of the glutamate neurotransmitter at the receptor's apical synapse with a bipolar cell. There are two types of cone bipolar cells. 'OFF' bipolar cells[7] have 'sign-conserving' synapses with cone photoreceptor cells, so the reduction in neurotransmitter release by the latter hyperpolarises these bipolar cells. 'ON' bipolar cells, in contrast, have 'sign-inverting' synapses with cones; they depolarise when the quantal release of glutamate by the cones is reduced. All rod bipolar cells tend to have a sign-inverting response to rod photoreceptor cell hyperpolarisation (Douglas & Lawnenson, 2016).

Rod and cone photoreceptors generate visual information across a large light intensity range. The rod system (i.e. rod cells and their connections within the retina) is particularly sensitive to light, partly because rod cells produce a reliable response to a single photon of light, whereas cone cells only produce a comparable response when exposed to over 100 photons (Purves et al., 2012). Furthermore, rod cells are far more convergent on bipolar cells than cones are (Purves et al., 2012). These properties of the rod system make it specialised for signalling at low-light levels. During starlight or exposures to similarly low irradiances, only the rods are active, so these conditions are classified as scotopic. During daylight or exposures to most artificial light, only the cones are active, so these conditions are classified as photopic (Purves et al., 2012; Tikidji-Hamburyan et al., 2017). Activity of the rod system is discounted under photopic conditions because the rods are said to be 'saturated'. That is, they are no longer capable of responding to increases in light intensity (Aguilar & Stiles, 1954). However, recent research has challenged established concepts about the irradiances at which rod saturation occurs, and about the extent and permanency of the saturation (see Tikidji-Hamburyan et al., 2017).

---

[7] OFF bipolar cells are not to be confused with the direction-selective OFF ganglion cells described in the sub-section above (1.3.3.1.2).

1.3.3.2.2 Comparative roles of the central and peripheral visual fields in space-motion signalling

Although the greater convergence of the rod system increases its sensitivity to light, it compromises the spatial resolution of the system (Purves et al., 2012). The cone system provides far greater visual acuity. Despite this and other trade-offs within the rod system, claims have frequently been made for a ‘peripheral dominance hypothesis’; specifically, that rod-dominated peripheral vision is more important than cone-mediated central vision for the perception of self-motion. This hypothesis stemmed from the work of Brandt and colleagues (1973), who found that occlusion of the central visual field caused minimal attenuation of vection - the illusion of self-motion elicited by an optokinetic stimulus (see section 1.5.3). In contrast, masking peripheral vision reduced this illusion. However, subsequent research called these findings into question. Importantly, in a similar study by Post (1988), no differences in vection experiences were found according to whether the optokinetic stimulus was located in the central, mid-peripheral or far-peripheral visual fields. Converging evidence indicates that central vision actually extracts more accurate self-motion information than peripheral vision alone (Bower, Bian, & Andersen, 2012; Warren & Kurtz, 1992). At least two reviews (Israël & Warren, 2005; Warren & Kurtz, 1992) have stressed that a focus on regions of retinal dominance overlooks the most important determinant of self-orientation and -motion perception from visual signals - the properties of the optical stimulation itself.

1.3.3.2.3 The optic array and optic flow

According to J. J. Gibson (1950, 1958), proprioceptive signalling by the visual system derives from the highly informative pattern and angle of light rays reaching the retina, called the optic array. Motion of the eye/head relative to the environment changes the optic array in ways that are unique to the nature of the occurrent motion. When the head moves and the environment is stationary, in other words during translocation of the self, the reconfiguration of the optic array signals that the environment is ‘flowing by’. This type of optic array reconfiguration is referred to as optic array flow (Gibson, 1958), or simply optic flow (e.g. Lee & Aronson, 1974; Schmidt & Lee, 2011). Particular patterns of optic array changes specify distinct kinds of movements of the self with respect to the environment or objects within it. For example, if the angle formed by light rays from two sides of an object remains constant over time, there is no motion of the observer relative to the object. If the angle between the light rays is increasing, the distance between the observer and object is decreasing. Conversely, if the angle between the light rays is decreasing, the separating distance is increasing. As a final example, if the angles of the light rays from two sides of an object are changing in the same direction, but the rate of change of the angles of the rays from the two sides is different, the observer could either be moving by the object, or turning away from it, in a specific direction (DeAngelis & Angelaki, 2012; Schmidt & Lee, 2011). Presumably all these sorts of changes in the optic array are detected, at least in part, by the direction-selective (DS) ganglion cells of the retina.

As the above examples suggest, optic flow contains information about self-motion velocity (Raudies & Neumann, 2013). However, a pertinent problem in attaining this information is parsing the changes in the optic array that are due to self-motion from those that are due to object motion (Warren & Kurtz, 1992). As Gibson (1958) implies, self-motion tends to generate global optic flow, whereas object motion tends to generate a reconfiguration of delimited regions of the optic array. Other nuances of optic array transformations are thought to cue self- versus object-motion perception. Stoffregen and Riccio (1990) proposed that there is a bias toward self-motion perception when the frequencies of optic flow reconfigurations are relatively low, matching the dynamics of normal postural and locomotor control, but a bias toward object-motion perception when there are higher rates of optical transformations.

Research has shown that the central visual field accurately transduces radial, rotary and lamellar flow, whereas the peripheral field only accurately transduces lamellar flow (Andersen & Dyre, 1989; Stoffregen, 1986; Warren & Kurtz, 1992). These findings are in-keeping with models of optic flow which predict that a variety of flow patterns can occur in the central field during natural movements, but that flow patterns are typically lamellar in the peripheral field (Warren & Kurtz, 1992). This ecological specialisation of retinal regions may be underpinned by different sensitivities of the medial superior temporal area to the locus of optic flow stimulation (Warren & Kurtz, 1992).

1.3.3.2.4 Adaptation to visual motion

Unlike the semicircular canal system, the visual system only partly adapts to stimulation associated with constant head velocity. Research suggests that visual adaptation of perceived speed in humans is described by an exponential decay to a steady level within a matter of seconds (Clifford & Langley, 1996). This may improve the detection of novel changes in speed but at the expense of maintaining an accurate representation of the occurrent, uniform optic flow (Clifford & Langley, 1996). The visual system probably dominates the vestibular system in mediating the perception of self-motion at constant velocities (Brandt et al., 1998; De Winkel, Katliar, & Bülthoff, 2017).

1.3.3.2.5 Polarity cues

The otolith organs of the vestibular system contribute to the perception of self-orientation by providing a graviceptive signal. The visual system also contributes to this perception; head position can be referenced to surfaces and vertical elements in the visual surround (Carpenter, 2003; De Winkel et al., 2018; Gibson, 1958), sometimes referred to as polarity cues (Howard, 1982). Carpenter (2003) points out that static, near-perfect, horizontal and vertical visual cues abound in urban environments, but may have been less readily available in the natural surroundings in which humans evolved. Therefore, inferring self-orientation from these cues may be solely due to perceptual learning throughout ontogenesis. Learning may be underpinned by changes in the computations which constitute the higher-level processing of space-motion information. Three important computations will be considered next.

1.4 The modulation of ascending space-motion information

Research into the modulation of ascending space-motion information has tended to focus on three main computations: predictive coding, optimal cue integration and temporal integration. Some of these computations appear to be rather unique to the perceptual and cognitive processing of visuo-vestibular information. For example, the responses of the neurons of the vestibular nuclei, which mediate the vestibulo-ocular reflex (PVP and FTN neurons - see section 1.3.2.1.2), do not conform with predictive coding (Cullen & Taube, 2017). In the main, these computations have been investigated and discussed in the literature in relative isolation of each other. This suggests that a comprehensive and clear theoretical framework for the processing of ascending space-motion information, which might link the computations together, is lacking (Ellis & Mast, 2017). The following sections will describe the computations and attempt to map them all onto a simplistic, informal model of motor control.

1.4.1 Predictive coding

Research into the ascending transmission of signals from the vestibular periphery, mainly in rhesus macaques, has revealed that the responses of VO neurons in the vestibular nuclear complexes (VNCs - see section 1.3.2.1.2) are markedly attenuated during active versus passive head movements (e.g. Carriot, Brooks, & Cullen, 2013; Roy & Cullen, 2001). More specifically, compared to angular or linear involuntary motions, the equivalent self-generated motions produce 70% less VO neuronal activity (Cullen & Taube, 2017). This attenuation during active head movement suggests that VO neurons receive not only vestibular afference, but also copies of the motor commands which drive the movement - so called efference copies. The latter may be subtracted from the former, effectively removing the expected vestibular feedback from the sensory signal.

Brooks, Carriot and Cullen (2015) investigated whether the attenuation was due to subtraction in this manner by applying velocity-dependent resistance to the voluntary head movements of a macaque, and studying the resultant responses of cells in both the VNC and a deep cerebellar nucleus (the rostral fastigial nucleus - rFN) while the macaque turned its head through 50º. The neuronal responses were compared to those recorded during unresisted passive and active head movements. The resistance would have changed the relationship between the motor command and both the resultant movement and afference. Compared to unresisted conditions, a more robust command would have been required to produce the 50º head turns when resistance was applied, yet vestibular afference would have been relatively unchanged. During initial active trials with resistance applied, neuronal responses were unattenuated and, therefore, similar to those measured during passive head movements. Over the course of 40-to-60 resisted head movement trials, neuronal activity gradually became suppressed, and more like that observed during unresisted active movement. In association with the adaptation of neuronal activity, the macaque's head velocities steadily increased, eventually matching the velocities recorded during normal active movement.

These results provide direct evidence that the sensitivity of specific VNC and cerebellar neurons is proportional to the difference between actual and predicted afference (Brooks et al., 2015). It would appear that VO neurons receive predictions of the expected consequences of the motor commands rather than raw copies of those commands (i.e.

efference copies) (Benazet, Thénault, Whittingstall, & Bernier, 2016). Presumably, VO neurons are sent predicted head velocity and acceleration information. The predictions are adaptive rather than fixed; that is, they are continually updated as a function of recent experience. A computation equivalent to subtraction of the predictions from the afference generates sensory prediction errors (Aitchison & Lengyel, 2017), which are specifically what the responses of the VO neurons encode (Cullen & Taube, 2017). This computation is commonly referred to as 'predictive coding' (e.g. Aitchison & Lengyel, 2017). The prediction errors, which the VO neurons transmit to higher centres, constitute a continuously updated representation of unexpected space-motion information that may serve to maintain perceptual stability (Brooks et al., 2015; Cullen & Taube, 2017).

Although much of the research related to space-motion perceptions has focused on predictive coding of vestibular afference, this computation also appears to modulate visual signals. Inaba et al. (2007) and Chukoskie and Movshon (2009) examined the responses of regions of extrastriate cortex, specifically the medial superior temporal (MST) and middle temporal areas, to large field visual motion (optic flow) during fixations and pursuit eye movements. The activity of MST cells were partially attenuated during the latter movements, indicating that they selectively suppress the (expected) optic flow component caused by self-generated pursuits (Green & Angelaki, 2010).

The adaptive transformation of efference copies into predictions, as evidenced by the findings of Brooks, Carriot and Cullen (2015), implies the brain implements a 'forward model'; an important component of internal model-based theories of motor control. A formulation of these theories will be discussed in more detail below (see section 1.4.4). Essentially, a forward model emulates the motor-to-sensory transformations which are implemented by the physical world and governed by the physics of the musculoskeletal system, environment and sensory receptors (Grush, 2004; Wolpert & Ghahramani, 2000). Internally representing these transformations, that is, the causal relationship between actions and their consequences, allows for the encoding of unexpected space-motion information which, in turn, enables organisms to adapt to changing environments, adjust to bodily changes and learn new skills. Building an internal model of the likely results of motor commands may also mitigate sensory delays (Forbes, Chien, & Blouin, 2018). The cerebellum has been proposed to be the substrate of a forward model that adaptively predicts the expected sensory consequences of self-generated action (Brooks et al., 2015; Cullen & Taube, 2017).

1.4.2 Optimal cue integration

Like all sensory cues, those from the vestibular and visual systems carry statistical uncertainty (Fetsch et al., 2010). Receptor transduction and neural transmission of sensory signals are intrinsically noisy processes (Faisal, Selen, & Wolpert, 2008; Fetsch, DeAngelis, & Angelaki, 2013; Riccio & Stoffregen, 1991; Stoffregen, Yoshida, Villard, Scibora, & Bardy, 2010). A large body of research indicates that the minimisation of error related to noise is achieved by a computation referred to as optimal cue integration (e.g. Alais & Burr, 2004; Ernst & Banks, 2002; Jürgens & Becker, 2006; Knill & Saunders, 2003). Essentially, the nervous system combines co-occurring or redundant sensory cues, derived from the same event, in a way that optimises what is inferred about that event (Ernst & Di Luca, 2011; Fetsch et al., 2013). One of the simplest models of cue integration, based on unrelated research by Cochran (1937), predicts that the inference or estimate with lowest variance (denoted $\hat{S}$), given a set of n sensory cues, is one based on a weighted sum of each of the single cues ($\hat{S}_i$):

Equation 1.1

$$\widehat{S} = \sum_{i=1}^{n} w_i \widehat{S}_i$$

The weights are proportional to each cue's reliability[8]. Where there are two cues, e.g. vestibular (A) and visual (B), the optimal estimate is:

Equation 1.2

$$\widehat{S}_{AB} = w_A \widehat{S}_A + w_B \widehat{S}_B$$

The weights are given by:

---

[8] In the field of sensory cue integration, the term reliability is frequently used, somewhat atypically, as a synonym for the precision or inverse variance ($1/\sigma^2$) of a measurement (Fetsch et al., 2013). Accuracy is defined as the probability with which information truly represents the magnitude of the real-world physical property that it pertains to (Ernst & Di Luca, 2011; Fetsch et al., 2013).

Equation 1.3A

$$w_A = \frac{1/\sigma_A^2}{1/\sigma_A^2 + 1/\sigma_B^2}$$

Equation 1.3B

$$w_B = \frac{1/\sigma_B^2}{1/\sigma_A^2 + 1/\sigma_B^2}$$

The reliability of the combined estimate is the sum of the reliabilities of the individual cues:

Equation 1.4

$$\frac{1}{\sigma_{AB}^2} = \frac{1}{\sigma_A^2} + \frac{1}{\sigma_B^2}$$

Re-formulated, the mean squared error (*MSE*) of the combined estimate is determined by dividing the product of the variance of the vestibular cue and the variance of the visual cue by the sum of these (squared) errors (Alais & Burr, 2004; Kaliuzhna, Prsa, Gale, Lee, & Blanke, 2015; Körding & Wolpert, 2004):

Equation 1.5

$$\sigma_{AB}^2 = \frac{\sigma_A^2 \sigma_B^2}{\sigma_A^2 + \sigma_B^2}$$

An equivalent model of optimal cue integration is based on Bayes' rule (Fetsch et al., 2010, 2013). Applied to space-motion processing, Bayesian models state that the goal of the multimodal balance system is to determine the value of a space-motion event of interest, X, that maximizes the posterior distribution P(X|A,B). That distribution describes the probability of each possible value of X, given the vestibular (A) and visual (B) cues. A simplification of Bayes' rule says that the posterior is proportional to the product of the joint likelihood function, P(A,B|X), and the prior, P(X). The former represents the probability of obtaining vestibular and visual information for different values of X. The latter describes the likelihood of observing each value of X before the vestibular and visual information is received.

If the sensory cues have independent sources of noise, the joint likelihood can be split into separate likelihoods for A and B, and Bayes' rule becomes:

Equation 1.6

$$P(X|A, B) \propto P(A|X) * P(B|X) * P(X)$$

The key terms of Bayes' rule are often assumed to be represented by probability distributions with Gaussian functions (Adams, Stephan, Brown, Frith, & Friston, 2013; Mast & Ellis, 2015; Wolpert, 2007). Given this assumption, the value of a space-motion event of interest that maximizes the posterior distribution, or the maximum *a posterior* (MAP) estimate, is a weighted sum of the peaks of the two likelihood functions and the prior function (Fetsch et al., 2010, 2013). Therefore, the latter function influences the final estimate, just as expectations about a space-motion event, based on previous exposure to similar circumstances, may influence one's inferences (Körding & Wolpert, 2004; Seriès & Seitz, 2013). However, often the prior is assumed to be uniform or flat (e.g. Alais & Burr, 2004; Ernst & Banks, 2002), implying there is limited prior knowledge of a space-motion event. As such, the predictions of the Bayesian model are indistinguishable from those of the model derived from Cochran (1937) (see equations 1.1 to 1.5). The Bayesian model constitutes a reliability-based, weighted, linear combination scheme (Fetsch et al., 2013; Rohe & Noppeney, 2018). The resultant space-motion estimate has a reliability that is reflective of, yet greater than, the most reliable of the two likelihood functions (Fetsch et al., 2010, 2013; Rohe & Noppeney, 2018), as depicted in Figure 1.1. Put differently, the most reliable sensory cue contributes more to the final inference or estimate. In that sense, the brain can be conceived as a Bayesian optimal integrator; it merges all of the available information into the most reliable composite estimate of a given event (Ma, Beck, & Pouget, 2011; Roach, Heron, & McGraw, 2006). However, the Bayesian model leads to a posterior distribution whose peak is located between the peaks of the likelihood distributions. That is, the posterior distribution is always biased to some degree by the less reliable cue (Ernst & Di Luca, 2011; Wolpert, 2007).

There is behavioural data in support of the optimal integration of visual and vestibular cues by the primate and human nervous systems (see De Winkel et al., 2015; Fetsch et al., 2013 for reviews). For example, Fetsch et al. (2009) investigated how human and monkey participants used visual and vestibular cues to perceive self-motion direction (heading). By manipulating the disparity between the cues, as well as their relative reliability (achieved by changing the coherence of the optic flow stimulus), it was possible to ascertain how much the individual cues contributed to the participants' heading judgements. Even when there was a relatively large conflict between the visual and vestibular information about self-motion direction, most participants biased the more reliable cue, as predicted by the optimal model of cue integration.

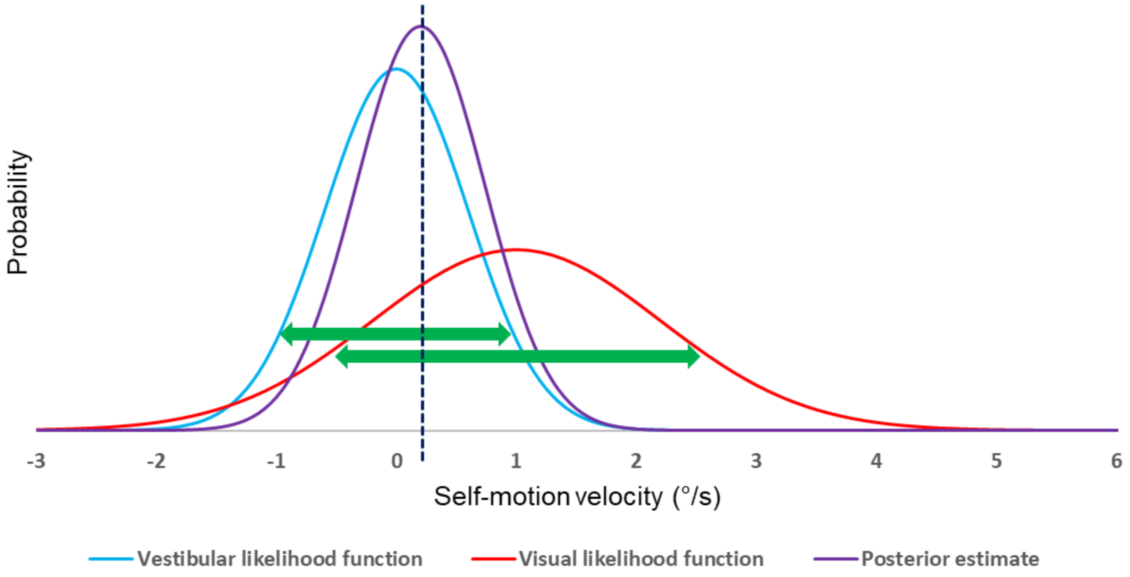


Figure 1.1: Schematic illustration of optimal cue integration.

The likelihood distributions for the vestibular (blue) and visual (red) cues, and the resulting posterior distribution (purple), relate to a relatively static space-motion event - the observer is stationary. The variances of the distributions correspond to their widths (green arrows); here, the vestibular cue has greater precision than the visual cue. The likelihood function for the former cue is concentrated over 0º/s. The likelihood function for the latter cue is more rightward shifted and imprecise, perhaps due to small field visual motion from right to left. The combination of these distributions through the application of Bayes' rule leads to *a posterior* distribution with even greater precision than the distribution for the vestibular cue. The rightward bias of the posterior expectation (see below) is extremely subtle and, therefore, stationarity is inferred, which is veridical.

The posterior curve is plotted by finding the 'joint probability' per x-axis data point (i.e. multiplying prior and likelihood probabilities for respective points), summing all of these joint probabilities, then normalising each one by dividing by the sum (Wolpert, 2007). The mean of the posterior distribution, determinable by its peak, is sometimes referred to as the posterior 'expectation' (Adams et al., 2013; Edwards, Adams, Brown, Pareés, & Friston, 2012), and is represented by the dashed line in the figure.

The dorsal aspect of the medial superior temporal (MSTd) area has been proposed to be a substrate for the optimal integration of vestibular and visual cues, but further research is required to corroborate this (Fetsch et al., 2010, 2013). Other researchers imply that optimal cue integration according to the models described above is too simplistic (e.g. Forbes et al., 2018; Laurens & Angelaki, 2017). They suggest that the sensory cues are subjected to gain adjustments by way of a Kalman filter as part of the predictive coding and/or integration processes. Indeed, there are very few accounts in the relevant literature of what form of vestibular and visual information is combined. Given that cue integration appears to occur in higher centres, following predictive coding, it seems plausible that vestibular prediction errors may be integrated with visual prediction errors. This is suggested by Peterka (2002) and by the schematics of Laurens and Angelaki (2017) and Forbes et al. (2018). Moreover, the study by Fetsh et al. (2009) - one of the first to provide empirical evidence of reliability-based integration - exposed participants to passive vestibular and visual stimuli only, meaning that prediction errors would certainly have been encoded. Aitchison and Lengyel (2017) highlight that predictive coding and Bayesian inference are compatible computations. No matter, according to Cullen (2018), it still remains unclear how attenuated vestibular signals are combined with other cues.

1.4.3 Temporal integration

The process of optimally integrating the vestibular and visual signals could be categorised as spatial integration or ‘input integration’ (e.g. Bartos, Alle, & Vida, 2011; Floresco, 2016), in order to differentiate it from ‘temporal integration’, which involves the accumulation of information over periods of time. Position is an integral of velocity over time. Converging evidence indicates that temporal integration of self-motion velocity cues from the vestibular and visual systems underpins self-location (position) perception (Arthur, Philbeck, & Chichka, 2009; Ionta et al., 2011; Israël, Bronstein, Kanayama, Faldon, & Gresty, 1996; Kaski et al., 2016; Mergner, Rumberger, & Becker, 1996). As mentioned in section 1.4.2.1.7, temporal integration might be linked to the right TPJ. In a recent study, problematic position judgements were only seen in patients with lesions specifically affecting this region (Kaski et al., 2016). Furthermore, only those same patients showed skewed judgements of motion duration.

Once again, it is unclear from the literature as to whether prediction errors rather than unmodulated cues are temporally integrated. Furthermore, it is uncertain whether vestibular and visual cues are combined with each other prior to the summation of information over time. The following simplistic description represents a formulation of ideas from the literature on the internal model of control, and is an attempt to show how temporal integration may relate to predictive coding and optimal cue integration. According to this simplistic formulation, these computations occur in series.

1.4.4 An internal model-based formulation of motor control pertaining to the whole body

Internal model-based theories of motor control have predominated for the past two decades or more. They stemmed from problem-solving approaches to overt action, whereby the interplay between the observer, task and environment creates a movement problem to be solved by the observer (Bouffard & Wall, 1990; Shumway-cook & Woollacott, 2007). Solving the movement problem and, thereby, reconfiguring the body into an intended state, represents the goal (Bernstein, 1967; Bouffard & Wall, 1990). Once the goal or desired state of the body has been established, the brain compares that state with the inferred current state of the body. As such, internal model-based theories imply a dependence of sensory processing on the occurrent task.

Formulating several variants of internal model theory, and in reference to overt movement of the whole body e.g. locomotion, if there is a discrepancy between the current state of the body (more specifically, the current perception of position or self-location) and the desired state or position, the sensorimotor circuitry for locomotion is activated. Signals encoding the discrepancy drive a controller or inverse model, which outputs efferent signals. These form the motor commands that activate the effector systems of the body so that purposive movements occur. The resultant temporo-spatial activity of the body is detected by the space-motion systems, namely the vestibular and visual systems (see sections 1.3.1 to 1.3.3).

The vestibular and visual signals are compared with the respective unimodal predictions. As described in section 1.4.1, these adaptive predictions are generated by a forward model, which processes copies of the efferent motor commands (efference copies) in a different branch of the sensorimotor circuit. The subtraction of the space-motion information contained in the unimodal predictions from the respective sensory information produces unimodal prediction errors (Aitchison & Lengyel, 2017). These are then combined in a reliability-based, weighted, linear fashion, such that the strongest unimodal prediction error has most influence on the resultant amodal prediction error formed at a higher level of the neuraxis (Friston, 2012). This prediction error, itself a stream of space-motion information e.g. about body velocity, is subsequently subjected to temporal integration so that the perception of body position is updated.

In its current form, this formulation is problematic given that, during active motion, sensory signals are attenuated at the first level of vestibular and possibly visual processing. With minimal unimodal and amodal prediction errors resulting from self-generated movement, there would be little information to temporally integrate or incorporate in higher cognitions (Cullen & Taube, 2017). Cullen & Taube (2017) suggest that the attenuated input during active motion could be up-weighted and/or combined with other signals, for example with efference copies. Laurens and Angelaki (2017) refer to the application of different weightings to the signals by a Kalman filter, seemingly in accordance with the balance of active versus passive motion. Possibly in addition to such weighting, the conundrum associated with signal attenuation might be overcome if the amodal prediction error were always added to an amodal prediction formed by the forward model. Purely active motion would mean that only the space-motion (e.g. velocity) data comprising the amodal prediction would be temporally integrated and, thereby, subserve the control process as a whole. Purely passive motion would mean only the amodal prediction error would be carried forward. If motor commands were generated, but, due to environmental perturbations, the resulting movement was greater or lesser than what had been intended, the amodal prediction error would be additive or subadditive, respectively, to the amodal prediction. The type of additivity would relate to the sign (positive or negative) of the error: positive during excessive motion and negative during inhibited motion. The temporal integration of the amodal prediction plus prediction errors might update one's self-location perception or current state. This is what may be recursively compared with the goal state until the latter has been achieved (Grush, 2004; Kessler & Thomson, 2010).

The formulation described throughout this section is a simplistic and informal (non-mathematical) account of information processing in an internal model-based, sensorimotor circuit for the purpose of goal-directed, overt whole-body movement. It is depicted schematically in Figure 1.2. A similar information processing scheme may underpin path integration; the process used by animals to determine their current position relative to their starting position (Taube, 2007). The process involves the summation of the vectors of distance and direction travelled from the starting point. The formulation may also apply to covert movements such as mental self-translocation, the theory of which will be discussed in section 1.7. Before that, it is pertinent to consider how experimentally-generated, incongruous sensory cues may give rise to aberrant space-motion information, and how the computations described in this section may allow such misinformation to propagate.

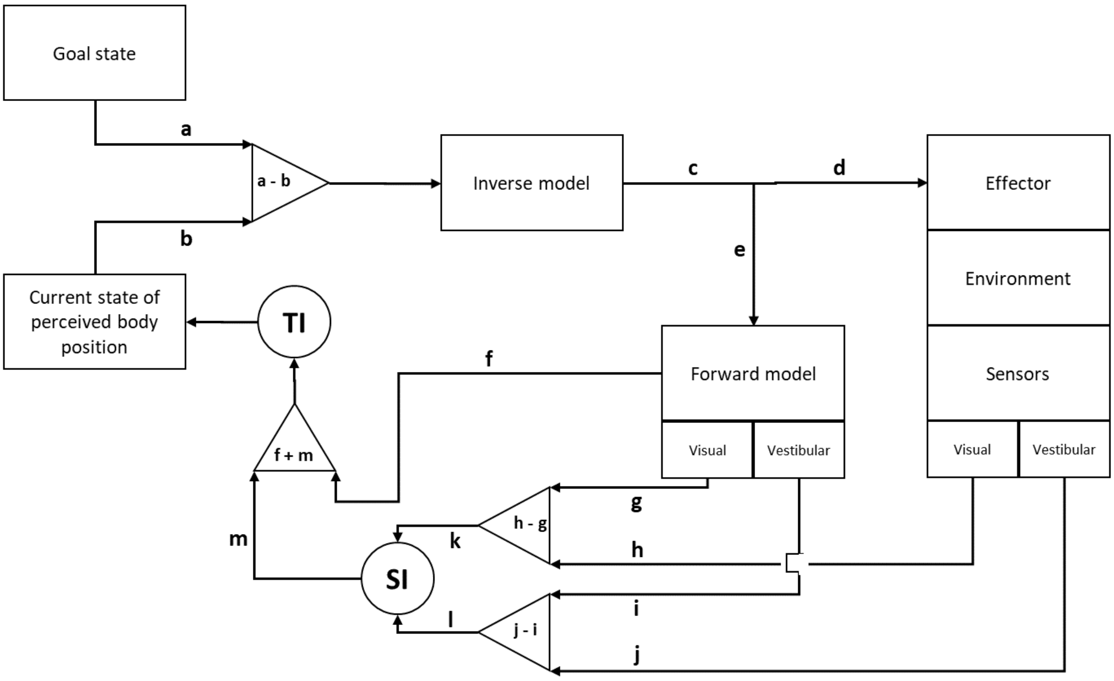


Figure 1.2: A simple schematic of the internal model-based sensorimotor circuit employed during whole-body movement, such as locomotion, and during path integration.

The outer loop of the circuit depicts the information processing stages relating to overt movement. Active movement and/or environmental perturbations of the body cause vestibular and visual afference. The inner loop represents the brain’s predictive processing. Efference copies instigate the forward model located in the central nervous system, which forms predictions about the vestibular and visual cues. Space-motion information comprising these predictions is deducted from the respective visuo-vestibular information resulting in unimodal prediction errors, which are weighted according to their reliability and combined into an amodal prediction error. Further weighting may be applied by a Kalman filter or by priors. The error is summed with an amodal prediction from the forward model. The resultant velocity signal is temporally integrated leading to a continually updated perception of self-location, which is compared with the goal state. This schematic is based on those of Miall and Wolpert (1996), Frith et al. (2000), Diedrichsen et al. (2010), Laurens and Angelaki (2017), and Forbes et al. (2018) and on the descriptions of Grush (2004). For simplicity, feedback loops necessary for the adaptation of the forward model, as a function of recent experience, have not been included.

a – goal signal; b – current state estimate; c – efference; d – motor command; e – efference copy; f – amodal prediction; g – unimodal (visual) prediction; h – visual afference; i – unimodal (vestibular) prediction; j – vestibular afference; k – unimodal (visual) prediction error; l – unimodal (vestibular) prediction error; m – amodal prediction error; SI – spatial (input) integration; TI – temporal integration

1.5 Aberrant space-motion information secondary to experimentally-induced visuo-vestibular cue incongruity

1.5.1 The propagation of aberrant space-motion information generated by incongruous cues

A corollary of optimal cue integration is that a strong and, therefore, reliable (Fetsch et al., 2013) cue may disproportionately influence the integrated estimate, even if that cue does not faithfully represent the action or environmental event of interest (Ernst & Di Luca, 2011). More specifically, a strong but inaccurate visual or vestibular cue may give rise to an inappropriate unimodal prediction error which biases the amodal prediction error. The probability distribution of the amodal prediction error would be concentrated over a region of the relevant temporo-spatial spectrum far removed from where it should actually be. The posterior expectation or mean of the error's distribution would be shifted or inaccurate. Ultimately, the observer would receive an inappropriate space-motion update. In effect, the computations described in section 1.4 serve to propagate the misleading information from a strong but irregular space-motion cue. Experimental manipulations of sensory stimuli can capitalise on this situation and, therefore, give rise to syndromic balance disorders. The two experimental manipulations used in the present series of studies, and their manifestations, are described next.

1.5.2 Impulse stimulation

Impulse stimulation[9] refers to the protocol during which an observer is exposed to a 'step stimulus' or 'impulse stimulus' (Baloh, Honrubia, & Kerber, 2011), and, consequently, to incongruous vestibular cues. The protocol is used in the clinical assessment of vestibular function and in experiments (see Baloh et al., 2011; Nigmatullina et al., 2015). The observer is rotated at a constant velocity, typically 90º/s, for at least one minute in a motorised chair. A rapid deceleration of the chair to 0º/s then follows. The change in velocity constitutes the velocity step or impulse. It stimulates the lateral semicircular canals, because the encapsulated endolymphatic fluid retains the direction of motion of the head when it was at constant velocity. This inertia of the fluid distorts the cupulae in the lateral canals, but in the opposite directions to that which they had been deflected during

---

[9] Participants in the final study undertaken as part of this research project were exposed to impulse stimulation - see Chapter 7.

the acceleration to constant velocity. Volleys of mutually antagonistic afferent signals are transmitted from the opposing lateral semicircular canals, and these volleys constitute a strong and reliable vestibular signal. Therefore, shortly after the abrupt deceleration, even though he or she is stationary as is faithfully signalled by the visual system, the observer perceives self-rotation in a direction opposite to the initial motion (Baloh et al., 2011; Carpenter, 2003; Laurens & Angelaki, 2011). Figure 1.3 depicts the preferential weighting given to the vestibular cue, or the respective prediction error, following an impulse stimulus, despite the fact that the visual cue more accurately represents the observer's stationarity.

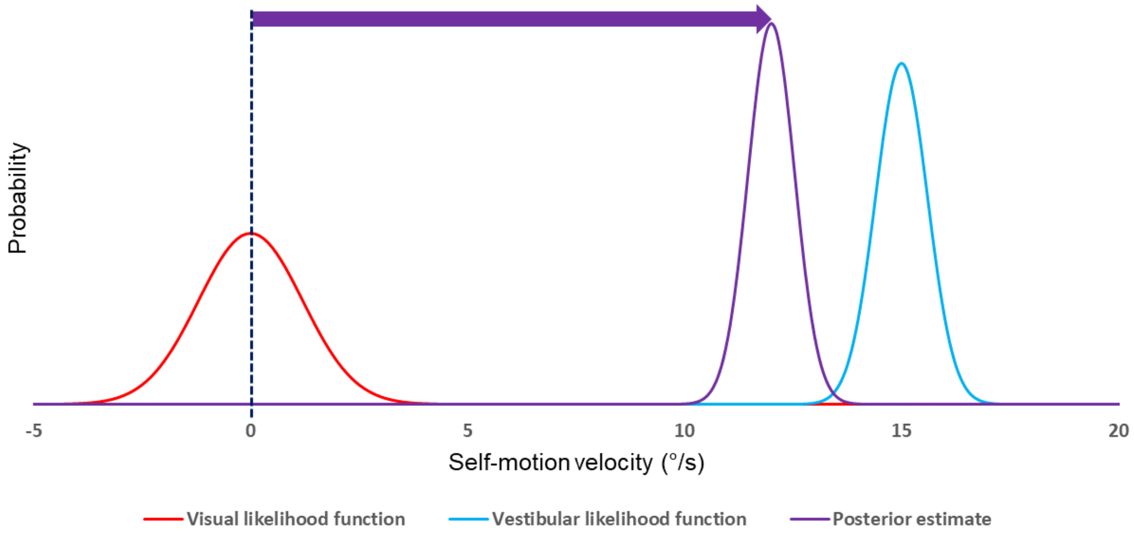


Figure 1.3: Visual representation of the biased amodal prediction error that occurs shortly after an impulse stimulus.

The healthy observer is stationary following the rapid deceleration, but there is strong signalling by the vestibular system, which is incongruous with visual signalling. A strong vestibular prediction error is generated. Visual prediction errors are minimal because both visual afference and the forward model's prediction encode stationarity. The match may up-weight the visual information more than predictive coding alone might predict. However, the vestibular prediction error still has greater reliability, so the mean or expectation of the combined prediction error is located towards the expectation of the vestibular-derived likelihood function. The expectation of the vision-derived likelihood function is veridical in this case (dotted line). The inaccuracy of the amodal prediction error is indicated by the purple arrow. Ultimately, the observer receives an inappropriate space-motion update and, therefore, erroneously perceives self-rotation. For simplicity, prior knowledge is assumed to be minimal, hence the prior distribution is flat and not depicted.

There are other, non-perceptual manifestations of the impulse-induced balance disorder. In particular, the strong vestibular cue gives rise to post-rotatory nystagmus, the slow phase velocity of which decays exponentially. The timing of this decay is usually described by its ‘time constant’, which is the time required for the velocity to drop to 1/*e* (exponential) or 37% of its maximum value (Baloh et al., 2011; Nigmatullina et al., 2015). Research has shown that, in healthy individuals not overly-trained at pirouetting, the decay of the perception of self-rotation is commensurate with the decay of the slow phase velocity (Nigmatullina et al., 2015; Okada et al., 1999). The time constant of both is around 15 s (Nigmatullina et al., 2015; Okada et al., 1999).

1.5.3 Optokinetic stimulation

Aberrant space-motion information can also arise due to visual or optokinetic stimulation (OKS). An optokinetic stimulus, defined as unidirectional motion of all or part of the optic array (Lackner & DiZio, 2005), can induce the illusory perception of self-motion known as vection. This illusion has been recognised since the late 1800s, having first been reported by Ernst Mach (1875). When a stationary observer is exposed to an optokinetic stimulus, the visual motion cue is strong and reliable, whereas the vestibular cue is quiescent and, therefore, relatively imprecise. According to the reliability-based combination rule, the brain reconciles these incongruous signals by preferentially weighting the visual cue (Fetsch, Gu, Deangelis, & Angelaki, 2011) or the prediction error associated with it. In effect, the situation depicted in Figure 1.3 would be reversed in terms of both the accuracy of the vestibular and visual prediction errors and the strength of the bias those cues would therefore have on the observer’s perception of self-motion.

The direction of the self-motion illusion is opposite that of the optokinetic stimulus, but the plane of the illusion tends to correspond with the plane of the pattern’s motion (Guerraz & Bronstein, 2008). Exposure to expanding, contracting, or laminar optic flow can give rise to ‘linear vection’ i.e. a feeling of self-translocation along a straight trajectory (Fetsch et al., 2011). After several seconds of viewing a pattern rotating at constant velocity, ‘circular vection’ is experienced i.e. a feeling of self-rotation in the roll, yaw or pitch planes dependent on the axis of the pattern’s rotation[10]. An optokinetic stimulus rotating in the roll plane evokes not only vection but also a misperception of self-orientation[11]. Study

---

[10] Participants in two studies undertaken as part of this research project were exposed to optokinetic stimulation in the roll plane - see Chapters 4 and 6.

[11] ‘Self-orientation misperception’ (Bringoux, Scotto Di Cesare, Borel, Macaluso, & Sarlegna, 2016) or its derivatives are used herein to refer to an observer’s distorted inference about his or her instantaneous attitude or long-axis alignment in relation to any given frame of reference. As such, this misperception is a facet of spatial disorientation alongside ‘self-location misperception’, which will be applied to an observer’s misrepresentation about his or her location within a given environment (Kaski, Malhotra, Bronstein, & Seemungal, 2012). Both of these misperceptions are separable from ‘self-motion misperception’, which is treated herein as an observer’s misrepresentative or distorted inference about

participants have been shown to make visual vertical judgements that were tilted in the direction in which the pattern was rolling (Guerraz et al., 2001; Lubeck, Bos, & Stins, 2016).

In addition to the perceptual manifestations of the balance disorder induced by optokinetic stimulation, postural displacements termed ‘visually evoked postural responses’ (VEPRs) can also occur (Guerraz & Bronstein, 2008). Whereas the onset of illusory self-motion is usually delayed by around 10 s after first exposure to such stimulation (Kleinschmidt et al., 2002), postural aberrations are measurable almost immediately (Guerraz & Bronstein, 2008; Tanahashi, Ujike, Kozawa, & Ukai, 2007). This could mean that the misperceptions of self-orientation and -motion occur as a result of postural instability rather than due to optokinetic stimulation *per se*. This line of reasoning is in accordance with the postural instability theory of motion sickness (Riccio & Stoffregen, 1991), which states that aberrant stimuli place constraints on postural control, and motion sickness represents awareness of the potential consequences of those constraints on goal achievements (Riccio & Stoffregen, 1991; Stoffregen et al., 2010). However, it is difficult to see how postural instability can be the sole basis of optokinetically-induced space-motion illusions given that there is behavioural and neuroimaging evidence of vection having occurred in participants who were sitting (Thilo, Kleinschmidt, & Gresty, 2003) or lying (Brandt et al., 1998; Kleinschmidt et al., 2002) while exposed to unidirectional motion sequences. Presumably postural control was less pressing for these participants because of their stable positions.

As hinted at by its delayed onset, vection is not ever-present during exposure to optokinetic stimulation. Rather, there are recurrent epochs of misperceived self-motion, each one lasting approximately 15 s (Kleinschmidt et al., 2002). These epochs are separated from each other by about 20 s (Kleinschmidt et al., 2002), during which time the observer recognises that it is really the visual pattern that is moving rather than him- or herself. As such, the observer perceives ‘object motion’ rather than self-motion (see section 1.3.3.2.3). Typically, at the onset and offset of vection epochs, there can be periods of ambivalence wherein the observer experiences coexisting interpretations of self- and object-motion (Thilo et al., 2003; Wertheim, 1994). Therefore, optokinetic stimulation gives rise to a situation where the perception of motion vacillates over time - the perception is

---

his or her instantaneous whole-body motion. Collectively, the misperceptions of self-orientation, -motion and -location will be termed ‘space-motion misperceptions’ after Indovina et al. (2014). They are formalisations of dizziness.

‘multistable’ (Blake & Logothetis, 2002). This is not predicted by the standard model of optimal cue integration, according to which the more reliable visual cue, secondary to persisting optic flow, should consistently hold greater influence over the perception of self-motion. Therefore, the standard model may be too simplistic. Indeed, the results of several studies, which were not specifically focused on visuo-vestibular cue integration, did not conform with optimality predictions (see Ernst, 2012 for a review).

One criticism of optimal cue integration is that it does not say anything about how the nervous system judges the accuracy of sensory cues and treats them accordingly (Ernst & Di Luca, 2011). Accuracy judgements may rely on top-down mechanisms, since, unlike reliability, cue accuracy cannot be directly assessed from sensory evidence (Ernst & Di Luca, 2011). Several recent studies and reviews have indicated that top-down influences may come into play in accordance with particular task demands (Kaliuzhna et al., 2015; Roach et al., 2006; Wei & Kording, 2011; Zaidel, Turner, & Angelaki, 2011). Such findings further highlight the task-specific processing of sensory information raised in section 1.4.4. Aberrant space-motion information may largely affect overt actions which involve translocation of the whole body. It may be possible to extrapolate this notion to covert actions of the body such as mental self-translocation, the theory of which will be described next.

1.6 Mental self-translocation and its theoretical dependence on space-motion information

The present section explores what mental self-translocation is, and then focuses on why it is a suitable cognitive process to study in order to determine whether aberrant space-motion information can directly affect higher cognition.

1.6.1 Definitions and associations of mental self-translocation

Mental self-translocation (MS-TL) is a higher cognitive function which involves the transformation of a mental image of body position. That is, MS-TL refers to imaginary changes of a representation of self-location (Blanke et al., 2005). These changes can occur in parallel with perceptual updating of physical body position (Cullen & Taube, 2017; Mast

& Ellis, 2015). Just as path integration involves the tracking, over time, of changes in body position due to overt movement (see section 1.4.4), MS-TL may involve the tracking of changes in imaginary body position with covert movement over time. Sometimes the mental representation of the body, which is manipulated during MS-TL, is referred to as the 'body schema' (e.g. Creem-Regehr, 2010; Falconer & Mast, 2012; Grabherr et al., 2007; Kessler & Thomson, 2010; Preuss, Harris, & Mast, 2013). According to Falconer and Mast (2012, p. 337), who give the fullest definition, "body schemas are internal spatial and biomechanical representations of the body, constructed from 'on-line' multisensory integration". MS-TL entails an imaginary change in one's perspective and, therefore, the cognitive process is sometimes referred to as 'perspective taking' (e.g. Frith & Frith, 2007). There are two main reasons why the term 'mental self-translocation' has been adopted in favour of 'perspective taking' in this thesis. First, 'self-translocation' highlights the fact that it is a representation of self-location (i.e. body position) which is the manipulandum during the cognitive process, based on the theory presented in section 1.6.2. Second, 'perspective taking' is often prefixed by one of several adjectives, for example 'spatial', 'visual', 'cognitive' or 'affective'. These prefixed versions of perspective taking specifically relate the cognitive process to discrete and explicit decisions or judgements. For example, 'spatial perspective taking' involves MS-TL, but specifically for the purpose of making laterality judgements. 'Visual perspective taking' uses the cognitive process as a precursor to the identification of specified objects. Use of the term 'mental self-translocation' is less confusing because it does not have multiple associations unlike 'perspective taking'.

MS-TLs can be categorised into more specific mental manipulations of self-location. Mental self-rotation and mental self-translation are the two main types of MS-TL. Given that all MS-TLs are manipulations of a mental representation of the body in space, they can be categorised as 'mental spatial transformations' within the bracket of spatial imagery. In addition to MS-TLs, mental spatial transformations include the range of covert rearrangements humans can make to representations of entities other than self-location. 'Mental object rotation' (MOR) is perhaps the most widely known and well-studied form of mental spatial transformation (Zacks & Tversky, 2005). This visuo-spatial ability involves the mental manipulation of images of two- or three-dimensional objects in one or more planes (Kaltner, Riecke, & Jansen, 2014; Shepard & Metzler, 1971) (see section 1.8 for further details). MS-TL, not MOR, was the higher cognitive function of interest during this research project because it may be the most susceptible to aberrant space-motion information. This is the prediction of a combined theory of MS-TL.

1.6.2 The internal model formulation of mental self-translocation

Grush (2004) and Mast and Ellis (2015) present mechanistic accounts of mental imagery based on internal model theory. Essentially, their accounts say that imagery processes capitalise on the sensorimotor circuitry for isomorphic, overt actions. In particular, the forward model in the circuitry is utilised. Mapping these ideas onto the preceding informal model of motor control (see section 1.4.4) yields an ‘internal model-based formulation of mental self-translocation’. According to this, a goal state would arise if an observer conceived a new position to mentally adopt. This goal state would be compared with his or her current representation of self-location (rather than with his or her current perception of self-location as described in section 1.4.4). Any discrepancy between the current state and goal state would activate the same sensorimotor circuitry as for analogous or isomorphic, overt whole-body movement. In all likelihood, therefore, this would be the locomotor circuitry of the brain. The inverse model within that circuitry would be instigated, leading to efferent signals. The motor command component of these, which is usually transmitted to the effector systems, has to be suppressed during MS-TL so that no overt movement occurs (Grush, 2004; Mast & Ellis, 2015).

The efference copies would not get suppressed. They would instigate the forward model, leading to amodal and unimodal predictions. Afference (Grush, 2004) or prediction errors (Mast & Ellis, 2015) would be actively attenuated because “any comparison between actual and fictive sensory signal [sic] would be undesirable” (Mast & Ellis, 2015, p. 10). Therefore, mainly the temporo-spatial (velocity) data comprising the amodal predictions from the forward model would get temporally integrated, resulting in a continually updated position of the body representation constituting the current state. When that mental image of body position matched the position the observer had originally intended to mentally adopt, the process of mental self-translocation would be terminated (Kessler & Thomson, 2010). Aspects of the sensorimotor circuit thought to be engaged during MS-TL are highlighted in Figure 1.4.

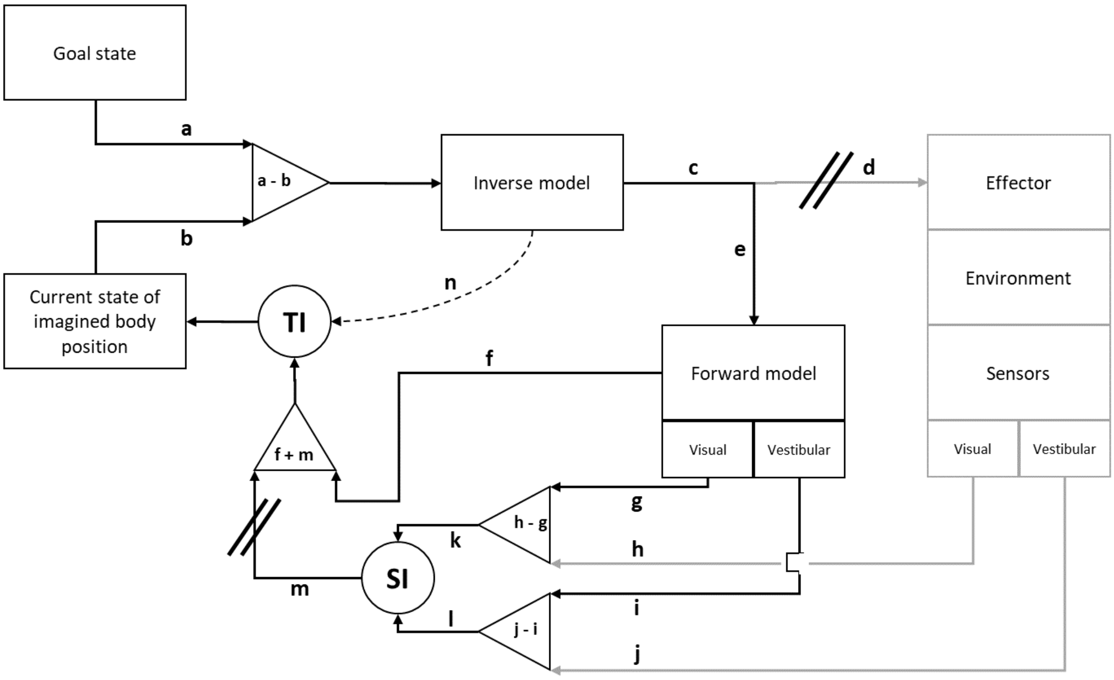


Figure 1.4: A schematic of the internal model-based sensorimotor circuit employed during mental self-translocation.

This modification of Figure 1.2 shows the suppression of motor commands from the inverse model to peripheral effectors and the attenuation of afference or prediction errors (Grush, 2004; Mast & Ellis, 2015). Hence, the inner loop of the circuit drives the transformation of the imaginary representation of self-location.

n – the pathway implied by simulation theory (Grush, 2004)

This internal model-based formulation of MS-TL is in line with emulation rather than simulation theories of motor imagery. The former emphasise the role of the forward model in emulating the motor-to-sensory transformations which would have been implemented by the physical world had the motor commands not been suppressed (Grush, 2004). Simulation theories imply that efference copies bypass the forward model (see Figure 1.4, pathway ‘n’); that is, motor imagery is hypothesised to be “the free-spinning of the controller [i.e. inverse model]” (Grush, 2004, p. 384). Mast and Ellis (2015) and Cullen and Taube (2017) imply that the inner loop of the circuit, which covertly drives the transformation of imaginary self-location, can be active at the same time as sensorimotor processing for overt action.

1.6.3 The preferential vulnerability of mental self-translocation to aberrant space-motion information

Given that prediction errors are most likely suppressed during MS-TL, it is not immediately clear how the process might be susceptible to aberrant space-motion information secondary to incongruous sensory cues. Indeed, the preceding theory of MS-TL implies that the process may be entirely implemented by an internal model (comprising inverse and forward model components), and only entail space-motion information generated by that model. Of relevance, at least three studies indicate that cognitive processes, which, like MS-TL (according to section 1.6.2), probably involve temporal integration specifically of space-motion information, benefit from an accurate space-motion context just prior to their onset (Arthur, Philbeck, & Chichka, 2007; Arthur et al., 2009; Israël et al., 1996). All three studies examined whether the availability of such a context enhanced the self-motion updating inherent in angular path integration. This refers to the specific ability to maintain an estimate of self-location after rotational displacement(s) (see section 1.4.4 for further details). To test this, the studies implemented whole-body yawing rotations in darkness. Prior to the rotations, participants either had clear or impoverished visual (or remembered) spatial referents. After the rotations, they had to judge the magnitude of the angular displacement relative to the initial heading. The studies showed that the precision of participants' perceptions had been higher when they had been provided with a space-motion context prior to whole-body rotations. For example, in the study by Arthur et al. (2009), there was a 93% increase in the standard deviation of participants' judgements when visual referents were not provided versus when they were.

The researchers concluded that accurate coding of one's initial temporo-spatial activity facilitates the subsequent integration of space-motion information (Israel et al., 1996; Arthur et al., 2007; Arthur et al., 2009). Without this coding, integration may accumulate more errors or noise in the velocity signal, leading to an increasingly imprecise estimate of one's position (Arthur et al., 2009). According to Israel et al. (1996, p. 411), an accurate space-motion context constitutes a "starting point", which might allow the temporal integrator to be reset and the relevant cognitive process to be initiated. However, they emphasised that the affordance of this starting point was not crucial to angular path integration, because their participants could still roughly judge the degree to which they had been displaced in its absence.

Temporal integration for MS-TL may similarly benefit from a starting point; that is, from accurate encoding of the foregoing space-motion context. This speaks to the traditional theories of mental object rotation (MOR) (e.g. Corballis, 1988; Shepard & Cooper, 1982). According to these, the following independent information processing stages can be differentiated in a MOR task: (1) perceptual preprocessing, (2) identification / discrimination of the image and identification of its orientation, (3) mental rotation itself, (4) judgement of the congruity, and (5) response selection and execution (Heil & Rolke, 2002; Kaltner & Jansen, 2014). Electrophysiological studies by Heil and Rolke (2002) provided support for these stages and their sequential organisation. It does not appear that the stages have been mapped on to MS-TL, but presumably similar chronopsychophysiological events occur during it. Establishing a starting point by referring to occurrent space-motion information might relate to stage 1. The starting point may constitute the 'current state'. Its comparison with the goal state, as per the internal model formulation of MS-TL (see section 1.6.2), may be equivalent to stage 2. Only from this stage onward may prediction errors be suppressed, and only then may MS-TL become entirely governed by the internal model as Grush (2004) and Mast and Ellis (2015) suggest.

The crucial role in this theory of an accurate starting point for MS-TL implies the process calls upon space-motion information and, therefore, is vulnerable to aberrant information caused by incongruous sensory cues. Such information may make the starting point inaccurate or even indiscernible. As with angular path integration following impoverished visual referents, visuo-vestibular incongruity may cause MS-TL to proceed based on a less precise, memory-based representation of the body's temporo-spatial activity. To make a visual or spatial judgement following MS-TL, for example on a visual or spatial perspective taking task, respectively, the observer would, in effect, have to sample from a wider distribution of possible body positions afforded by the noisier translocation process (Arthur et al., 2009). Therefore, the accuracy or efficiency of the dependent visual or spatial judgement may be disrupted. While MOR and other mental spatial transformations may also involve starting points, and the subsequent temporal integration of information, these processes are less likely to call upon the space-motion context of the body as a whole. That is, they may not refer to space-motion information constituted by the occurrent, ascending and modulated visuo-vestibular inputs. Therefore, in comparison to these other imagery processes, MS-TL may be hypothesised to be dependent on space-motion information. This hypothesis will be re-visited in section 1.8.2.

1.7 Empirical support for a sensorimotor basis of mental self-translocation

1.7.1 The behavioural correlates of spatial perspective taking tasks

If MS-TL does use the sensorimotor circuitry for overt whole-body movement - a prerequisite of its hypothesised dependence on space-motion information - it should yield performance patterns similar to those observed during analogous, overt body movements.

MS-TL is typically evoked in experiments by having participants undertake spatial perspective-taking (SPT) tasks. In so-called ‘classical SPT tasks’, participants are presented with an array of objects within a designated area (van Elk & Blanke, 2014). The participants must remember the relative positions of the objects within the array. Thereafter, they are required to imagine standing in a new position and/or orientation within the area, then to identify where certain objects would be located relative to their new perspective (e.g. May, 2004). This classical method of evoking MS-TL, sometimes referred to as the ‘spatial updating paradigm’ (Creem-Regehr, 2010), has been criticised for the burden it places on working memory (Kessler & Thomson, 2010; May & Wendt, 2013). Such tasks, which are devoid of a target avatar, were not employed in this research project to reduce the memory imperative.

The SPT tasks, which will be focused upon herein, typically require participants to specify the laterality of a demarcated body part, manipulandum or environmental feature from an on-screen avatar’s perspective. These SPT tasks can be categorised according to whether their stimulus sets comprise avatars incrementally tilted in the roll plane or turned in the yaw plane. Both groups of tasks are designed to evoke mental self-translocation or, more specifically, mental self-rotation - the covert isomorphism of overt, physical self-rotation. That is, they supposedly encourage observers to imagine their own bodies rotating to match the orientations of the visually-presented avatars so that they can make a laterality judgement about the demarcated entity. According to the internal model formulation of MS-TL, the time taken to make the laterality judgement should vary as a function of the orientation disparity between the observer's and avatar's positions. For larger disparities, more iterations of the sensorimotor loop would be required before the observer's representation of self-location (current state) matches his or her intended self-location (goal state). The actual performance patterns yielded from the two groups of SPT tasks will be discussed separately below with a focus on seeing if these predictions hold.

1.7.1.1 SPT tasks comprising avatars tilted in roll and their behavioural correlates

In tasks that present the single avatar rear-facing in every trial, but with its on-screen orientation systematically varied in the roll plane through 360º, response times (RTs) remain stable for avatar tilts between 0º (fully upright) and approximately 50º in the clockwise or anticlockwise directions (Kaltner et al., 2014; Kessler & Thomson, 2010; Michelon & Zacks, 2006; Preuss et al., 2013). Beyond 50º tilts, RTs increase monotonically until the avatar is tilted 180º (fully inverted) (Kaltner et al., 2014; Kessler & Thomson, 2010; Michelon & Zacks, 2006; Preuss et al., 2013). This confinement of the monotonic RT function to larger angles of rotation suggests that participants only engage in mental self-rotation for greater angular disparities between their own and the avatar's positions. Kessler and Thomson (2010) suggested that participants are able to make a direct visual classification of the laterality of the avatar's limb, or other demarcated entity, for smaller angular disparities (of approximately 50º or less). That is, for smaller disparities between the observer and avatar, mental self-rotation is simply not necessary (Kessler & Thomson, 2010; Surtees, Apperly, & Samson, 2013). The reason why RTs, which are recorded when the angular disparity between the avatar and observer is 180º (i.e. when the avatar is fully inverted), are usually the longest of all is that observers seem to imagine themselves rotating along the shortest path according to Parsons' (1987) observations.

Overall, SPT tasks with stimulus sets comprising only rear-facing avatars tilted in the roll plane appear to adequately evoke MS-TL if monotonic performance is a hallmark of it, as the internal model formulation suggests. The same cannot be said for SPT tasks with stimulus sets comprising only front-facing avatars tilted through 360º in roll. There tends to be no discernible monotonic function in the response time data for these specific tasks (Jola & Mast, 2005; May & Wendt, 2013; Zacks, Mires, Tversky, & Hazeltine, 2002). Even when the angular disparity between the avatar and observer is 180º (typically when the avatar is fully inverted), response times are little different than when the angular disparity is 0º (typically when the avatar is fully upright). Such findings contradict the predictions of the internal model formulation of MS-TL. In Jola and Mast's (2005) study, participants reported that they imagined rapidly flipping their bodies in the pitch plane when presented with inverted, front-facing avatars; a quicker strategy than imagining rotating their bodies in the roll plane. This could account, in part, for the non-monotonic RT function. But participants may also learn that the laterality of the demarcated limb or entity from the avatar's perspective, when it is near or fully inverted, simply requires an ipsilateral manual response (May & Wendt, 2013) (see section 1.7.2 for further details). Essentially, participants probably adopt one or both of these 'shortcut' strategies when presented with inverted, front-facing avatars. These strategies obviate the need for them to engage in mental self-rotation; a more cognitively-demanding process than the shortcuts. SPT tasks, which feature inverted, front-facing avatars, are not valid means of evoking MS-TL. Performance on these tasks may not be especially susceptible to aberrant space-motion information.

Returning to the SPT tasks with rear-facing avatars tilted in roll; even though these yield a (partial) monotonic RT function indicative of the evocation of MS-TL, the ecological validity of these tasks remains questionable. Imagining taking the perspectives of partially- or fully-inverted conspecifics is not commonplace for humans. Therefore, it can be argued that all SPT tasks comprising avatars tilted through 360º in the roll plane, not just those with front-facing figures, are not well-suited to the task of clarifying whether balance disorders, and the misinformation they entail, can have a direct effect on higher cognitions.

1.7.1.2 SPT tasks comprising two-dimensional, front- and rear-facing avatars and their behavioural correlates

The group of SPT tasks, wherein the avatar is displayed in different orientations in yaw as opposed to pitch, are more ecologically valid. These tasks have also been employed in a range of studies. In many of them, a two-dimensional avatar was simply shown front- or rear-facing (e.g. Arzy, Thut, Mohr, Michel, & Blanke, 2006; Blanke et al., 2005; Gardner

& Potts, 2011). As with SPT tasks comprising avatars tilted in roll, participants were required to identify the laterality, from the avatar's perspective, of a demarcation on or near one of the avatar's hands. It has been consistently shown that the time needed to make this laterality judgement is longer when the avatar is shown front-facing; that is, when the avatar's position differs from the observer's by 180º. However, this does not necessarily indicate that this form of SPT task evokes mental self-rotation or MS-TL more generally. Participants may merely learn to transpose left and right whenever confronted with front-view figures (Gardner, Brazier, Edmonds, & Gronholm, 2013). This shortcut strategy would still manifest longer response times for front- versus rear-facing avatars because of stimulus-response incompatibility (May & Wendt, 2013) (see section 1.7.2 for further details). To try to circumvent this shortcut strategy, further variability was introduced into the stimulus sets of some studies by presenting the avatars randomly displaced in the roll plane, but through a maximum range of -60 to +60º in order to maintain ecological validity (e.g. Candidi et al., 2013; Gardner et al., 2013; Gardner, Stent, Mohr, & Golding, 2017; Zacks, Rypma, Gabrieli, Tversky, & Glover, 1999).

1.7.1.3 SPT tasks comprising three-dimensional avatars incrementally turned in yaw and their behavioural correlates

In other studies of MS-TL (e.g. Kessler & Thomson, 2010; Michelon & Zacks, 2006; Surtees et al., 2013; Tadi, Overney, & Blanke, 2009; van Elk & Blanke, 2014), three-dimensional (3-D) avatars have comprised the stimulus sets. The figures' extra spatial dimension meant that they could be displayed trial-on-trial in different yawing increments, rather than just in front- or rear-facing orientations. Opting for a 3-D image afforded the following series of views of the avatar in several studies: 0º of rotation (avatar fully rear-facing); 45º of rotation to the left or right; 90º of rotation to the left or right; 135º of rotation to the left or right, and; 180º of rotation (avatar fully front-facing). The most common finding has been a linear increase in RT with each successive 45º increment. More specifically, converging evidence from several studies indicates that participants are quickest to make laterality judgements about an avatar with 0º of rotation, but become progressively slower to respond as the avatar's yawing orientation increases in one direction or other towards 180º (Michelon & Zacks, 2006; Surtees et al., 2013; Tadi et al., 2009). Kessler and Thomson (2010) opted for slightly finer incremental yawing rotations of the avatar in their SPT task. They found that participants' RTs only started to progressively increase for avatars rotated beyond 80º in yaw. This confinement of the monotonic RT function to larger angles of rotation is similar to the pattern of performance on SPT tasks with rear-facing avatars rotated in roll (see section 1.7.1.1). Mental self-rotation may not be necessary when the angular disparity in yaw between observer and avatar is relatively small.

The monotonic RT functions across most, if not all, of the angular disparities between observer and avatar suggest that these SPT tasks with 3-D avatars can evoke MS-TL. They are probably the most ecologically valid SPT tasks as well - imagining taking the perspectives of conspecifics in various angles of turn is commonplace for humans (Gardner et al., 2017). So far, no investigations into the effect of balance disorders on MS-TL have employed SPT tasks with stimulus sets comprising 3-D avatars displayed trial-on-trial in different yawing increments. Doing so might be insightful about the potential direct effect of aberrant space-motion information on higher cognition.

1.7.2 Alternative explanations for monotonic response-time functions

Throughout the section above (i.e. 1.7.1 and all its subsections), monotonic RT functions were heralded as the hallmark of the internal model formulation of MS-TL. More specifically, these functions have been explained in terms of a greater number of iterations of the sensorimotor loop for larger disparities between the observers' and avatar's positions. However, this explanation for RT monotonicity is not universally accepted. Those researchers who dispute that participants engage sensorimotor circuitry thus deny that perspective-taking tasks evoke MS-TL. May and Wendt (2013) argue that a series of problems stand in the way of the claim that observers solving SPT-related problems imagine transforming their own perspectives into those of the avatars. Almost all SPT tasks, which have been employed in published research to date, have required laterality judgements (as explained in section 1.7.1). This means it is difficult to separate performance costs genuinely associated with MS-TL from costs associated with stimulus-response compatibility (May & Wendt, 2013). It is well-recognised in perception-based research that responses are faster and less error-prone when there is greater correspondence between the location of a stimulus and the location of the required response (Gardner & Potts, 2011; May & Wendt, 2013). Therefore, spatial compatibility effects should facilitate laterality judgements about rear-facing avatars (May & Wendt, 2013), which may explain, in part or in full, why it has been consistently shown that the time needed to make left-right judgements is longer when the avatar is shown front-facing (see section 1.7.1.2). May and Wendt (2013, p. 2) even suggest that the monotonic RT function found when avatars appear in incremental yawing orientations (see section 1.7.1.3) may be due to "graded compatibility effects".

Evidence pointing towards an influence of spatial compatibility on perspective-taking performance can be found in Gardner and Potts' (2011) data, which show that vocal laterality responses, known to produce smaller spatial compatibility effects than manual responses, reduced the difference in RT for rear- versus front-facing avatars. Furthermore, the non-monotonic RT function associated with SPT tasks employing front-facing avatars with different roll plane tilts (see section 1.7.1.1) could also attest to a strong spatial compatibility influence on patterns of performance. When front-facing avatars are fully inverted, there is no longer a spatial conflict between the laterality of the demarcated limb, or other salient feature, and the laterality of the required response (May & Wendt, 2013). Hence, the latency of responses made about front-facing, inverted avatars matches response times for upright avatars.

It has also been suggested that response monotonicity on SPT tasks could stem from imaginary manipulations of the avatar's rather than the observer's orientation (e.g. May & Wendt, 2013). Since behavioural data, even those indicating monotonic RT functions, may not be adequate evidence for the evocation of MS-TL, it is particularly useful to review the relevant neuro-imaging and -stimulation data. The internal model formulation would predict the activation of cortical vestibular processing areas (CVPAs) during tasks that elicit MS-TL given that the cognitive process should utilise modulated space-motion information. Evidence for such activations during the performance of SPT tasks would lend support to the hypothesis that MS-TL calls upon space-motion information and, therefore, is vulnerable to misinformation.

1.7.3 The neuro-imaging and -stimulation correlates of spatial perspective taking tasks

1.7.3.1 Functional neuro-imaging data

Zacks and colleagues' (1999) study remains the only one to have employed functional magnetic resonance imaging (fMRI) while participants undertook a spatial perspective taking (SPT) task with a stimulus set comprising on-screen avatars. More specifically, the participants were presented with two-dimensional, front- and rear-facing avatars tilted at random 10º increments in the roll plane through a maximum range of -50 to +50º. Three scans were performed, and the tasks employed during each were varied. During the first scan, the participants had to alternate between two strategies from trial-to-trial; they had to identify the laterality of an on-screen target from either the avatar's perspective or from their own. The laterality responses the participants made from their own perspective served as a control task. Compared to the control task, the SPT task, with its supposed imperative for MS-TL, led to activity centred around the temporoparietal junction (TPJ) and adjacent extrastriate cortex (Zacks et al., 1999) - the forebrain regions that contain many of the CVPAs and, therefore, are involved in the processing of space-motion information (see section 1.3.2.1.8). The specific cortical regions that were preferentially activated included the posterior cuneus, the precuneus, the occipital and lingual gyri, the superior parietal lobule and the middle frontal gyrus (BA 9), with much stronger activity in the left than in the right hemisphere. Because the control task did not rule out brain activations simply due to incompatible stimulus-response mappings, the findings of the first scan do not make a compelling case for TPJ engagement that is unique to the process of MS-TL.

During the second scan in the study by Zacks et al. (1999), the avatar was presented either upright or inverted. No matter its orientation, participants had to judge the laterality of the on-screen target from the avatar's perspective. Similar cortical regions were activated during the two different orientations, but stronger activations were observed during the inverted presentations in several of those regions. The authors argue that these findings are in-keeping with separable neural substrates for MS-TL and mental object rotation; participants may have imagined rotating the inverted avatars into an upright position before they engaged in MS-TL to make the laterality judgements (Zacks et al., 1999). However, due to the overlap of neural activations associated with the upright and inverted presentations, it is not clear whether stimulus-response mappings can be completely discounted as a cause of TPJ / CVPA engagement. A third and final scan was performed (Zacks et al., 1999) while participants made rote-learned, spatially incompatible responses, but performance on this task was not compared directly with performance on the SPT task employed during the first two scans. Overall, the results of this fMRI study are equivocal as to the separability of CVPA activations due to stimulus-response mappings or MS-TL.

The same uncertainty also compromises the results of the evoked potential study by Blanke et al. (2005). Therein, 11 right-handed participants undertook Zacks and colleagues' (1999) SPT and control tasks, albeit without the roll-plane tilts of the avatars, during continuous electroencephalographic recordings. Evoked potential mapping based on the temporoparietal electrodes revealed a pronounced evoked potential component, which suggested different cortical processing of the SPT and control tasks. During the SPT task, activation of the TPJ was found in 10 of the 11 subjects (Blanke et al., 2005).

Two subsequent studies, which also employed evoked potential mapping (Arzy et al., 2006; Tadi et al., 2009), were able to show that TPJ activity is a hallmark of SPT tasks, therefore probably of MS-TL, and does not just represent incompatible stimulus-response mappings. Arzy et al. (2006) used the same SPT task as Blanke et al. (2005) but adapted the control task. Instead of identifying the laterality of the on-screen target from their own perspective, participants had to imagine that the on-screen avatar was their mirror image and make the laterality judgements accordingly (Arzy et al., 2006). Therefore, this version of the control task necessitated spatially incompatible responses during half of the trials, whereas the simpler control task employed by Blanke et al. (2005) did not. Only during the SPT task was there a predominance of TPJ activity on the right side, which occurred 330 to 400 ms after the avatars were displayed. In the other study, Tadi et al. (2009) used tasks with 3-D rather than 2-D avatars, which appeared in a range of increments in yaw. During the SPT task, the avatars were presented upright, but during the control task, they were shown inverted. The latter task matched the SPT task for stimulus-response compatibility and, therefore, served to control for related confounds. Similar to the results of Arzy et al. (2006), Tadi et al. (2009) found activation in temporo-occipital and medial parieto-occipital cortices between 350 and 460 ms after stimulus onset, which specifically related to mental self-translocations into upright avatars.

1.7.3.2 Neuro-stimulation data

The results of neuro-stimulation studies may also provide insight into whether the dependence on space-motion information is valid, as predicted by the inverse-forward formulation of MS-TL. Recently, van Elk et al. (2017) found that transcranial direct current stimulation (tDCS) of the right TPJ preferentially impaired performance on a SPT task, which incorporated three-dimensional avatars incrementally turned in yaw, compared with performance on a simple laterality task, which involved left-right judgements from participants' own perspectives. Unfortunately, the simplicity of the control task means it is not possible to differentiate whether there was a tDCS-induced disruption of MS-TL or of incompatible stimulus-response mappings more generally.

In addition to their evoked potential study (see 1.7.3.1), Blanke et al. (2005) also undertook a transcranial magnetic stimulation (TMS) study, which incorporated seven right-handed participants. In separate experimental sessions, the participants performed the SPT task comprising front- and rear-facing avatars (see 1.7.3.1) or a 'letter transformation' (LT) task. During the latter, the participants were presented with the letter F either in its canonical orientation or in a flipped orientation, as if the character had been rotated by 180° in yaw. A black square was imprinted on one or other end of the character's horizontal bar. The participants were instructed to imagine rotating the character into its canonical orientation in order to judge whether the black square was on its left- or right-hand-side (Blanke et al., 2005). The LT task controlled not only for spatial compatibility effects but also for mental rotation effects. TMS was applied over the right TPJ as well as over a control site at the intraparietal sulcus (IPS). Stimulation of the former region caused prolonged RTs, but only with respect to laterality judgements made about front-facing figures in the SPT task. The authors concluded that the activation of the TPJ during MS-TL is differentiable from the mere perception of the human body and from spatially incompatible left-right decisions (Blanke et al., 2005).

In conclusion, the neuro-imaging and -stimulation data indicate that activity in discrete cortical regions, including CVPAs, correlates specifically with MS-TL. In particular, MS-TL is associated with activation of the TPJ in one or both hemispheres. As proposed by Kaski et al. (2016), the (right) TPJ may be the temporal integrator, which updates the perception of self-location from trains of velocity- and/or acceleration-related signals (see sections 1.3.2.1.7 and 1.4.3). This temporal integration is fundamental to MS-TL according to the internal model formulation and may benefit from a discernible and accurate ‘starting point’ (see sections 1.6.2 and 1.6.3). As there is some empirical support for space-motion processing during MS-TL, the cognitive function may well have a comparative dependence on related information and the starting point it provides.

1.8 The contrasting bases of mental self-translocation and other mental spatial transformations

1.8.1 Mental rotation of objects, bodies and body parts

In the classical mental object rotation (MOR) tasks, sometimes referred to as chronometric mental rotation tasks (e.g. Kaltner et al., 2014), two or more misaligned polygons are presented side-by-side on paper or on screen. Typically, the left shape serves as the “standard” or “target” image, and the observer has to decide as quickly and as accurately as possible whether each of the “comparison” shapes to the right is the same as, or different to, the target (Parsons, 1987). Essentially, the observer must work out whether the target and comparison shapes have rotational symmetry, in which case they are the same, or mirror symmetry, in which case they are different. From trial-to-trial, angular disparities between target and comparison shapes are varied systematically, and response times (RTs) and error proportions serve as dependent variables (Kaltner et al., 2014). Two-dimensional body-part and whole-body pictures have been used as visual stimuli, in place of inanimate polygons, in many studies since the 1980s (e.g. Candidi et al., 2013; Falconer & Mast, 2012; Grabherr et al., 2007; Kaltner et al., 2014; Preuss et al., 2013). Target and comparison body forms are usually presented with disparate orientations in the picture (roll) plane.

Even when bodies or body parts are displayed, these MOR tasks should be differentiated from ‘mental body part rotation’ (MBPR) tasks, which only display a single appendage (e.g. hand, shoulder, foot etc.) per trial. The observer’s goal is to identify the laterality of the body part with reference to the anatomical position. There is no accompanying body part in relation to which a same-different judgement can be made. Parsons (1987) observed that participants tend to imagine their own appendage moving into the position of the one displayed on-screen in order to make the left-right judgement. This strategy is clearly different from that evoked during MOR, which does not make explicit reference to one's own body and its parts. The difference in the cognitive processing elicited by MBPR and MOR tasks is further emphasised by research showing that RTs recorded during MBPR but not MOR tasks vary with the "implicit awkwardness of stimulus orientation (i.e. extent of anatomical and physiological constraints on movement to that stimulus orientation)" (Parsons, 1987, p. 178). The neural substrates of performance on MBPR and MOR tasks have also been shown to be dissociable (Kosslyn, DiGirolamo, Thompson, & Alpert, 1998; Tadi et al., 2009).

However, Wohlschläger and Wohlschläger (1998) identified an important similarity between the cognitive processes for MOR and overt movements of the hand. They had 92 right-handed participants undertake a MOR task while simultaneously executing one of four hand motions. Interference was observed when the manual and mental rotations were coplanar. Ipsi-directional hand rotation facilitated, whereas contra-directional hand rotation inhibited, MOR (Wohlschläger & Wohlschläger, 1998). These results, which were replicated by Wexler et al. (1998), indicate that MOR and physical motion of the body's appendages share a common process. This implies that the cognitive bases of performance on MBPR and MOR tasks may not be completely distinguishable after all. For this reason, the theoretical and behavioural aspects of MOR will be focused upon below to provide a contrast to MS-TL.

1.8.2 The internal model formulation of mental object rotation

An internal model formulation may also apply to mental rotation, according to Grush (2004) and Mast and Ellis (2015). Whereas MS-TL may utilise space-motion information and locomotor circuitry, it has been proposed that the imaginary rotation of objects (as in MOR) capitalises on the sensorimotor circuitry for controlling overt, manual manipulations of objects (Grush, 2004; Kessler & Thomson, 2010; van Elk & Blanke, 2014; Wexler et al., 1998; Wohlschläger & Wohlschläger, 1998). This circuitry would be activated if an observer conceived a new (imaginary) location or position for an object (goal state) which differed from its current position (current state). The forward model in the circuit would receive copies of suppressed motor commands that would otherwise manually rotate an analogous manipulandum. In turn, the forward model would issue amodal predictions about the state of the upper limb performing the (imaginary) manipulation. The temporo-spatial data constituting these predictions would be temporally integrated enabling the observer to continually update his or her representation of limb configuration and, therefore, of object position. However, before temporal integration were initiated, a starting point would be constructed from the limb's actual or physical state. Unlike in MS-TL, where the starting point depends on visuo-vestibular (i.e. space-motion) information, the starting point for MOR would derive from muscle proprioceptor and somatosensory (i.e. body segment) information. Accordingly, MOR would not be expected to be as susceptible to aberrant space-motion information as MS-TL.

Alternatively, MOR may be based on the processing of stored information, or remembered spatial representations of objects (Arthur et al., 2009), rather than on the processing of body segment information (Grush, 2004). A starting point for temporal integration of this 'cognitive information' may remain beneficial, and that starting point may still be determinable in the face of incongruous visuo-vestibular cues due to its detachment from the temporo-spatial activity of the whole body. Both accounts of the mechanisms underpinning MOR are consistent with the task-specific processing of sensory information, as described in sections 1.4.4 and 1.5.3.

1.8.3 The behavioural and neuro-imaging correlates of mental object rotation tasks

As predicted by the internal model formulation of mental rotation, the time needed to make a decision about the congruity of two misaligned polygons has been shown to be a function of the angular disparity between the two objects. The greater the disparity, the longer the time needed to make a response. This monotonic RT function has indeed been likened to the linear increase in time taken to physically rotate objects by increasing magnitude, so long as a constant rotational velocity is maintained (Shepard & Metzler, 1971). The monotonicity was initially shown for incremental angular disparities between polygons in the depth (yaw) plane and, separately, in the roll plane (Shepard & Metzler, 1971). Subsequently, it was demonstrated that a monotonic RT function occurs even when increasing angular disparities between two polygons are generated by systematic re-orientations of the comparison polygon in the yaw and roll planes simultaneously (Jola & Mast, 2005). Furthermore, a positive linear relationship between RT and angular disparity also tends to be derived from MOR tasks in which misaligned body forms - either pairs of body parts or whole bodies - are displayed side-by-side (Creem-Regehr, 2010). The RT monotonicity for whole bodies certainly occurs when both target and comparison image are either bodies viewed from the front (front-facing) or bodies viewed from the back (rear-facing) (Kaltner et al., 2014). The RT pattern derived from misaligning whole bodies in roll, while also manipulating the direction the bodies are facing in, is less clear from the literature. Researchers tend to call less attention to the error patterns that MOR and other transformation tasks give rise to. However, increases in the angular disparity between two shapes typically lead to increases in errors, as well as in RTs (Jola & Mast, 2005; Kaltner et al., 2014), suggesting the slower responses are not simply a trade-off for higher accuracy.

MOR tasks have been consistently reported to be more effortful, denoted by participants' slower responses and reduced accuracy, than SPT tasks (Creem-Regehr, 2010; Kessler & Thomson, 2010; Preuss et al., 2013). The greater difficulty of MOR versus SPT tasks, plus the more assured monotonic RT functions that the former tasks yield, indicate that MOR and MS-TL are behaviourally differentiable, which may relate to separable informational dependences. The potential lesser reliance of mental rotation on space-motion information may also be reflected by neuro-imaging data, which show activations of differing sensorimotor areas of the cortex during MOR and SPT tasks (Creem-Regehr, 2010; Zacks & Michelon, 2005). More specifically, previous investigations into the neural substrate of MOR have shown bilateral occipito-parietal and frontal activations, not the predominant TPJ activation found during MS-TL (Creem-Regehr, 2010; Tadi et al., 2009; Zacks & Michelon, 2005). Blanke et al. (2005) theorised that MOR is associated with activity in the intraparietal sulcus rather than the TPJ (see section 1.7.3.2).

In conclusion, MS-TL is well-suited to the goals of this project; it should serve investigations into whether the aberrant space-motion information inherent in balance disorders can directly affect higher cognition. Tasks with similar stimulus-response mappings that evoke MOR or other cognitive processes, but do not involve the temporal integration of sensory information pertaining to the temporo-spatial activity of the whole body, may serve as useful controls. Greater disruption of SPT than control task performance might suggest that balance disorders can have an unmediated effect on cognition (see section 2.3 for further details).

1.9 Synopsis

In this chapter, space-motion information was defined as encoded temporal and spatial activity of the head and body as a whole. It is extracted mainly by the vestibular and visual systems. Research has shown that vestibular and possibly visual cues are compared with predicted sensory feedback. Those predictions are effectively deducted from the respective afferent signal so that the space-motion information, which ascends the neuraxis, represents prediction errors. Related research has also shown that the predictions are modified as a function of recent experience, which suggests that they derive from adaptive forward models. These are components of the sensorimotor circuitry for motor control according to internal model theory. During locomotion or other changes in whole-body position, the central nervous system monitors whether the intended translocation has been achieved by temporally integrating space-motion information processed by the motor control circuitry. Temporal integration may benefit from an accurate, initial context based on visuo-vestibular cues.

The second half of this chapter focused on the higher cognitive function known as mental self-translocation. This refers to imaginary changes of a representation of one's body position or self-location. Internal model theories propose that the process capitalises on the sensorimotor circuitry for locomotion. The circuitry is used 'off-line' so dynamic transformations of imaginary self-location take place in the absence of overt whole-body movement. Therefore, temporal integration of space-motion information may be inherent in covert as well as overt body movements. Internal model theories predict that performance on tasks, which evoke mental self-translocation e.g. spatial perspective-taking tasks, may be particularly susceptible to aberrant space-motion information. This is because temporal integration may be impaired by the lack of accurate visuo-vestibular referents at the outset. Behavioural and neuro-imaging studies provide some empirical support for the sensorimotor basis of mental self-translocation, and imply the cognitive function might have a particular susceptibility to aberrant space-motion information. Therefore, comparing the integrity of this and other cognitive processes in participants exposed to incongruous visuo-vestibular stimuli was adopted as a method for determining whether balance disorders, and the aberrant space-motion information they entail, can directly affect higher cognition.

Chapter 2. Delimited introduction: Narrative review of the effect of experimentally-induced balance disorders on spatial perspective-taking and comparison tasks

2.1 Overview

According to the theories set out in Chapter 1, spatial perspective-taking (SPT) tasks evoke mental self-translocation and, therefore, depend on accurate space-motion information. A preferential disruption of SPT task performance might indicate that balance disorders, and the aberrant space-motion information they entail, can have a direct, unmediated effect on higher cognition. Five studies, which provide empirical data of relevance to this hypothesis, are reviewed in the present chapter. All of the studies exposed participants to both regular and irregular vestibular or visual stimulation while they undertook SPT and comparison tasks. Therefore, the participants were subjected to two levels of a 'space-motion cue congruity factor' (congruous versus incongruous cues). A significant interaction between this factor and task on cognitive but not on physiological or subjective variables would indicate that aberrant space-motion information can directly affect cognition.

Four of the studies provide converging evidence for a disruption of mental self-translocation by aberrant stimulation. However, only two of the studies showed a statistically significant interaction between task and cue congruity on task performance variables. None of the studies adequately measured and analysed the cardinal manifestations of the stimulation-induced balance disorders. Therefore, it is not possible to discern whether aberrant space-motion information can directly disrupt cognition because the effects of potential mediator variables have not been adequately controlled to date. There is scope to extend the existing research with the objective of clarifying whether aberrant space-motion stimulation can have an unmediated effect on higher cognition. Details are provided of some of the methods necessary to pursue and fulfil this objective.

2.2 Introduction

According to the theories set out in Chapter 1, tasks that evoke mental self-translocation (MS-TL) depend on accurate space-motion information. Performance on such tasks may be susceptible to aberrant information, whereas performance on comparator tasks may be less so. Such a differential disruption of task performance might indicate that balance disorders, and the aberrant space-motion information they entail, can have a direct, unmediated effect on higher cognition. Empirical studies of particular relevance to this hypothesis are reviewed in the present chapter. All of the studies examined the effect of experimentally-induced balance disorders on spatial tasks (see Falconer & Mast, 2012; Gardner, Stent, Mohr, & Golding, 2017; Gresty, Golding, Le, & Nightingale, 2008; Lenggenhager, Lopez, & Blanke, 2008; Preuss, Harris, & Mast, 2013). It is the particular fact that the balance disorders under investigation were experimentally evoked that makes the studies so pertinent. There is less potential with experimentally-induced balance disorders, than with their pathological counterparts, for confounding interactions between the resultant dizziness, anxiety, imbalance and other cardinal manifestations, as explained in section ii of the Preface.

The review that follows omits studies which employed spatial perspective-taking (SPT) tasks based on the spatial updating paradigm (e.g. Dilda, MacDougall, Curthoys, & Moore, 2012) (see section 1.7.1 for the rationale). It only includes studies which exposed healthy participants to strong (i.e. reliable and, therefore, compelling) but erroneous (i.e. inaccurate) vestibular or visual stimulation. Usefully, the studies also exposed the participants to control conditions wherein there was veridical and matching visuo-vestibular stimulation. Hence, each study featured different types of space-motion stimulation (after Indovina, Riccelli, Staab, Lacquaniti, & Passamonti, 2014); that is, different levels of a factor that will be referred to herein as ‘space-motion cue congruity’. These studies are separable from those which focused on the effects of strong and accurate space-motion stimulation (e.g. Deroualle, Borel, Devèze, & Lopez, 2015; van Elk & Blanke, 2014), or of profound depletion of space-motion cues (e.g. Grabherr et al., 2007). It is questionable as to whether the latter studies, and the stimuli they featured, induced sensory prediction errors (see section 1.4.1) or other discordance which perturbed the starting point for temporal integration during MS-TL (see section 1.6.3). The fact that, previously, the effects of balance disorders on higher cognition do not appear to have been considered in terms of mediation models of analysis hinders a systematic search for, and synthesis of, data on the direct effect of aberrant space-motion information.

The specific aims of the present chapter are:

- To evaluate the directness of the effect of aberrant space-motion information on higher cognition, based on published evidence of relevance, and,
- To delineate the methodological requisites for the experiments covered in this thesis.

The five studies, or their subsidiary experiments, reviewed below are aggregated by the type of aberrant space-motion stimulation that gave rise to participants' experimentally-induced balance disorders. The five types of stimulation that featured in these studies were: caloric vestibular stimulation (CVS), galvanic vestibular stimulation (GVS), actively-generated impulse stimulation, visual stimulation and cross-coupled acceleration stimulation (CCS). The studies' methods and results will be summarised and then appraised with reference to experimental designs and analytical methods or models that might be particularly revealing about the direct effect of misinformation. Therefore, these designs and models will be covered first.

2.3 Applicable designs and analytical models

To ensure that participants engage satisfactorily in MS-TL and, therefore, benefit from veridical space-motion information, valid SPT tasks should be employed. Section 1.7.1 discussed how SPT tasks, which have stimulus sets comprising avatars in different yawing orientations, may be more valid than those tasks with avatars tilted in the roll plane. Evidently, the comparison tasks, which evoke cognitive processes other than MS-TL, also need to be valid. Having independent groups of participants, who are designated to undertake either the SPT or comparison tasks, may reduce the carryover of cognitive strategies from one task to another and, thereby, prevent attenuation of the intended cognitive processes (Gardner, Brazier, Edmonds, & Gronholm, 2013; Gardner et al., 2017; Zacks, Rypma, Gabrieli, Tversky, & Glover, 1999). In so doing, an independent-groups design would help to ensure that performance on the tasks remained variably susceptible to aberrant space-motion information. Performance outcomes on the cognitive tasks, for example response time (RT) and error proportion (P_e), should serve as primary dependent variables (DVs).

It is important to reiterate that the cardinal, often co-occurring manifestations of balance disorders, including those induced by experimental sensory manipulation, can include postural instability, disordered eye movements, anxiety, nausea and dizziness (Brandt, 2000; Gresty et al., 2008; Kennedy & Fowlkes, 1992; Kennedy, Lane, Lilienthal, Berbaum, & Hettinger, 1992; Luxon, 2004; Luxon & Bamiou, 2007; Smith & Zheng, 2013). All of these manifestations could potentially mediate the relationship between a balance disorder and higher cognitive function. Therefore, validated measures of each manifestation should be utilised then analysed as secondary DVs.

Structural equation modelling (SEM) is the accepted method of analysing the range of effects inherent in a combined parallel-sequential multiple mediator model such as that depicted in Figure ii of the Preface (Hayes, 2013; Singh, Chen, & Wegener, 2014). However, this technique typically requires a large sample that scales with the number of variables included. Subjecting each of the primary and secondary DVs to factorial analysis of variance (ANOVA) would seemingly be a more inclusive analytical strategy for the purpose of screening the indirect effects of potential mediator variables which it might not be practical to incorporate in a regression-based strategy[12]. More specifically, each variable could be submitted to an ANOVA incorporating no less than the two factors 'task' and 'space-motion cue congruity'. The levels of the former would depend on the number of tasks employed in the study, but would need to include 'SPT'. The two levels of the latter factor would comprise 'congruous space-motion cues' versus 'incongruous space-motion cues'. This analytical strategy would be particularly revealing if there was a significant interaction effect between the factors (task by space-motion cue congruity) on one or more primary DVs but not on any of the secondary DVs, as depicted in Figure 2.1[13]. This pattern of results would indicate a disproportionate disruption of one cognitive function, necessarily of MS-TL, by the aberrant space-motion stimulation without a commensurate inordinate disturbance of physiological or subjective state. The assumption inherent in this interpretation would be that the cognitive tasks differed only in regard to their susceptibility to misinformation resulting from the aberrant stimulation. The

---

[12] ANOVA-based analytical strategies, not SEM, were used in previous research of relevance.

[13] The line graphs in figure 2.1 depict the situation wherein a decrease in the magnitude of a parameter represents a disruptive effect of aberrant space-motion stimulation on that parameter. The reverse may be true for some parameters of cognitive performance i.e. an increase in the magnitude of such parameters may be representative of disruption.

implication would be that misinformation can have a direct, unmediated impact on higher cognition.

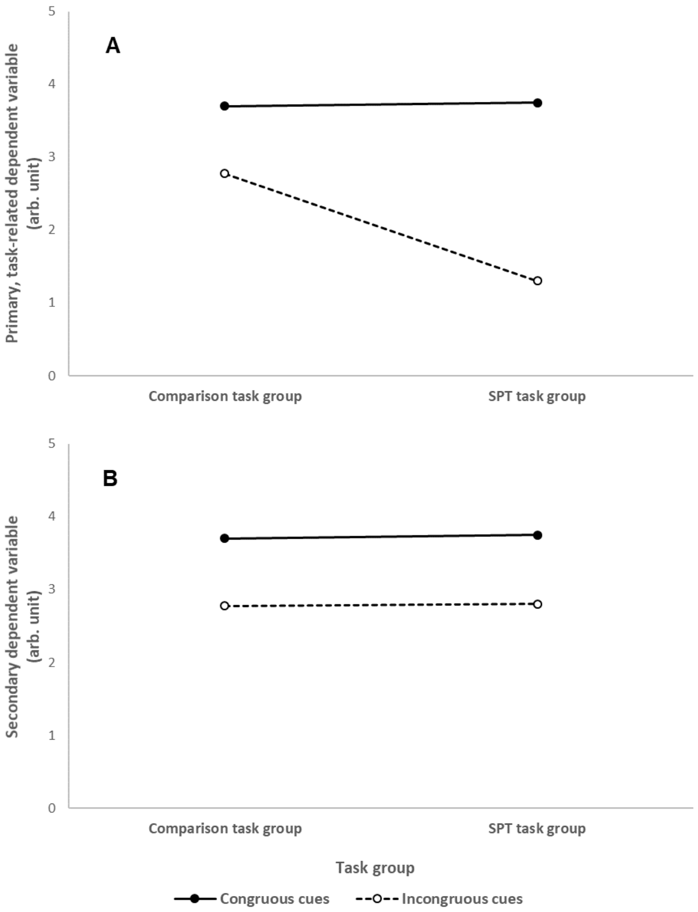


Figure 2.1: Line graphs depicting a significant interaction effect of ‘task’ and ‘space-motion cue congruity’ factors on a primary, task-related dependent variable [A], but not on a secondary, physiological / subjective variable [B].

This overall pattern of results, owing to the greater dependence of mental self-translocation on veridical space-motion information, would indicate that aberrant information can directly affect cognition.

However, the experimental design and analytical strategy described above would not necessarily rule out the potential mediating effect of attentional diversion. Consequently, conclusions regarding the directness of the effect of aberrant space-motion information would be ‘unsafe’. As discussed in the Preface, the cardinal manifestations of balance disorders may moderate the amount of attention devoted to cognitive task performance (for example, see the comment on the ‘posture-first principle’ in section ii). A selective diminution of attentional allocation to the SPT task could explain the pattern of results portrayed in Figure 2.1. Directly measuring effort by self-report may provide insight into attentional allocation, since effort and attention are commonly conflated (e.g. Kahneman, 1973). However, this conflation is controversial (Bruya & Tang, 2018). An alternate method of ascertaining the impact of attentional diversion on cognitive task performance might be to translate the 'observed' or behavioural variables of cognitive task performance into 'unobserved', mechanistic variables, and submit these as additional primary DVs to factorial ANOVAs as well.

This translation can be achieved by way of cognitive process models such as the EZ-diffusion model (Wagenmakers, van der Maas, & Grasman, 2007). According to Wagenmakers et al. (2007), the EZ-diffusion model was designed to yield the three most important mechanistic variables: the rate of decision-related information accumulation (represented by drift rate 'v'); response conservativeness or caution (represented by boundary separation 'a'), and; the duration of non-decision processes (represented by non-decision time 'T_{er}' or NDT - see section 3.11.2.1.2 for further details) (van Ravenzwaaij, Dutilh, & Wagenmakers, 2012). It is generally accepted that attentional diversion leads to a decrease in drift rate (O'Callaghan et al., 2017; Teichert, Ferrera, & Grinband, 2014; van Ravenzwaaij et al., 2012). Therefore, if a primary DV other than drift rate was disrupted by incongruous space-motion stimulation, the pattern of results depicted in Figure 2.1 would provide a compelling case for a direct effect of misinformation.

There are additional benefits of applying a diffusion model. Non-decision time represents afferent and efferent delays, as well as sensory encoding before decision-making processes are implemented (Dully, McGovern, & O'Connell, 2018; O'Callaghan et al., 2017; Teichert et al., 2014). Therefore, it could be a proxy for the amount of visual encoding required by the cognitive tasks. An interaction effect of task and space-motion cue congruity on non-decision time, with the more visually complex task(s) most disrupted, could indicate a differential vulnerability of the tasks to the disordered eye movements associated with an experimentally-induced balance disorder. This would represent a violation of the assumption stated above; that the cognitive tasks differed only in regard to their sensitivity to space-motion information. However, linking non-decision time to visual encoding is conjectural. Like most cognitive process models, the EZ-diffusion model largely assumes that information flow during decision-making can be broken down into individual, serial stages (Teichert, Grinband, & Ferrera, 2016). The mechanistic variables it derives have not been mapped on to the processing stages of MS-TL as far as the author of this thesis is aware.

The path-analytic method of mediation analysis devised by Montoya and Hayes (2017) complements the ANOVA-based analysis strategy described above by enabling simplistic mediation models to be tested. Based on regression analysis, this variant of Structural Equation Modelling can ascertain the direct effect of a predictor variable on an outcome variable by controlling for the effects of one or more mediator variables.

2.4 Methods and results of the relevant research

2.4.1 Caloric vestibular stimulation

Falconer and Mast (2012) administered bona fide and sham caloric vestibular stimulation (CVS) to 14 participants while they undertook MST tasks. CVS typically involves periods of unilateral aural irrigations with water or air, the temperature of which differs by specific amounts from body temperature. The irrigations transfer a temperature gradient from the outer ear to the inner ear by conduction. This gradient alters the specific gravity of endolymphatic fluid in the segment of the lateral semicircular canal nearest the outer ear causing fluid movement, which, in turn, deflects the cupula thereby modulating the afferent discharge in the ipsilateral vestibular nerve[14] (Baloh, Honrubia, & Kerber, 2011). Falconer and Mast (2012) delivered bilateral rather than unilateral air irrigations to participants' external auditory canals. During bona fide stimulations, the left and right canals received consistent air temperatures of 20 and 47ºC, respectively. The aim was to induce an illusory body rotation to the right by eliciting antagonistic vestibular afferences.

In pseudorandom order, during irrigations, participants completed blocks of a SPT task and two comparison, mental rotation tasks. In the former, a line-drawn avatar was repeatedly displayed in various orientations (front- or rear-facing) and tilts (0, 90, 180 or 270º from upright). Either its left or right arm was horizontally abducted or adducted. Participants were instructed to imagine adopting the avatar's position, in order to determine which of its arms was not in the anatomical position. One of the comparison tasks was a mental body part rotation (MBPR) task. A single, line-drawn hand was presented in configurations equivalent to the permutations of the avatar in the SPT task. Participants had to determine

---

[14] Debate surrounds the theoretical basis of caloric vestibular stimulation referred to here (see Scherer & Clarke, 1985).

the laterality of the hand by aligning their “hand axis to the posture of the viewed image” (Falconer & Mast, 2012, p. 334). The other control task was a mental object rotation (MOR) task. Its stimulus set comprised four letters of the alphabet. These were presented in canonical or mirror format and in one of four different orientations (0, 90, 180 or 270º from upright). Participants were instructed to judge the chirality of each letter presented.

RTs and P_es served as primary dependent variables and were analysed by repeated measures ANOVA, which included the factors ‘task’ (SPT, MBPR, MOR) and ‘stimulation’ (sham CVS, bona fide CVS). The latter is equivalent to the ‘space-motion cue congruity’ factor discussed above (see section 2.3). Eye movement recordings were made by way of videonystagmography (VNG) during test irrigations before or after the experiment to check that the irrigation technique elicited nystagmus. Slow phase velocities were not recorded during actual task blocks. Participants completed a short questionnaire after both bona fide and sham stimulation conditions. The questionnaire, based on that used by Stephan et al. (2005), comprised items pertaining to the nature and intensity of the dizziness experienced during the preceding period of stimulation. The items had a 7-point response scale. Separate non-parametric pairwise comparisons (Wilcoxon signed-rank tests) were carried out on questionnaire data from the two stimulation conditions for each of the tasks.

The ANOVA on RTs revealed a significant interaction between the task and stimulation factors. This and further ‘within-task’ analyses indicated that RTs got quicker during bona fide CVS, but only on the SPT task. There was a significant main effect of task on P_e indicating that participants were least error-prone on the MOR task. Based on all of the analyses, Falconer and Mast (2012) argue for a selective facilitatory effect of the aberrant space-motion stimulation (CVS) on MS-TL.

2.4.2 Galvanic vestibular stimulation

The effect of galvanic vestibular stimulation (GVS) on MSTs was studied by Lenggenhager and colleagues (2008) in 11 participants. GVS is administered by attaching electrodes to both mastoid processes. A constant current output is delivered, which typically increases the firing rate in vestibular afferents on the cathodal side, and decreases the firing rate on the anodal side. These alterations in vestibular discharge cause self-motion misperceptions (Fitzpatrick & Day, 2004). Lenggenhager et al. (2008) delivered both right and left GVS, which refer to right and left anodal stimulation, respectively. They also administered sham GVS by attaching the electrodes towards the bases of participants' necks so that vestibular discharge was not modulated by current flow. In the SPT task, a greyscale avatar was only ever shown rear-facing with either its left or right arm abducted. It was presented in one of six different orientations in the roll plane (0, 60, 120, 180, 240 and 300º). A single plant was shown instead of the avatar in what was intended to be a MOR task. The plant had a large leaf projecting to the right or left side of its stem. The laterality of the leaf had to be determined. Participants completed randomised blocks of both the SPT and MOR tasks during four periods of bona fide and sham GVS with the anode on the left or right side.

RTs and P_es were collected but only the former were analysed by way of a repeated measures ANOVA, which included 'task' (SPT, MOR) and 'stimulation' (sham GVS, bona fide GVS) as factors. In addition to the primary, task-related DVs, Lenggenhager et al. (2008) collected subjective visual vertical (SVV) estimates at the start of each experimental period. These estimates provide insight into a participant's self-orientation perception (see section 1.3.2). The SVV data were subjected to the same ANOVA. At the end of each of the four experimental periods, participants were asked to disclose the main cognitive strategy they had adopted during the SPT and MOR tasks using a questionnaire modified from Zacks and Tversky (2005). A separate questionnaire was employed to ascertain the nature and intensity of the dizziness experienced during the preceding period. Participants also completed a modified version of the Simulator Sickness Questionnaire (SSQ) providing further insight into their dizziness, plus their nausea and ocular motor symptoms (Kennedy, Lane, Berbaum, & Lilienthal, 1993) (see section 7.4.2.5.1 for further details). All of the self-report data was analysed descriptively rather than inferentially.

RTs for the MOR task were significantly longer than for the SPT task. The questionnaire responses revealed that approximately half of the participants had adopted a MS-TL strategy for both the SPT and MOR tasks. The other half of the participants had mainly used mental rotation to solve both tasks. Therefore, an additional 'strategy' factor was added to the ANOVA. It interacted with the stimulation and 'laterality of stimulation' factors, but only for the MOR task. Lenggenhager et al. (2008) contended that incongruous stimulation by bona fide GVS on the right preferentially disrupted MS-TL.

Only pooled descriptives for the SSQ are presented in the manuscript. Symptom scores pertaining to each level of the space-motion stimulation factor are not discernible.

2.4.3 Actively-generated impulse stimulation

In the study by Gresty and colleagues (2008), participants were subjected to different types of aberrant space-motion stimuli in three separate experiments. In their first one, 16 healthy participants were exposed to an impulse stimulus of sorts. They actively circumducted their heads for 20 s causing endolymph motion in the vertical semicircular canals (see section 1.4.2.1.1 for anatomical clarification). In itself, this would have been a relatively strong and compelling yet unfamiliar form of vestibular stimulation. After the 20 s, the participants ceased moving. Presumably, the endolymph initially retained the direction of the prior head motion due to inertia, distorting the cupulae in the vertical canals, but in the opposite direction to that which they had been deflected during the initial head rolls. The cessation of head movement may, therefore, have caused the participants to perceive self-rotation in a direction opposite to the initial head motion (see section 1.5.2 for further details about impulse stimulation). All participants completed a SPT task and a spatial control task in a counterbalanced order immediately after the head rolls. Half of the participants were relatively familiar with the tasks by that point; that is, they had already completed blocks of the tasks with their heads still (i.e. under congruous space-motion conditions). The other half were relatively unfamiliar with the tasks, and were yet to perform the tasks under stationary conditions.

The SPT task employed in the study by Gresty et al. (2008) was the ‘Manikin Test’ (Benson & Gedye, 1963). This is a slightly simpler version of the SPT task used in the study by Falconer and Mast (2012) (see section 2.4.1). The avatar was shown front- or rear-facing and either upright or inverted. It held different objects in its hands. One of these objects was also shown beneath the avatar. Per trial, participants had to identify which of the avatar’s hands held the duplicated object. The spatial control was a choice reaction time task. Participants simply had to press the arrow key which corresponded with the on-screen position of a cross.

DVs for both tasks included the total number of correct responses and RT. These were submitted to a repeated measures ANOVA comprising the factors ‘stimulation’ (head stationary, head motion) and ‘task familiarity’ (familiar, unfamiliar). There were no between-task analyses, hence no ‘task’ factor. There were significant interactions between stimulation and task familiarity, affecting all DVs for the SPT task only. These interactions and the results of simple effects analyses indicated that impulse stimulation disrupted performance by those participants who were less familiar with the SPT task; that is, by the participants who were counterbalanced to perform the head rolls at the start of the experimental procedure. A modified version of the SSQ was administered to participants just after the stimulation and prior to both blocks of trials. Additional motion sickness ratings, using a six-point ordinal scale, were also collected. It appears that subjective responses were eyeballed but not analysed any further. Participants’ symptoms were minor in general.

2.4.4 Static and dynamic visual stimulation

In the second experiment by Gresty and colleagues (2008), participants undertook the same SPT and spatial control tasks with and without concurrent exposure to large-field, optokinetic stimuli (see section 1.5.3). The latter were generated by different motions of a landscape that was projected onto a large screen surrounding the smaller one on which the tasks were displayed. For the first 12 participants, the landscape was either still or rotated at 20º/s in the pitch plane during the tasks. Some weeks later, almost exactly the same group of participants repeated the experiment, but this time the landscape rotated in roll (at 90º/s) rather than in pitch. All participants were seated throughout experimentation to remove the imperative for postural control.

The data collection and analysis strategies employed by Gresty et al. (2008) in this experiment were the same as those they had adopted in their first experiment. Once again, there were significant interactions between stimulation and task familiarity, affecting all DVs for the SPT task only. More specifically, the number of correct responses was fewer and RTs were longer when participants, who were less familiar with the SPT task, completed it during roll OKS.

In a separate study by Preuss et al. (2013), incongruous space-motion stimulation was generated by aberrant, static visual polarity cues (see section 1.3.3.2.5). Sixteen participants were seated upright in an enclosure, which could be rotated in roll about the participants’ antero-posterior axes. The enclosure contained multiple fixtures which typically act as polarity cues, such as a table and chairs, shelves and a full-sized, seated manikin. During experimentation, the enclosure was randomly orientated so that the polarity cues differed from the participants' upright orientations by 0, 90, 180 (inverted) and 270º. During these random changes in their surrounds, participants completed SPT and MBPR tasks very similar to those employed in the study by Falconer and Mast (2012) (see section 2.4.1). The SPT task comprised line-drawn avatars randomly tilted by 0, 90, 180 or 270º from upright. Each trial of the MBPR task comprised a single, line-drawn hand in one of those orientations at random. These simplistic body and hand images were displayed on a screen fixed to the wall of the enclosure, which faced the participants.

RTs and P_es comprised the primary DVs. Separate repeated measures ANOVAs were completed per task. Therefore, 'task' was not one of the factors but 'room orientation' was. This was akin to the 'space-motion cue congruity' factor discussed in section 2.3. Regarding error proportions, solely on the SPT task, there was an interaction between enclosure orientation and avatar orientation. Simple effects revealed that participants had been significantly more error-prone whenever there had been a 180º disparity between the orientations of the enclosure and avatar. Based largely on this result, Preuss et al. (2013) suggested that aberrant visual polarity cues disrupt the construction of the body schema and, thereby, specifically perturb MS-TL. At the end of the experiment, once trial blocks had been completed with the enclosure in all four orientations, participants were asked whether they had perceived themselves or the room as being upside down, solely when the room had been fully inverted. These data were reported descriptively; 14 of the 16 participants said they had felt as if they had been upside down.

2.4.5 Cross-coupled acceleration stimulation

In the third and final experiment by Gresty and colleagues (2008), six participants undertook the SPT and spatial control tasks described above (see section 2.4.3) with and without preceding exposure to cross-coupled stimulation (CCS). This exposure is achieved by rotating an observer at constant angular velocity about one axis, then requesting he or she perform a head movement about a second axis. The observer will misperceive his or her self-motion and verticality, typically about the third axis, due to strong but aberrant stimulation of the semicircular canals (Tribukait & Eiken, 2006). In this particular study (Gresty et al., 2008), participants were constantly rotated in yaw at 90º/s in a motorised chair. They received specific but randomly-ordered instructions to move their heads in the sagittal and coronal planes. Three of the six participants developed moderate-to-severe nausea as a result. A simple effect of CCS was found, just with regard to the total number of correct responses when participants were less familiar with the SPT task. This indicates that less well-trained participants make fewer correct responses on the perspective-taking task under incongruous as compared to congruous space-motion conditions.

Almost exactly the same form of CCS was employed in a separate study by Gardner and colleagues (2017). The 39 participants in that study moved their heads in the sagittal and coronal planes while being rotated at 60º/s rather than at 90º/s. This aberrant space-motion condition was counterbalanced with a stationary, hence congruous, condition. During both of these, half of the participants completed a SPT task, referred to as the 'Own Body Transformation' (OBT) task. Those participants were presented with front- or rear-facing avatars, which were randomly tilted by 10º increments in the roll plane through a range of -50 to +50º. Per trial, the avatar held a ball in each hand. One of the balls was always black, but the hand in which it was held by the avatar was randomised across trials. Participants were instructed to imagine adopting the avatar's perspective in order to determine which of its hands held the black ball. The other half of the participants undertook a spatial choice-reaction time task involving rote-learned, manual response transpositions. Hence, this control task was referred to as the 'Transpose' task. It controlled for the stimulus-response incompatibility associated with front-facing avatars in the OBT task, but did not require the participants to mentally self-translocate in order to make their responses. Further details on the OBT and Transpose tasks will be given in section 4.3.3.

The primary DV was the 'Inverse Efficiency Score' (IES), which is a composite of RT and P_e (see Townsend & Ashby, 1978). Omnibus (four-way) and follow-up (two-way) mixed ANOVAs were completed, and all included the factors 'task' (OBT, Transpose) and 'stimulation' (stationary, motion). The omnibus analysis revealed no main effect of task, indicating that the OBT and Transpose tasks were of matching difficulty. For data collected during the first minute post-CCS, there was a significant interaction of task and stimulation. Simple effects revealed that cognitive disruption resulting from CCS was present for the OBT but not the Transpose task.

Participants were asked to rate their level of nausea on a six-point Likert scale after all four task blocks. They were also asked to rate their perceived effort relative to a practice block on a seven-point scale. The nausea scores were not analysed inferentially, but the ordinal-level effort ratings were subjected to a two-way mixed ANOVA in which task was a between-subject factor, and stimulation was a within-subject factor. This revealed no main or interaction effects.

2.5 Synthesis of the evidence for a direct effect of aberrant space-motion information

All of the reviewed studies found that incongruous space-motion cues, secondary to aberrant vestibular or visual stimuli, had some degree of effect on performance of one or more of the spatial tasks employed. The analyses of Gresty and colleagues (2008) and of Preuss et al. (2013) provided particularly nuanced results, which indicate that incongruous cues preferentially disrupted SPT task performance, hence MS-TL. This interpretation of their results would be more compelling had an interaction effect been found between task and congruity factors. However, no between-task analyses were conducted as part of these studies.

However, had Gresty et al. (2008) and Preuss and colleagues (2013) found a significant interaction, it may have been relatively difficult to interpret because their studies employed SPT tasks which incorporated inverted avatars. Such avatar configurations have often been shown not to yield monotonic RT functions and, therefore, do not obey the predictions of the internal model formulation of MS-TL (see sections 1.6.2 and 1.7.1.1). Preuss et al. (2013) specifically comment that RTs for rear-facing avatars were always faster than for front-facing ones, but not when the avatars were inverted. This highlights the problem with inverted avatars; participants adopt shortcut strategies, rather than engaging in MS-TL, when presented with them. Hence, in their study, and possibly in that of Gresty et al. (2008), there may have been no difference in the reliance on veridical space-motion information between performance on the SPT and comparison tasks.

Lenggenhager et al. (2008) did find a significant interaction effect, which suggested that participants, who adopted MS-TL to solve the MOR task but not the SPT task, were hindered when bona fide GVS was administered with the anode on the right mastoid. Although this finding has some resemblance to the results depicted in the top half of Figure 2.1, it is ambiguous or equivocal. Had MS-TL been selectively vulnerable to the aberrant space-motion stimulation constituted by the right-sided GVS, the same interaction effect should have been found when data from the SPT task were analysed. The fact that it was not suggests that extraneous factors may have influenced these findings. Indeed, the SPT and MOR tasks were not equivalent in terms of difficulty. Participants were slower to respond to the latter. It is possible that the features of the plant were more visually complex, which meant the plant not only took longer to encode but also made the MOR task more susceptible to nystagmus. While it was advantageous, in terms of the engagement in MS-TL, that the avatars were only shown rear-facing during the SPT task, the interleaving of stimuli from the SPT and MOR tasks appears to have led to carryover of cognitive strategies between the two tasks. This is evidenced by the fact that half of the sample engaged in mental rotation during the SPT task. The lack of an independent task-groups design detracted from MS-TL engagement. Another potential limitation of the study by Lenggenhager et al. (2008) was the small sample size. The significant interaction effect alluded to above was yielded from 10 participants' RT data. Small sample size risks elevating Type I error (e.g. Button et al., 2013).

There were fewer limitations of the study by Falconer and Mast (2012). Their analyses revealed a clear interaction between the task and cue congruity factors. This interaction was indicative of a facilitatory effect of aberrant stimulation on MS-TL, particularly when that cognitive process was evoked by an avatar orientated in the same direction as that of the self-motion (mis)perception elicited by the CVS. This result appears to be at odds with the findings of the other studies reviewed in this chapter, which all suggest that perverse space-motion stimulation causes some degree of disruption of MS-TL. Moreover, Lenggenhager et al. (2008) found no directional effects of GVS on co-planar MS-TL. Falconer and Mast's (2012) findings also appear to be inconsistent with those of other studies beyond the scope of this review. Previous research by one of the same authors (Mast, Merfeld, & Kosslyn, 2006) found that CVS disrupted performance on a MOR task, which was not the case in the study by Falconer and Mast (2012). Furthermore, CVS has been shown to distort perceptions of body form (Lopez, Schreyer, Preuss, & Mast, 2012) and to trigger nausea in approximately one third of patients with dizziness (Seemungal, Green, Bronstein, Golding, & Gresty, 2009). All of these results strongly imply a disturbing rather than facilitatory effect of CVS no matter the co-directionality of the illusory body motion and the mental transformation. Had Falconer and Mast's (2012) results been replicated, their interaction effect may have been more telling about the potential direct effect of aberrant space-motion information.

The interaction between task and congruity found by Gardner et al. (2017) is more in-keeping with the results of related research in that the effect signified a selective disruption by CCS of MS-TL. While this effect clearly resembles the results depicted in the top half of Figure 2.1, there would have been a more compelling argument for a direct effect of misinformation had complementary analyses of participants' nausea ratings been undertaken. In the third experiment by Gresty et al. (2008), wherein participants were also exposed to CCS, a negative association was reported between simulator sickness symptoms and performance on their SPT task. More specifically, those participants, who gave low sickness ratings, were faster and more accurate in responding to the cognitive task. Therefore, it is plausible that an indirect effect via nausea, rather than an unmediated effect of aberrant space-motion information, may have underpinned the significant task by cue congruity interaction in the study by Gardner et al. (2017). Aside from nausea, no measures of the cardinal manifestations of the CCS-induced balance disorder were collected. Some of the other studies reviewed above were more rigorous in this regard. For example, the SSQ was administered in three studies (Falconer & Mast, 2012; Gresty et al., 2008; Lenggenhager et al., 2008), providing the respective researchers with information on participants' levels of dizziness / disorientation, nausea and ocular motor symptoms. However, the SSQ data were not subjected to inferential analyses in any of these studies.

Overall, relatively little attention was paid across all five studies to the polysymptomatic or syndromic nature of the disorders that arise from aberrant experimental space-motion stimulation (Kennedy & Fowlkes, 1992; Kennedy et al., 1992). None of the studies' procedures incorporated real time collection of objective measures of nystagmus, anxiety or postural stability. Although participants were seated or recumbent in all cases, perceived instability may still draw on attentional resources (Ehrenfried, Guerraz, Thilo, Yardley, & Gresty, 2003). There were no reports of diffusion modelling or similar analyses, which may have provided insight into the mediating effect of attention.

In summary, none of the research to date has yielded a pattern of data which completely matches that depicted in Figure 2.1. A tenable synthesis of the extant data is that experimentally-induced balance disorders cause a modest disruption of MS-TL. More relevant than that, it is not possible to discern whether aberrant space-motion information causes that disruption directly because the mediating effects of the cardinal manifestations, and of attentional diversion, have not been adequately controlled to date. Therefore, there is scope to extend or build on the existing research and clarify whether misinformation about the body's temporo-spatial activity can have an unmediated effect on higher cognition.

2.6 Synopsis

In this chapter, five studies, which investigated the effect of aberrant vestibular or visual stimulation on spatial tasks evoking mental self-translocation (MS-TL) and tasks measuring other cognitive processes, were reviewed. The aberrant, experimental stimulations included caloric vestibular stimulation, galvanic vestibular stimulation, actively-generated impulse stimulation, visual stimulation and cross-coupled acceleration stimulation. All of these typically lead to a multitude of perceptual and non-perceptual disturbances. Hence, they cause experimentally-induced, syndromic balance disorders. Sham or absent stimulations during the studies resulted in congruous space-motion cues, which had no disturbing manifestations. Hence, all of the studies tested two levels of a 'space-motion cue congruity factor' (congruous versus incongruous cues), as well as different levels of a 'task' factor (MS-TL task versus non-MS-TL task(s)).

The methods and results of the five studies were summarised and then appraised with reference to experimental designs and analytical models that might provide insight into whether aberrant space-motion information can have a direct effect on higher cognition. Factorial analysis of variance (ANOVA) of cognitive task performance variables, specifically response time and error proportion, and of variables pertaining to perceptual and non-perceptual sequelae of aberrant stimulation, might be particularly insightful. Given the proposed dependence of MS-TL on space-motion information, a direct effect of misinformation would be deducible if there was a significant interaction effect between task and cue congruity factors on task performance variables but not on subjective or physiological measures, which capture the perceptual and non-perceptual sequelae.

Four of the studies (Gresty et al., 2008, Lenggenhager et al., 2008, Preuss et al., 2013, Gardner et al., 2017) provide converging evidence for a subtle preferential disruption of MS-TL by aberrant vestibular or visual stimulation. Only one of those studies (Gardner et al., 2017) showed an interaction effect between task and cue congruity factors on task performance variables, consistent with a preferential disruption of MS-TL. None of the studies adequately measured and analysed the cardinal manifestations of the experimentally-induced balance disorders under investigation. Therefore, it is not possible to discern whether aberrant space-motion information can directly affect cognition because the effects of potential mediator variables have not been adequately controlled to date.

There is scope to extend the existing research with the objective of clarifying whether aberrant space-motion information can have an unmediated effect on cognition. This narrative review has indicated that this objective might only be fulfilled if the following methods are adopted: ecologically valid MS-TL tasks plus well-matched comparison tasks; an independent groups design with between- by within-subjects analyses; detailed subjective and objective measurements of all the cardinal manifestations of balance disorders; diffusion modelling to determine mediation by inattention.

2.7 Thesis preview

The goals of this research project were pursued by way of four main studies, which are described in separate chapters following the General Methods presented in Chapter 3. More specifically:

- Chapter 4 presents Study 1 which examined the effect of OKS on the performance of two tasks hypothesised to have different dependences on space-motion information: the ‘Own Body Transformation’ (OBT) task, a SPT task entailing MS-TL, and the Transpose task, a choice-reaction time (i.e. spatial control) task. This hypothesis was called into question by the results of Study 1, prompting the development of new tasks.
- Chapter 5 presents Study 2 which was carried out to determine the validity of the new SPT task, the ‘Single Avatar Stimulus Set’ (SASS) task, and to establish whether the new control tasks (the ‘Single Object Stimulus Set’ [SOSS] task, a candidate spatial control task, and the ‘Double Avatar Stimulus Set’ [DASS] task, a

candidate mental object rotation task) might have comparable cognitive loads, without evoking MS-TL.

- Chapter 6 presents Study 3 which examined the effect of OKS on the performance of the three new tasks. Support for a direct effect of aberrant space-motion information on higher cognition was precluded by the study's small sample size.
- Chapter 7 presents Study 4 which investigated nystagmus intensities shortly after abrupt deceleration from constant velocity rotation, then examined the effect of such impulse stimulation on the performance of the SASS, SOSS and DASS tasks. This study had the strongest internal and external validity and allowed for new insights into the directness of the effect of aberrant space-motion information on higher cognition.
- Chapter 8 presents the General Discussion; a synthesis of the research findings.

Chapter 3. General Methods

3.1 Overview

This chapter focuses on the methods that were common to two or more of the experiments. The health and well-being of participants was closely monitored throughout experimentation, particularly while they were exposed to aberrant space-motion stimulation. Optokinetic stimulation, by way of anticlockwise rotation of a large photorealistic image, gave rise to incongruous visuo-vestibular cues in two of the studies. Participants had to complete a randomly allocated cognitive task with and without background optokinetic stimulation. Trait measures were collected before experimentation started, and state measures were systematically collected during it. The data were categorised as primary, secondary or tertiary outcome variables. The same hypotheses were set for three of the studies. The hypothesis tests comprised two-way ANOVAs, t-tests and path-analytic mediation analyses. These and supplementary analyses of individual study results helped to refine the trajectory of the research.

3.2 Introduction

To pursue the project's aim and objective, as set out in the Preface (see section iii) and discussed in the Delimited Introduction (see section 2.6), systematic investigations into the effect of aberrant space-motion stimulation on mental self-translocation and comparative cognitive processes were undertaken. The studies all had between- by within-subjects designs, and many other aspects of their methods were kept consistent.

The specific aim of this chapter is:

- To detail those methods that were common to at least two of the studies[15].

---

[15] Some methods, which were shared by two or more studies, are not presented in this chapter, since it is preferable, for the sake of coherence, to outline these later in the thesis.

3.3 Ethical considerations and recruitment

The experimental procedures for all four studies were approved by the Psychology Departmental Ethics Committee of the University of Westminster, UK. Therefore, the procedures were designated to be in accordance with the 1964 Declaration of Helsinki. Participation in the studies was deemed not to induce negative consequences beyond those which may be encountered in normal daily life. The repetitive nature of both the cognitive assessments and the aberrant space-motion exposures in each of the studies was the only hazard which required due attention both prior to the applications for ethical approvals and during experimentation. As will be elaborated on in the Experimental Procedure (see section 3.10), participants were given regular breaks during testing sessions and ready access to drinking water. They were requested to rate their levels of mental effort and malaise throughout the experimental procedures (see sections 3.7.3 and 3.7.4). These scores helped to check that the participants remained in a fit state as experimentation progressed. At the beginning, they were reminded of their right to withdraw from the study without the need for justification.

Healthy participants were sought for all of the studies (see sections ii of the Preface and 2.2 for the rationale). They were recruited following the recruitment practices that are regularly adopted within the Psychology Department. Principally, they were recruited via the Research Participation Scheme (RPS). This is the Department's well-established and well-governed scheme for involving undergraduate students in local studies, thereby exposing them to relevant research protocols and topics. The RPS is administered by a senior lecturer via an on-line, password-protected portal. Students can log-in and find out about ethically-approved studies ongoing within the Department. They are able to access Participant Information Sheets for all of the studies listed, and can request further information about those they may develop an interest in. Once they feel sufficiently informed, they are able to sign-up to study testing sessions of their choosing.

The Participant Information Sheets produced for the studies undertaken in this research project highlighted that participation was voluntary and that all data collected would be kept confidential and anonymous. Contact details of both the researcher and Director of PhD Studies (formerly Professor Tony Towell and latterly Dr Mark Gardner) were provided in the information sheets, so that participants could ask questions or convey their concerns before or after participation. Also listed in the Participant Information Sheets were health-related eligibility criteria. These stipulated that individuals would only be selected to take part if they were fit and healthy, aged between 18 and 65 years, and had no uncorrectable visual problems. Furthermore, to be eligible, individuals had to have no history either of vertigo lasting longer than an hour or of vertigo bouts occurring on more than one occasion no matter the duration. Everyone who attended a testing session for any of the studies completed a paper-based health screening questionnaire (see Appendix A) in order to double-check his or her eligibility. This also screened for pregnancy and for a history of unstable neurological, cardiovascular and psychiatric conditions, which were contraindicated. Finally, the health screening questionnaire enquired as to whether respondents had any current issues with minor illness, lack of sleep, or nausea associated with recent overeating. Only after signing an unblemished questionnaire were individuals asked to complete a paper-based Consent Form (see Appendix A). Since the health screening questionnaire ensured that the participants in all of the studies were healthy adults without impaired communication or comprehension, there were no concerns at any stage that informed consent had not been obtained. Participants' data were anonymised using a numbering system which only the researcher could decode. All necessary steps were taken to ensure tight data security.

Unless specified in the upcoming chapters, sample sizes for the studies were set pragmatically. The design and methods of the first study were similar to those employed by Gardner et al. (2017), who found a significant interaction effect between space-motion cue congruity and task (see sections 2.3 and 2.4.5). Eighteen participants had undertaken the spatial perspective-taking (SPT) task in that study. In view of the potentially less persistent space-motion misperceptions that were expected from the visual stimulation (see section 1.5.3) in Study 1 of this project, 24 participants were recruited per task group for the first study. Sample sizes were gauged iteratively from there.

3.4 Aberrant space-motion stimulation

Two types of aberrant space-motion stimulation were studied throughout this research project: visual (optokinetic) stimulation [OKS] and impulse stimulation. Details of the latter will be given in Chapter 7 for the sake of coherence. The former was utilised in the first and third studies (see Chapters 4 and 6, respectively), and is described below. The reasons for choosing OKS will be given in the introduction to Chapter 4.

Aberrant visual stimulation was by way of uni-directional, hence optokinetic, large field visual motion in the roll plane. It was intended to perturb participants' self-orientation perception, specifically their subjective visual vertical estimates (see section 1.5.3). It was also intended to induce the illusory perception of self-motion known as vection (see section 1.5.3). Participants stood 1.8 m away from, and centrally aligned with, a photographic still of a riverscape, which was projected onto a screen. The projected image filled the 2.5 m x 1.8 m area of the screen's white canvas (horizontal and vertical screen dimensions, respectively). Buildings lined the banks of the river depicted in the image. The riverscape had been captured from a bridge at an elevation of approximately 3 m. The horizon of the photograph was just below the vertical centre of the screen, which was 1.7 m above the floor as it hung. The luminance of the riverscape ranged from 10 to 50 candles per square metre (candles/m^2). When in motion, photorealistic and large-field images, like the projected riverscape, have been shown to increase the irresistibility of illusory self-tilt and -rotation (Allison, Howard, & Zacher, 1999; Trutoiu, Mohler, Schulte-Pelkum, & Bülthoff, 2009; Warren & Kurtz, 1992).

The image was front-projected from a distance of 2.2 m away from the screen. The projector (hereafter the 'large field' [LF] projector), was 2.1 m above the ground and centrally aligned with the screen. The centre and lower quadrant of the LF projector's lens was occluded by a metal object so that participants' shadows did not fall on the screen and potentially provide them with visual feedback about their balance, which could have augmented their postural control. Participants wore custom goggles which reduced their view of the screen to 2.05 m by 1.3 m (horizontal and vertical dimensions, respectively). Therefore, their field of view subtended approximately 60º by 40º with the goggles in situ. The blinker goggles prevented the participants from seeing the border of the projection screen. This might have otherwise provided an Earth-fixed frame and, thereby, decreased the effect of OKS on postural sway and verticality deviations (Lubeck, Bos, & Stins, 2016).

Continuous anticlockwise rotation of the riverscape in the roll (i.e. picture) plane, through 360°, constituted the optokinetic stimulus. This was incongruous given that participants stood still while viewing the image, hence their vestibular systems were relatively quiescent. Roll motion was chosen ahead of yawing visual motion because of the possibility that the participants may have been more accustomed to the latter due to daily exposures to planar OKS e.g. during train travel. Furthermore, OKS in the pitch plane was found to be less cognitively disruptive than roll OKS (Gresty, Golding, Le, & Nightingale, 2008) (see section 2.4.4).

The angular velocity of the rotation was fixed at 72°/s, equating to a tilting frequency of 0.2 Hz. This was slightly slower than the 90°/s roll motion of the image projected in the study by Gresty et al. (2008) (see section 2.4.4). It has previously been reported that vection is prominent in the low frequency range below 0.2 Hz (Berthoz, Lacour, Soechting, & Vidal, 1979; Warren & Kurtz, 1992). However, the 0.2 - 0.3 Hz frequency range is when there is maximum ambiguity as to whether vestibular signals represent tilt or translation (see section 1.3.2.2.2) (Golding & Gresty, 2016). Therefore, visual motion in this frequency range may be particularly compelling, perhaps because the vestibular system's own ambiguities mean it is not used to differentiate whether the visual signal represents object- or self-motion. The disadvantage of employing visual motion with a tilting frequency of 0.2 Hz was that it had the potential to be particularly nauseogenic (Bles, Bos, de Graaf, Groen, & Wertheim, 1999; Golding & Gresty, 2016). Nausea might moderate attention which, in turn, might mediate the effect of balance disorders on cognition (see Preface section ii). Therefore, repeated, direct measures of participants' nausea and general malaise were carried out throughout experimentation (see section 3.7.3).

The projected image and its rotation in roll were generated by a desktop computer, connected to the LF projector, running the Morfit 3-D engine (Ilea Damsker of 3DSTATE, New York, NY, USA)[16]. Participants stood slightly elevated above the floor, with feet together on a force platform (Accusway, AMTI, Watertown, MA, USA). Figure 3.1 shows a blinkered demonstrator, stood atop the force platform, facing the large field rotating riverscape image projected from above and behind the participant's head (LF projector out-of-view).

---

[16] The riverscape image was originally built in the Morfit application by Professor Michael Gresty, Honorary Visiting Professor at Imperial College London, UK.

Figure 3.1: Demonstrator exposed to aberrant visual stimulation.

Forethought had been given to the stance participants were asked to adopt during experimentation. With their feet together, participants had a narrow base of support, which taxed their postural control (Ehrenfried, Guerraz, Thilo, Yardley, & Gresty, 2003). It was assumed that this would mean the participants would have to utilise all of their proprioceptive signals in order to maintain balance. With a wider base of support, and the resultant diminution of the postural demand, it was reasoned that the participants would be able to (subconsciously) down-grade their reliance on visual proprioceptive signals and, thereby, evade the space-motion misperceptions generated by the OKS. It was predicted that the anticlockwise visual roll motion would cause a tendency for leftward sway (i.e. Visual Evoked Postural Responses - VEPRs - to the left; see section 1.5.3) in the onlooking participants. Hence, as a safety precaution, the researcher stood just to the left of the participants during all trial blocks in case of uncorrected loss of balance in that direction. Given that VEPRs might moderate attention which, in turn, might mediate the relationship between aberrant stimulation and cognition (see Preface section ii), participants' postural control was measured throughout all trial blocks by instrumented stabilometry (see section 3.7.5).

3.5 Cognitive tasks

Two different spatial perspective-taking (SPT) tasks were employed throughout this project. In Study 1, one group of participants undertook an established SPT task and the other group completed a spatial control task which had been designed to match the stimulus-response mappings of the SPT task. Both tasks will be described in further detail in Chapter 4 (see section 4.3.3). From Study 2 onward, a new SPT task and comparison tasks were implemented. These will be detailed in Chapter 5. All tasks comprised computer-generated visual images or stimuli about which the participants had to make laterality judgements and accordant manual responses. The tasks were implemented using the E-Prime 2.0 experiment generator software (Schneider, Eschman, & Zuccolotto, 2002), running in the Windows 7 environment (Microsoft, Redmond, WA, USA) on a laptop (Toshiba, Tokyo, Japan).

In studies 1 and 3 (see Chapters 4 and 6), the laptop was connected to a projector (hereafter the 'small field' [SF] projector) which was positioned 0.9 m from the projector screen. Hence, the SF projector was in-between the screen and the participants (see section 3.4). The SF projector was positioned on a stand 0.6 m above the floor so that it did not obscure the participants' line of sight to the screen. It threw a small field, circular image of the E-Prime program's renderings into the very centre of the screen. This projection had a diameter of 21 cm, hence subtended 7° of the participants' field of view at 1.8 m from the screen. Therefore, the cognitive tasks' stimuli did not fully exclude the riverscape image from participants' central vision. The latter has been estimated to subtend approximately 20° of the field of view (Warren & Kurtz, 1992). It was important that the roll motion of the riverscape was visible in participants' central fields since this region of vision transduces rotary flow more accurately than peripheral vision and, therefore, may provide for stronger vection (Andersen & Dyre, 1989; Stoffregen, 1986; Warren & Kurtz, 1992) (see section 1.3.3.2.3). The projection from the SF projector had visual prominence relative to the surrounding riverscape image. The luminance of the former measured between 750 and 850 candles/m^2. Therefore, the riverscape appeared to be in the background relative to the centrally-projected cognitive stimuli. This was also intended to increase the vection illusion caused by the rotating riverscape (Howard & Heckmann, 1989; Israël & Warren, 2005).

In Studies 1, 2 and 3 (see Chapters 4, 5 and 6, respectively), the response devices were two computer mice of the same brand and model, and had no manufactured adaptations for left- or right-handed use. However, custom adaptations had been made to the mice such that one was only operable by the right index finger (the right button had been removed), and the other was only operable by the left index finger (the left button had been removed). Throughout testing in Studies 1 and 3, participants held the appropriate mouse in each hand, with arms resting down by their sides, as they stood with feet together on the force platform.

3.6 Trait measures

In at least two of the studies, the following measures were used to gauge participants' psychological traits or other general proclivities. These paper-based measures were completed by all participants just after they provided informed written consent. At the end of study recruitment, scores were compared across task groups (by independent samples t-test in Study 1 and one-way ANOVA in Study 3) in order to check that they comprised participants with a similar spread of traits and proclivities. Blank copies of all of the trait measures listed here are provided in Appendix A.

3.6.1 State-Trait Inventory for Cognitive and Somatic Anxiety (STICSA)

The STICSA was developed by Gros et al. (2007) to assess anxiety as a transitory emotion (or state) and as a stable disposition (or trait). The state-trait anxiety distinction of this measure is in line with the structure and principles of Spielberger's (1983) well-established inventory - the State-Trait Anxiety Inventory or STAI. However, the STICSA also makes the distinction between cognitive and somatic symptoms of anxiety which the STAI does not (Gros et al., 2007). Compared with the STAI, the STICSA was more strongly correlated with the anxiety subscale of the Depression Anxiety Stress Scales (Lovibond & Lovibond, 1995) and was less strongly correlated with its depression subscale (Gros et al., 2007). The STICSA may, therefore, be a purer measure of anxiety than the STAI is.

The state and trait scales of the STICSA both have 21 self-report items, 11 of which are for the somatic subscale. Respondents rate each item on a four-point Likert scale, ranging from 1 (not at all) to 4 (very much so). Only the trait scale was of interest in this project.

The total ‘STICSA Trait’ score is found by summing all 21 items. Subscale totals are the summation of scores on corresponding items. The cognitive and somatic subscales of the STICSA Trait have demonstrated excellent internal consistency, with Cronbach’s alpha coefficients of .87 for both (Gros et al., 2007). According to Van Dam et al. (2013), a total STICSA Trait score between 40 and 43 (out of 84) indicates a possible anxiety disorder, and a score above 43 suggests a probable disorder. Scores above 23 on the cognitive subscale and 18 on the somatic subscale indicate probable cognitive and somatic anxiety components, respectively (Van Dam et al., 2013).

3.6.2 Situational Vertigo Questionnaire (SVQ)

Participants in two of the studies (see Chapters 4 and 6) rated their quotidian susceptibility to visually-mediated disorientation on the SVQ (Guerraz et al., 2001). This is a simplified version of the Situational Characteristics Questionnaire devised by Jacob et al. (1989). The SVQ has 19 items which ask the respondent to rate how much ‘vertigo’ they experience in environments bearing intense visual information, e.g. supermarket aisles, and/or conflicting visual and vestibular information, e.g. moving scenes at the cinema. Vertigo is very broadly defined in the SVQ as encompassing symptoms ranging from light-headedness to unsteadiness. So-called ‘validity items’ also feature. These may be endorsed by individuals with space or motion phobias which are not necessarily or solely visually triggered e.g. standing in a lift while it moves at a steady speed (Jacob et al., 1989). Respondents rate each item on a five-point Likert scale ranging from 0 (not at all) to 4 (very much). A ‘not tried’ response option is also available should respondents have no experience of the situation specified in a given item. The total score on the SVQ is calculated as the sum of all answered items (excluding ‘not tried’ responses) divided by the total number of answered items. Based on the results of Pavlou et al. (2006), a normalised score above 0.7 indicates that a respondent may have ‘visual vertigo’ (Bronstein, 1995); that is, a disproportionate burden of dizziness and postural instability in environments with incongruous visual stimuli. The psychometric properties of the SVQ are less well-established than those of the original Situational Characteristics Questionnaire. Initial reliability and validity investigations have been carried out on the Italian version of the SVQ (see Colnaghi et al., 2017).

3.6.3 Balance confidence scale

Balance confidence or efficacy may change with the postural threat posed by a specific activity, and can influence postural control during the respective activity (Adkin, Frank, Carpenter, & Peysar, 2002; Carpenter, Adkin, Brawley, & Frank, 2006; Huffman, Horslen, Carpenter, & Adkin, 2009). In order to check for parity of balance confidence levels between task groups in two of the studies (see Chapters 4 and 6), all participants in those studies completed task-specific confidence ratings. The scale that was used was based on that employed in a series of studies designed to look at interactions between psychological factors and postural control (e.g. Adkin et al., 2002; Carpenter et al., 2006; Davis, Campbell, Adkin, & Carpenter, 2009; Hauck, Carpenter, & Frank, 2008; Huffman et al., 2009). Participants were required to indicate their confidence by way of a modified, horizontal visual analogue scale, which had 50 equally-spaced graduations from 0 (no confidence) to 100 (complete confidence). Every fifth graduation of the scale was emboldened to highlight 10-point intervals. Specifically, participants were asked for the level of confidence they had in their ability to maintain balance and stand as still as possible in forthcoming trial blocks. They had to circle just one of the 50 graduations on the scale, then write down the value of the graduation they had circled. By having the participants duplicate their confidence rating in this manner, it was deemed there would be less scope for misinterpretation on the researcher's behalf.

In both studies of relevance, each participant gave five balance confidence ratings in total. The first was a practice rating and preceded the balance practice trial block (see Experimental procedure; section 3.10). It was not subjected to inferential tests. Two sets of ratings were gathered before both the first and third experimental trial blocks. Prior to the first trial block, participants were told about the congruous and incongruous visual stimuli they were about to experience during the two upcoming trial blocks. They were asked for a confidence rating for each condition, based purely on the verbal descriptions provided by the researcher. When they gave their balance confidence ratings prior to the third experimental trial block, participants were no longer naive to the conditions that were upcoming. After experimentation, confidence ratings were averaged according to condition. Hence, a single score was obtained per participant both for the lower (congruous visual stimulation) and higher (incongruous visual stimulation) postural threat conditions. Between-group comparisons of both scores were undertaken to check for parity.

3.7 State measures

In most of the studies, a series of measures were collected during or immediately after every experimental trial block, in order to carefully record participants' subjective and physiological states. This was important for monitoring the participants' well-being and safety throughout experimentation. In addition, it provided insight into whether the aberrant stimulation affected the cognitive processes under investigation in isolation of, or in combination with, commensurate physical or psychological changes. The following self-report and instrumented measures of participants' states were collected in at least two of the studies. Blank copies of all of the self-report measures listed here are provided in Appendix A.

3.7.1 Perceived stability and fear-of-falling scales

Separate ratings of task-specific, perceived stability and fear of falling were collected from participants after trial blocks using the modified visual analogue scales employed by Huffman et al. (2009). These scales were much like the balance confidence scale described in section 3.6.3. To ascertain their perceived stability, participants were asked to rate how stable they felt 'when balancing with feet close together, while performing the left-right judgement task'. The 50 graduations on the scale ranged from 0 (not stable at all) to 100 (completely stable). Participants rated their fear-of-falling on a separate scale where 0 and 100 represented 'not fearful at all' and 'completely fearful', respectively. Previous reviews have stressed that fear of falling, perceived stability, balance confidence and state anxiety are separate constructs (Hauck et al., 2008; Jørstad, Hauer, Becker, & Lamb, 2005; Moore & Ellis, 2008), so they should be measured individually.

3.7.2 Modified Sport Anxiety Scale (mSAS)

A modified version of Smith and colleagues' (1990) Sport Anxiety Scale (SAS), as employed by Geh et al. (2011), was issued after each trial block to ascertain participants' state anxiety. Participants scored each of the 10 items using a nine-point scale ranging from 1 (I did not feel this at all) to 9 (I felt this extremely). Six items of the mSAS form a 'somatic subscale' and the remaining four constitute the 'worry subscale'. Due to a strong correlation between the subscale scores, previous research has just analysed the total mSAS score, which is calculated by simple summation of the responses for all items (Carpenter et al., 2006).

3.7.3 Malaise scale

As the objective was not to induce unsettling levels of sickness or other motion-induced symptoms, participants were asked to report any feelings of malaise (defined as ‘any feelings of vertigo, fullness of head, or other dizziness feelings; stomach awareness, nausea, or other general discomfort; eyestrain, headache, fatigue, or other difficulties focusing or concentrating’) on a custom four-point scale shortly after every trial block (no malaise; mild malaise; moderate malaise, or; severe malaise).

3.7.4 Mental effort scale

Based on Gardner et al. (2017), participants were also repeatedly asked to rate the mental effort they perceived they had exerted as compared to the effort they put in during the practice trial block. This mental effort rating was made on a seven-point scale (a lot; moderately; mildly less/more effort, or; no difference).

3.7.5 Instrumented stabilometry

Recordings of the participants’ stability or postural control were taken during all experimental trial blocks in two of the studies, in order to gauge their physiological states in real-time. The recordings were collected by the portable force platform on which the participants stood during experimentation (see section 3.4 and Figure 3.1). Participants were always required to start trial blocks with their stockinged feet together and centralised on the platform. In order to standardise this centralised, feet-together position from one block to the next, tracings of each participant’s feet were made towards the start of his or her experimental session. On each tracing, a line was drawn from the anterior border of the hallux to the posterior border of the foot. The centre of this line was found and then aligned with the origin of the platform’s y axis. The medial borders of the heel and forefoot tracings were aligned with the origin of the platform’s x axis. Once both tracings were aligned in this manner, they were fixed to the platform with tape.

Forces (Fx, Fy, Fz) and moments (Mx, My, Mz) outputted by the force platform were captured by the 'Balance Clinic' program (AMTI, Watertown, MA, USA) at a sampling frequency of 100 Hz. Subsequently, this data were exported to Excel (version 2016; Microsoft, Redmond, WA, USA) for smoothing with a macro-based, 10 Hz, fourth order, low-pass Butterworth filter (Van Wassenbergh, 2007). The coordinates in x (medio-lateral) and y (fore-aft) of the net centre of pressure (COP_{net}) were then calculated for each data point, according to the manufacturer's recommendations (Samaan, 2016), which are based on a standard formula (see Latash, Ferreira, Wieczorek, & Duarte, 2003). Finally, the mean velocity of interval period COP displacement (average COP velocity; 'COP_{vel}') was calculated for all experimental blocks. COP_{vel} represents the total path length of COP displacement per block normalised for block duration. It is representative of the degree of muscular activity about the ankle, but is often erroneously interpreted to be a surrogate of postural sway rather than postural control (Winter, 1995).

3.8 Strategy measures

After all of the experimental blocks had been completed, participants were probed as to what strategies they had used to solve their allotted cognitive tasks. Further details about how this information was gleaned will appear in the Methods sections in the upcoming chapters.

3.9 Space-motion misperception measures

Based on Gresty et al. (2008), participants in two of the studies (see Chapters 4 and 6) were asked whether they had experienced the vection illusion during incongruous visual stimulation, and, if so, how pervasive and strong it had been. The specific questions, which the participants had to respond to at the end of experimentation about their experience of vection, are given in Appendix A. Accordingly, vection duration was rated as either brief (allocated a score of 0) or sustained (allocated a score of 1). Vection strength was rated as either weak, moderate or strong. These responses were converted to scores of 1, 2 and 3, respectively. These conversions allowed inferential tests to be applied to participants' responses (see section 3.14.4).

3.10 Experimental procedure

Every testing session began with a slide-based briefing on the study, in order to ensure participants felt sufficiently well-informed about the study's aims and the procedures involved. They were asked to complete the health screening questionnaire (see section 3.3), and then provide written consent if they were content to do so, and as long as they met all of the selection criteria (see section 3.3). Following consenting, participants in most of the studies were requested to specify their dominant upper limb, according to the one they wrote with, and to provide their age and occupation. Height and mass measurements were collected using metre rules and standard weighing scales, respectively. Participants completed the STICSA and SVQ (see section 3.6). They were then randomly allocated to undertake just one of the cognitive tasks. Randomisation was accomplished using a dedicated randomisation website (Dallal, 1997), which implements the method of randomly permuted blocks. The independent-groups design was selected because previous research has shown that there can be carry-over of task strategies from one spatial task to another if participants perform more than one during the same experiment (Gardner, Brazier, Edmonds, & Gronholm, 2013; Wraga, Thompson, Alpert, & Kosslyn, 2003; Zacks, Rypma, Gabrieli, Tversky, & Glover, 1999) (see section 2.5).

Having rated their balance confidence for the first time (see section 3.6.3), the laboratory lights were turned off, and participants practised maintaining a steady posture in standing with feet together on the force platform while simultaneously performing a simple spatial task – the 'Which Side' task (Gardner & Potts, 2011; Zacks et al., 1999). This required manual responses about the laterality, as judged from the participants' perspectives, of a black ball when it appeared on the screen. Inter-trial intervals were the same as those demanded by the cognitive tasks the participants were to complete in the experimental trial blocks. Thus, the numbers of responses were comparable. After the balance practice period, the participants practised their allocated task while sitting facing the projector screen. The number of practice trials they completed will be specified in the upcoming chapters. They were under instruction to respond as quickly but as accurately as possible. After the task practice, participants were asked to rate, based on a 4-point scale implemented by Gardner and colleagues (2017), how much effort they had exerted while practising (mentally at rest; minimal mental effort; moderate mental effort, or; maximal mental effort). During both the balance practice and task practice periods, only the projection from the SF projector illuminated the room (see section 3.5). The LF projector remained switched off throughout the practices, so the riverscape image was not in view (see section 3.4). The participants were first shown the riverscape image on a laptop screen, just after the practice periods. They watched it in its stationary and rotating formats until they could envisage how these would be rendered on the larger projector screen during the upcoming experimental blocks. All participants remained naïve to rotation of the riverscape in large field format until the first block wherein that condition was scheduled.

The experiment proper comprised four blocks of trials of the allocated cognitive task. Each block had a fixed duration of two minutes. In an interleaving manner, two of the blocks were conducted with a static visual surround (i.e. the large field riverscape was stationary – denoted 'congruous'), and two blocks with the visual surround rotating continuously in roll (denoted 'incongruous'). These two visual conditions constituted the two levels of the within-subject factor 'space-motion cue congruity'. Whether the first block comprised congruous or incongruous space-motion cues was counterbalanced between participants in the same task group.

Before the first and third experimental trial blocks, and with the lights on, participants rated the confidence they had in their ability to maintain balance in the two upcoming and visually different blocks (see section 3.6.3). In preparation for every experimental block, participants stepped on to the force platform, and positioned their stockinged feet together and centralised (see section 3.7.5). Once in position, participants donned the blinker goggles (see section 3.4), and were then handed the two computer mice, modified for use in the right or left hand (see section 3.5). The participants held these with their arms resting down by their sides. The researcher then turned off the main lights in the laboratory and a trial block was started.

After every two-minute block, participants removed the goggles, sat down and the laboratory lights were turned on. They completed the mSAS (see section 3.7.2) and the perceived stability and fear-of-falling scales (see section 3.7.1), in order to ascertain their subjective and physiological states. They rated their level of malaise (see section 3.7.3), and how much mental effort they had exerted during the most recent block in comparison to the first time they practised their allocated task in sitting (see section 3.7.4). Completing all of these self-report, state measures after each block took over two minutes, and allowed for any after-effects of the visual stimulation to dissipate. After all of the experimental blocks had been completed, participants were probed as to what strategies they had used in order to solve their allocated tasks (see section 3.8). Finally, the participants were asked whether they had experienced the vection illusion during 'incongruous' blocks, and, if so, how pervasive and strong it had been (see section 3.9). Their levels of malaise were evaluated every five minutes at the very end of the experiment, in order to ensure that all participants returned to an asymptomatic baseline before departing the laboratory.

3.11 Variables

3.11.1 Independent variables

The independent or predictor variables (IVs) were 'space-motion cue congruity' and 'task'. The former was a within-subject factor with two levels (congruous space-motion cues versus incongruous space-motion cues; see section 3.10). The latter was a between-subject factor. The number of levels it had depended on how many independent groups were recruited to in a given study. Further clarification about the levels of the 'task' factor will be given in the Methods sections of each of the upcoming study chapters.

3.11.2 Dependent variables

In most of the studies, dependent variables (DVs) were categorised as primary, secondary and tertiary outcome variables.

3.11.2.1 Primary, task-related outcome variables

The primary outcome variables were those which pertained to participants' performance on the cognitive tasks (see section 3.5). They were further divided into observed or "behavioural" variables and unobserved or "mechanistic" variables.

3.11.2.1.1 Behavioural variables

All of the cognitive tasks employed in the studies were two-choice response-time tasks. The behavioural variables for such tasks are response time (RT) and response accuracy or error proportion (P_e) (Wagenmakers, van der Maas, & Grasman, 2007). These were readily determinable from the outputs of the experiment generator software (see section 3.5), and were subjected to the hypothesis tests (see section 3.14.3).

3.11.2.1.2 Mechanistic variables

As discussed in section 2.3, inferential analysis of mechanistic variables might provide further insight into the direct effect of aberrant space-motion information on higher cognition. Hence, such variables were calculated, by way of the EZ-diffusion model, for inclusion in the hypothesis tests. The EZ-diffusion model is a cognitive process model (Wagenmakers et al., 2007), the formulae for which were implemented in Excel. The underlying assumption of such models is that the brain extracts the signal and, inevitably, some noise from a stimulus, and accumulates these over time, as depicted in Figure 3.2. The accumulated information represents the evidence for a decision with two possible response options. When the evidence for one response option reaches a preset criterion or boundary, the respective response is initiated (Bitzer, Park, Blankenburg, & Kiebel, 2014; Dutilh, Wagenmakers, Visser, & van der Maas, 2011).

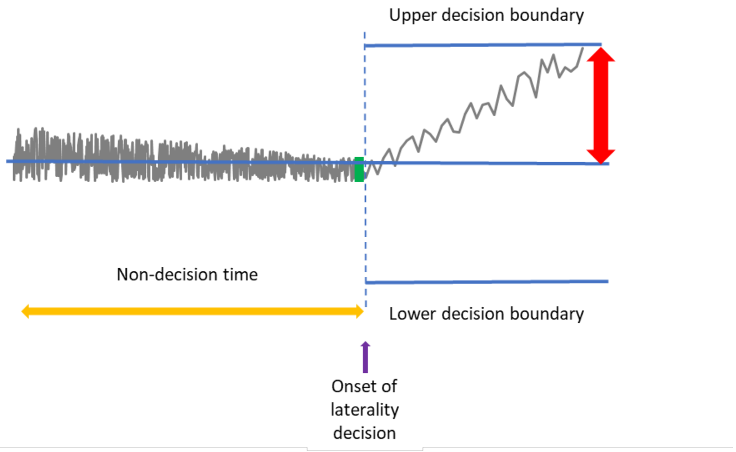


Figure 3.2: The drift diffusion model, adapted from Teichert et al. (2016).

The process of accumulating evidence for a decision is described by the position of a particle that drifts over time towards one of two response boundaries. Its drift is deflected by noise (Nesti, De Winkel, & Bülthoff, 2017). A decision process ends when the particle reaches one of the boundaries. The noisy grey line exemplifies a single trial wherein the decision process reached the correct (upper) boundary. The solid green vertical bar at decision onset represents the distribution of the decision variable at the time of decision onset (i.e. when the accumulation or integration of evidence begins). The red arrow indicates the boundary separation. The total response time is the sum of decision and non-decision time.

The EZ-diffusion model takes as input three measures: mean response time, the variance of response time and decimalized response accuracy. According to Wagenmakers et al. (2007), it outputs the three most important mechanistic variables associated with the assumption described above: the rate of decision-related information accumulation (represented by drift rate ‘v’), response conservativeness or caution (represented by boundary separation ‘a’), and the duration of non-decision processes (represented by non-decision time ‘T_{er}’ or NDT) (van Ravenzwaaij, Dutilh, & Wagenmakers, 2012). The units for drift rate and boundary separation are arbitrary; “they carry no meaning that can be directly translated into response time” (Verhaeghen, 2014, p. 65). However, a reduction in drift rate (i.e. a slowing of information accumulation) is associated with increases in both RT and P_e. Reductions in boundary separation (i.e. decreases in response caution) are also linked with higher error but quicker rather than slower RTs (Voskullen, Ratcliff, Fennell, & McKoon, 2017).

As discussed in section 2.3, the mechanistic variables outputted by the EZ-diffusion model or other drift diffusion models (DDMs) have not been mapped on to the processing stages of MS-TL as far as the author is aware. It may be problematic or even inappropriate to do so given that MS-TL can only be readily evoked by tasks which involve an additional spatial, visual, cognitive or other judgement. Spatial perspective-taking (SPT) tasks, for example, require both MS-TL then a laterality decision. In effect, SPT tasks may comprise two perceptual decisions; a latent or implicit decision as to whether the position of one's mental representation of the body has or has not yet matched the position of the avatar, then an overt or explicit decision as to whether the demarcated object is on the left or right of the newly positioned body representation (De Winkel, Katliar, & Bülthoff, 2017). DDMs typically apply to a single perceptual decision. It may be possible to determine which mechanistic variables relate to MS-TL or to the laterality decision by determining which ones show monotonicity as a function of the angular disparity between the observer and avatar. Although this data does not appear to be available for SPT tasks, one study (Molenaar, Tuerlinckx, & van der Maas, 2015) indicated that NDT increased monotonically on a MOR task. This would suggest that NDT encapsulates stages 1 (perceptual preprocessing), 2 (identification / discrimination of the image and identification of its orientation), 3 (mental rotation itself) and 5 (response selection and execution) as per traditional theories of MOR. Presumably drift rate and boundary separation relate to stage 4 (judgement of the congruity) (see section 1.6.3). Similarly, NDT data yielded by SPT tasks may be largely representative of MS-TL[17]. Therefore, drift rate and boundary separation may depend on the noisiness of the body position estimate determined from the process of MS-TL, assuming these two mechanistic variables mainly relate to the laterality decision during SPT tasks.

Even if drift rate pertains more to the laterality decision than to MS-TL, a decrease in this parameter may still be a useful way of determining whether attentional diversion is at play during aberrant space-motion stimulation (see section 2.3). Diffusion models, like the EZ-diffusion model, are relatively simple compared to Bayesian models, but the former can be

---

[17] Based on this line of reasoning, non-decision time (NDT) will be referred to, throughout the rest of the thesis, as a marker of 'non-explicit decision processing'. In tasks involving just a single perceptual decision, NDT is often referred to more simply as 'non-decision processing'. However, this may not capture the possibility that an implicit decision may be made in advance of the explicit laterality or chirality decision in SPT and MOR tasks, respectively.

mapped onto the latter (Bitzer et al., 2014; FitzGerald, Moran, Friston, & Dolan, 2015). One of the drawbacks of the EZ-diffusion model is that it cannot be applied when participants achieve perfect accuracy (Arnold, Bröder, & Bayen, 2015; Voss, Nagler, & Lerche, 2013).

3.11.2.2 Secondary outcome variables

In most of the studies, there were several secondary outcome variables, which were subcategorized as either physiological or subjective variables. The physiological variable was recorded in real-time during trial blocks, whereas the subjective variables were obtained by self-report after trial blocks. As with the primary DVs, all of the secondary outcome variables were subjected to the factorial analyses that constituted the hypothesis tests. However, within-subjects, simple-effects analyses of the secondary DVs formed part of the supplementary analyses not the hypothesis tests.

3.11.2.2.1 Physiological / mediator variable

Average COP velocity (see section 3.7.5) constituted the physiological variable in two studies (see Chapters 4 and 6). In those studies, average COP velocity was also modelled as the mediator variable. That is, this measure was included as the intervening variable in the mediation analyses which formed part of the hypothesis tests in Studies 1 and 3.

3.11.2.2.2 Subjective (self-report), non-categorical variables

The subjective, non-categorical variables, which constituted the remaining secondary DVs in Studies 1 and 3, included perceived stability and fear-of-falling ratings (see section 3.7.1), and the total mSAS score (see section 3.7.2).

3.11.2.3 Tertiary outcome variables

Several categorical datasets, derived from self-report instruments, constituted tertiary outcome variables. For two of the studies, these datasets related to ratings obtained on the malaise (see section 3.7.3) and mental effort (see section 3.7.4) scales. They also related to responses given by participants to questions regarding task strategy (see section 3.8) and space-motion misperception (see section 3.9). All tertiary outcome variables, bar task strategy responses, were subjected to between- and within-subjects analyses as part of the supplementary analyses (see section 3.14.4).

3.12 Hypotheses

The following null hypotheses were tested in studies 1, 3 and 4B (see Chapters 4, 6 and 7, respectively):

- H_o1: There will be no interaction effects of the independent variables (task and space-motion cue congruity) on primary or secondary outcome variables,
- H_o2: There will be no within-subjects, simple effects of space-motion cue congruity on primary outcome variables without or with the physiological / mediator variable controlled.

These hypotheses were commensurate with the aim and objective of the research project set-out in the Preface (see section iii). In reference to section 2.3, the hypothesis tests would need to reveal both of the following findings in order to imply that higher cognitive sequelae of balance disorders are the direct result of the aberrant space-motion information inherent in such disorders:

1. A statistically significant task by space-motion cue congruity interaction effect on one or more primary outcome variables, but not on any secondary outcome variables, plus,
2. A statistically significant simple and disruptive effect of space-motion cue congruity on the implicated primary outcome variables derived only from the SPT task, even with the physiological / mediator variable controlled.

3.13 Reduction of bias

For the sake of transparency, the data collected in all of the studies were treated in the same way to remove outliers and counteract violations of statistical assumptions. Moreover, the same hypothesis tests were applied in Studies 1, 3 and 4B. Those tests will be described in section 3.14.3. The present section will focus on the procedures that were used to reduce the impact of bias.

3.13.1 Removal of outliers

The experiment generator software was set-up in all of the studies such that participants had up to 2100 ms to respond to each task stimulus (see section 4.3.3). This ensured that only speeded judgements were collected and, relatedly, that excessively long RTs were not possible. In order to control for possible ‘aphysiological’ responses, which had been made too soon after initial presentation of the stimuli by mistake or in anticipation, any responses with RTs shorter than 100 ms were excluded. Given that participants were constrained to make speeded responses by the brevity of the stimulus display periods, it was possible that excessive error was induced. To offset this, only RTs for correct responses were averaged and further analysed. This procedure was in-keeping with that employed in previous, related research (e.g. Gardner et al., 2017; Zacks & Tversky, 2005). Also, based on the methods of Teichert et al. (2014) and van Elk and Blanke (2014), all data collected for any particular participant, whose overall error proportion was greater than their group’s mean error proportion by 1.96 standard deviations, were excluded from further analysis.

3.13.2 Techniques for counteracting violations of normality

The non-categorical data were scrutinised for normality by a combination of means using IBM SPSS v24 (IBM Corp., USA). Histograms were generated, values for skewness and kurtosis were calculated, and the Kolmogorov-Smirnov test was implemented. Bootstrapping (Efron & Tibshirani, 1993) was applied during all pairwise comparisons of data pertaining to the primary and secondary outcome variables. This procedure was favoured over data transformation methods, e.g. arcsine square root transformation, since it has been argued to be the procedure that best combats problems with data normality while maintaining the interpretability of the tests to which the procedure is applied (Field, 2013). Furthermore, bootstrapping is the suggested method of reducing the potential bias associated with mechanistic variables (Wagenmakers et al., 2007). Similarly, using bootstrap confidence intervals to infer the indirect effects of X on Y in path-analytic mediation analyses (see section ii of the Preface) is the recommended approach (Montoya & Hayes, 2017). Montoya and Hayes (2017, p. 13) emphasise that the sampling distribution of the indirect effect(s) is not typically normal, since “the product of two normally distributed random variables is not normal”. Based on Field (2013) and Montoya and Hayes (2017), the bias corrected and accelerated bootstrap (BCa) method, with 2000 bootstrap samples, was selected for all relevant analyses. Unless stated otherwise, all probability (*p*) values given in the upcoming Results sections for pairwise comparisons are derived from the BCa method.

3.14 Analytical treatments

The statistical analyses carried out on data from Studies 1, 2 and 4B (see Chapters 4, 6 and 7) were segregable as: comparisons of baseline characteristics, hypothesis tests, supplementary analyses or exploratory analyses. Each of these different groupings of statistical treatments is discussed next. All analyses were carried out using IBM SPSS v24 (IBM Corp., USA). In the Results sections of the upcoming chapters, typically only the outputs of those analyses that yielded significant results are given. This is in order for those results to be conspicuous. Effect sizes are usually only presented for statistically significant results. Partial eta squared (η_p^2) values are given as the effect sizes pertaining to ANOVAs. These values are interpreted based on Richardson (2011). Pearson's correlation coefficient, *r*, is given as the effect size for pairwise comparisons based on the recommendations of Field (2013).

3.14.1 Comparisons of baseline characteristics

Scores on the trait measures (see section 3.6) and other baseline characteristics, specifically participants' heights and weights, were compared across the groups. As there were only two groups in Study 1, the comparisons were achieved by way of independent samples t-tests. In the remaining studies, there were three groups. Hence, baseline measures were submitted to one-way ANOVAs, where 'task' was the between-subjects factor.

3.14.2 General descriptives

Averages were calculated for most of the DVs to aid preliminary inspection of the data. Ordinal data pertaining to task strategy (see sections 3.8 and 3.11.2.3) were treated differently. Participants in the group, which performed the SPT task, were simply categorised according to their reported use of MS-TL. Further details about how participants were proportioned according to strategy will be given in the Methods sections in the chapters to follow.

3.14.3 Hypothesis tests

In three of the studies (Studies 1, 3 and 4B), the same analyses were employed to test the null hypotheses:

- H_o1 was tested by two-way ANOVAs where 'space-motion cue congruity' was a within-subject factor and 'task' was a between-subject factor (see section 3.11.1). Each primary and secondary outcome variable was individually analysed.
- H_o2 was tested by way of paired t-tests between congruous and incongruous levels of the space-motion cue congruity factor. To control for the physiological / mediator variable, 'standard' t-tests were supplemented by the regression-based, path-analytic method of mediation analysis devised by Montoya and Hayes (2017). This method was implemented by way of the MEMORE (Mediation and Moderation for Repeated Measures v1.1) macro for SPSS (Montoya & Hayes, 2017). Data subjected to all of these analyses were for primary outcome variables only.

To protect against Type I error, the chances of which may have otherwise been heightened by the two sets of hypothesis tests, Bonferroni correction was applied by dividing the alpha level (.05) by two. Hence, the alpha was adjusted to $p \leq .025$. Values from .025 up to and including .05 were considered to be borderline significant, based on Carpenter et al. (2006). Probability values greater than .05 were deemed to be non-significant. In the forthcoming chapters, significant interaction effects are depicted by interaction (line) graphs. Regarding simple effects, significant *p* values are denoted '*<' or '>*' in tables and simply '*' in figures. Borderline simple effects are denoted '≤' or '≥' in tables and '~*' in figures.

3.14.4 Supplementary analyses

Paired t-tests were also carried out to infer the effects of space-motion cue congruity on secondary outcomes, that is, on COP velocity, total mSAS score, stability and fear-of-falling ratings obtained in Studies 1 and 3. In addition to these pairwise comparisons, the Supplementary analyses comprised analyses of the tertiary outcome variables. Between-task comparisons of malaise, mental effort, vection duration and vection strength scores, with the space-motion cue congruity factor collapsed, were carried out by way of either Mann-Whitney U tests (Study 1) or Kruskal-Wallis tests (Study 3). Within-subjects comparisons of just the malaise and mental effort scores, specifically between levels of the space-motion cue congruity factor, were carried out on respective data from Studies 1 and 3 using Wilcoxon signed-rank tests. No inferential tests were carried out on the ordinal data pertaining to task strategy (see sections 3.8 and 3.14.2).

3.14.5 Exploratory analyses

Based on all of the preceding tests and analyses, exploratory data analysis was conducted on data for some of the studies. The aim of these unplanned tests was to investigate unexpected findings and/or to facilitate the objectives and design of the next study. Further details will appear where relevant in the upcoming chapters.

3.15 Synopsis

This chapter described many of the methods which were common to two or more of the upcoming experiments. The methods were kept relatively consistent across all of the studies so that the research was as rigorous and systematic as possible. Ethical considerations were explored prior to each application for ethical approval. During experimentation, the health and well-being of participants were viewed as paramount. Two types of space-motion stimulation were studied throughout the project. This chapter focused on the methodology with which optokinetic stimulation was generated. A large photograph rotated in the roll plane at a low frequency, intermittently giving rise to the vection illusion. Images associated with the cognitive tasks were projected into the centre of the larger, rotating photograph. Participants were randomly allocated to undertake just one of the cognitive tasks to prevent carryover of task strategies. They stood on a force platform with feet together, and responded to the stimuli linked to their allocated cognitive task by clicking on designated mouse buttons.

A series of self-report trait measures were collected before practice and experimental trial blocks got underway. These allowed for between-group comparisons of baseline levels of anxiety, balance confidence and susceptibility to visually-mediated disorientation. During or immediately after trial blocks, state measures were collected to ascertain participants' physiological and subjective conditions as experimentation proceeded. One of these state measures served as a mediator variable in the hypothesis tests conducted on completion of each study. The primary dependent or outcome variables related to participants' performance on their allocated cognitive tasks. The independent variables were space-motion cue congruity and task. Two hypotheses were set for three of the studies which accorded with the aim and objective of this research project. The hypothesis tests comprised two-way ANOVAs, t-tests and path-analytic mediation analyses. These tests were supplemented by between- and within-subjects analyses of secondary and tertiary outcome variables, in order to discern whether interpretations of the hypothesis tests might be confounded. The results of the analyses for one particular study helped to delineate the materials and methods for the next study.

Chapter 4. Study 1:
The effect of optokinetic stimulation on spatial perspective-taking and comparison tasks with 2-D task stimuli

4.1 Abstract

Purpose:

To investigate whether balance disorders, and the aberrant space-motion information they entail, can directly affect higher cognition, this study examined the effect of optokinetic stimulation (OKS) on the performance of two tasks hypothesised to have different dependences on space-motion information. Roll-plane OKS was selected as the means of inducing a balance disorder in healthy participants, in order to minimise the potential for nystagmus to mediate disruptions of cognition.

Methods:

Forty-eight participants were randomised into independent groups to undertake the ‘Own Body Transformation’ (OBT) task, invoking mental self-translocation (MS-TL), or the ‘Transpose’ task, requiring equivalent spatial mappings but without the necessity for imaginary changes in self-location. Both cognitive tasks were administered in two-minute trial blocks, four times in a row, with alternating exposure to static and rotating visual surrounds. Participants stood feet together atop a force platform during experimentation and, afterwards, completed several self-report measures. One of these gauged the cognitive strategies the participants had adopted while performing their allotted task.

Results:

During OKS, there were longer response times on both the OBT and Transpose tasks, plus higher error and lower drift rates just on the latter task. Importantly, there was no difference between performance on the OBT and Transpose tasks in terms of the degree of disruption by OKS of the primary, task-related outcome variables. Participants in the OBT task group reported a low uptake of MS-TL.

Discussion:

The lack of a differential disruption of OBT versus Transpose task performance means that it is not possible to determine whether aberrant space-motion information can have a direct, unmediated effect on cognition. However, the participants' low uptake of MS-TL indicates that the OBT task was not a valid means of engaging this cognitive process. Therefore, performance on the OBT task was probably no more vulnerable to misinformation than performance on the Transpose task. In effect, the materials of this study precluded insight into whether balance disorders can directly affect higher cognition. An important next step for this research is to develop new spatial perspective-taking and comparison tasks with clearer differences in demands for MS-TL and, thus, for space-motion information.

4.2 Introduction

The preceding narrative review highlights the requirement for detailed measurement and analysis of the cardinal manifestations of experimentally-induced balance disorders to discern whether the aberrant space-motion information, which those disorders entail, can directly affect higher cognition (see Chapter 2, specifically section 2.6). The design and methods of the first study were largely governed by this requirement. There was no facility for measuring nystagmus, a common cardinal manifestation which may lead to unstable visual fixation and, in turn, to attentional diversion (see Preface section ii and section 2.5). Hence, roll-plane optokinetic stimulation (OKS) was selected as the aberrant space-motion stimulation to which participants would be exposed during interleaving trial blocks (see section 1.5.3 for further background on this form of stimulation). While visual motion in roll can generate nystagmus about the optical (antero-posterior) axis (Baloh, Honrubia, & Kerber, 2011), Brandt et al. (1998) reported that such torsional eye movements were small and irregular when roll-plane OKS was presented to participants at a relatively short viewing distance. Moreover, Dilda et al. (2012) suggested that, even if torsional eye movements are induced during OKS in roll, participants are still readily able to see task-related visual stimuli because visual acuity is relatively independent of ocular torsion about the optical axis. In summary, it was thought that roll-plane OKS would provide suitable space-motion cue incongruity in the first study, yet minimise the potential for nystagmus to mediate disruptions of cognition. Any dizziness, nausea, postural instability and anxiety associated with OKS would be relatively simple to measure and interpret.

Also based on the findings of the narrative review (see section 2.6), the SPT task chosen as the means of evoking MS-TL in the present study was the ‘Own Body Transformation’ (OBT) task (Blanke et al., 2005). The stimulus set of this task comprises front- and rear-facing avatars randomly tilted by 10° increments in the roll plane through a range of -50 to +50°. The restricted tilt angles of the avatars mean that the OBT task has acceptable ecological validity, since participants do not have to imagine inverting themselves. Moreover, the tilt angles may reduce the chances of participants foregoing MS-TL for a rote strategy (see section 1.7.1.2). Therefore, the OBT task probably evokes MS-TL more continually than other commonly-used SPT tasks, particularly those with two-dimensional (2-D) avatars. To date, this is the only SPT task of its kind[18] to have been studied using fMRI (see section 1.7.3.1). Zacks et al. (1999) found that the neural substrate of OBT task performance and, therefore, probably of MS-TL engagement, is centred around the parietal-temporal-occipital junction - the forebrain region that contains many of the CVPAs.

An added advantage was that a spatial control task - the ‘Transpose’ task (Gardner & Potts, 2011) - has been designed which matches the OBT task for difficulty and controls for stimulus-response compatibility effects associated with it. During the OBT and other similar SPT tasks, when the avatar is displayed with its front facing the participant, the on-screen location of the black ball (i.e. the target - see section 4.3.3) is contralateral to the correct response button (Gardner & Potts, 2011). A spatially incompatible response is therefore required from the participant. This is not the case when the avatars are displayed rear-facing. Were OKS to selectively disrupt responses to front-facing avatars, it might simply be due to a perturbation of the extra cognitive processing required to make incompatible responses, rather than due to a disturbance of the extra mental self-rotation required to assume the avatars’ positions. By simultaneously studying the effect of OKS on Transpose task performance, it is possible to distinguish performance costs genuinely associated with MS-TL from costs associated with stimulus-response incompatibility (see section 1.7.2). Gardner et al. (2017) employed the OBT and Transpose tasks in their study

---

[18] Other SPT tasks, based on the spatial updating paradigm, have been submitted to fMRI research. Such tasks are not the focus of this thesis (see section 1.7.1 for the rationale).

(see section 2.4.5), but exposed participants to cross-coupled stimulation, rather than OKS, while they undertook these.

With reference to section 3.12, the present study was designed:

- To establish if OKS has any differential effects, between the independent task groups, on primary or secondary outcome variables, and,
- To determine if OKS specifically causes disruption of primary outcomes derived from either of the cognitive tasks, and, if so,
- To ascertain if the disruptive effects may be accounted for indirectly by any of the consequences of the aberrant stimulation, in particular the disturbance of postural control.

4.3 Methods

4.3.1 Ethical considerations and recruitment

As detailed in section 3.3.

4.3.2 Aberrant space-motion stimulation

As detailed in section 3.4.

4.3.3 Cognitive tasks

Participants were randomly allocated to undertake either the OBT or Transpose tasks. During the former, the participants were recurrently presented with a two-dimensional (2-D), line-drawn avatar holding a black ball in one hand and a white ball in the other. The avatar was randomly tilted by 10º increments in the roll plane through a maximum range of -50 to +50º. More importantly, the avatar was either facing toward (front-facing) or away from (rear-facing) the participant, while the black ball was either in its left or right hand. Therefore, there were four main permutations of the avatar's on-screen appearance. Front- and rear-facing avatars shared the same outline but the former were distinguishable from the latter by simple facial features and buttons. The participants randomised to undertake the OBT task were instructed to imagine themselves in the avatar's body position each time it appeared, in order to judge whether it held the black ball in its left or right hand. Participants had to register their judgements by tapping the mouse button with their corresponding index finger (see section 3.5). As discussed in section 4.2, the correct response was ipsilateral (i.e. compatible) with the on-screen location of the black ball when the avatars were rear-facing, but contralateral with the location of the black ball for front-facing stimuli.

During the Transpose task, participants were recurrently presented with black and white balls, tilted in the same manner, and of the same size and angular separation as in the OBT task, but no avatar was holding them. Instead, the balls were shown either without (referred to as ‘cue-absent’ stimuli) or with (referred to as ‘cue-present’ stimuli) a random array of the facial features and buttons which distinguish front- from rear-facing avatars in the OBT task. For cue-absent stimuli, which were displayed during half of the trials, participants were required to click ipsilaterally to the on-screen location of the black ball. However, for cue-present stimuli, they were instructed to transpose or cross their response and, thereby, click contralaterally to the location of the black ball. Hence, the spatial mappings of the Transpose task were of equivalent compatibility to those of the OBT task, but the participants who undertook the former did not need to engage in mental self-translocation.

For both tasks, each trial commenced with the presentation of a black fixation cross which appeared centre-aligned for 1400 ms. This was followed immediately by the stimulus which terminated after a response had been made, or after 2100 ms, whichever was sooner. Thereafter, visual feedback was displayed about whether the response was correct or incorrect. This feedback stayed on-screen for 1500 ms, and was followed by the fixation cross for the next trial. Therefore, fresh task stimuli were presented at least every five 5 s.

All elements of both tasks (i.e. their stimuli, the fixation cross and feedback text) were centred within a circular, white surround. The perimeter of this encirclement was smudged into a black outer border. This format meant that just the central circular portion of the cognitive tasks, comprising the line drawings of the OBT and Transpose stimuli, stood proud of the large field, riverscape image (see sections 3.4 and 3.5). Furthermore, it meant that there were no obvious vertical or horizontal borders enframing the stimuli which might have otherwise given the participants polarity (verticality) cues (see section 1.3.3.2.5). Examples of the stimuli shown in both the OBT and Transpose tasks are displayed in Figure 4.1. The correct response is given below each example. Further details about the cognitive tasks and about the order and number of trial blocks can be found in sections 3.5 and 3.10, respectively.

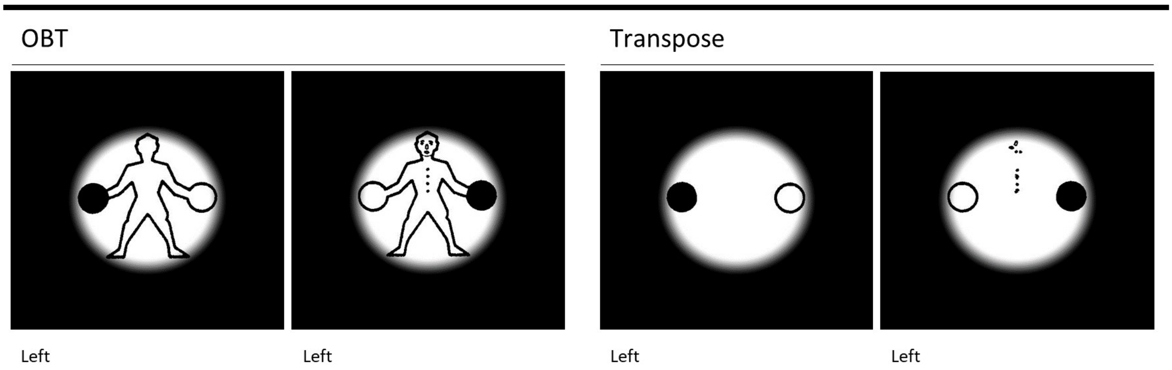


Figure 4.1: Sample stimuli presented as part of the OBT and Transpose tasks.

Correct laterality judgements are given under each stimulus, noting that stimuli requiring right-sided responses are not depicted.

4.3.4 Trait measures

As detailed in section 3.6.

4.3.5 State measures

As detailed in section 3.7.

4.3.6 Strategy measures

Once all of the experimental blocks had been completed, participants were asked questions about the strategies they had used in order to make the necessary laterality judgements during the OBT or Transpose tasks. More specifically, participants in the OBT group were asked to read a short passage taken from Gronholm et al. (2012), which described two common strategies reported by participants in previous research. One of these strategies was the one they had been instructed to adopt; that is, to imagine themselves in the avatar's body position each time it appeared, in order to judge whether it held the black ball in its left or right hand. The other was the rote strategy whereby participants learn merely to transpose or flip left and right whenever confronted with front-facing avatars. Having read the passage, the OBT task group participants rated how often they used the proposed strategies on a 5-point scale (Always imagined myself taking the figure's position; Usually imagined myself taking the figure's position; Used both strategies equally often; Usually used the flipping left and right strategy; Always used the flipping left and right strategy). They were also asked to recall at what point during the entire experiment they started to use the transposing/flipping strategy, if at all. If participants were uncertain about how to respond to one or both questions about their strategies, they were asked for further free text comments.

Based on Gardner and Potts (2011), participants in the Transpose task group were simply asked whether they had attributed any meaning to the stimuli they had been presented with throughout the task. They were given dichotomous (yes or no) response options. If they had felt that the images, particularly the 'cue-present' stimuli, were not just abstract features but had some real-world association, the participants were asked for further free text comments about the association.

4.3.7 Space-motion misperception measures

As detailed in section 3.9.

4.3.8 Experimental procedure

The procedure for this study is given in detail in section 3.10. The only addendum is that participants in both the OBT and Transpose task groups undertook 44 practice trials of their allocated task in a single block while sitting down. This meant they experienced every configuration of the tasks' stimuli once each (four permutations by 11 possible tilt angles).

4.3.9 Variables

The variables incorporated into this study are listed in section 3.11. The only addendum is that the independent or predictor variable 'task' had two levels: 'OBT' and 'Transpose'.

4.3.10 Hypotheses

As detailed in section 3.12.

4.3.11 Reduction of bias

As detailed in section 3.13.

4.3.12 Comparisons of baseline characteristics

As detailed in section 3.14.1.

4.3.13 General descriptives

Details of the descriptive statistics calculated from the data are given in section 3.14.2, but further clarification is required as to how participants in the OBT task group were categorised as ‘high self-translocators’ or ‘high transposers’. The categorisation was made based on participants’ responses to the strategy-related questions (see section 4.3.6). Those who disclosed that they had always or usually imagined themselves taking the figure’s position were grouped as high self-translocators. Whereas, those participants who reported that they had always or usually used the ‘flipping left and right strategy’ were grouped as high transposers. The number of participants in each category was converted to a percentage of the total number of participants in the OBT task group.

In a similar manner, the number of participants in the Transpose task group who had reported attributing some meaning to the array of facial features and buttons associated with ‘cue-present’ stimuli, was summed and converted into a percentage of the total number of participants in the Transpose task group.

4.3.14 Hypothesis tests

As detailed in section 3.14.3.

4.3.15 Supplementary analyses

As detailed in section 3.14.4.

4.4 Results

4.4.1 Participants and comparisons of their baseline characteristics

In total, 48 student volunteers from the University of Westminster took part in this study, having met the eligibility criteria and provided written informed consent. Both the OBT and Transpose task groups comprised 24 randomly-allocated participants. The proportion of errors participants in both groups made across all four experimental blocks was low (*M* = 5.4%; *SD* = 4.3%). However, three participants demonstrated particularly high cumulative error compared to other members of their groups. More specifically, their error proportions were more than 1.96 standard deviations greater than the mean proportions for their groups. Two of these participants had been in the OBT task group, and the remainder had been a member of the Transpose task group. All data for these three participants were excluded from the analyses given that their task performance was atypical, and in the attempt to reduce bias (see section 3.13.1).

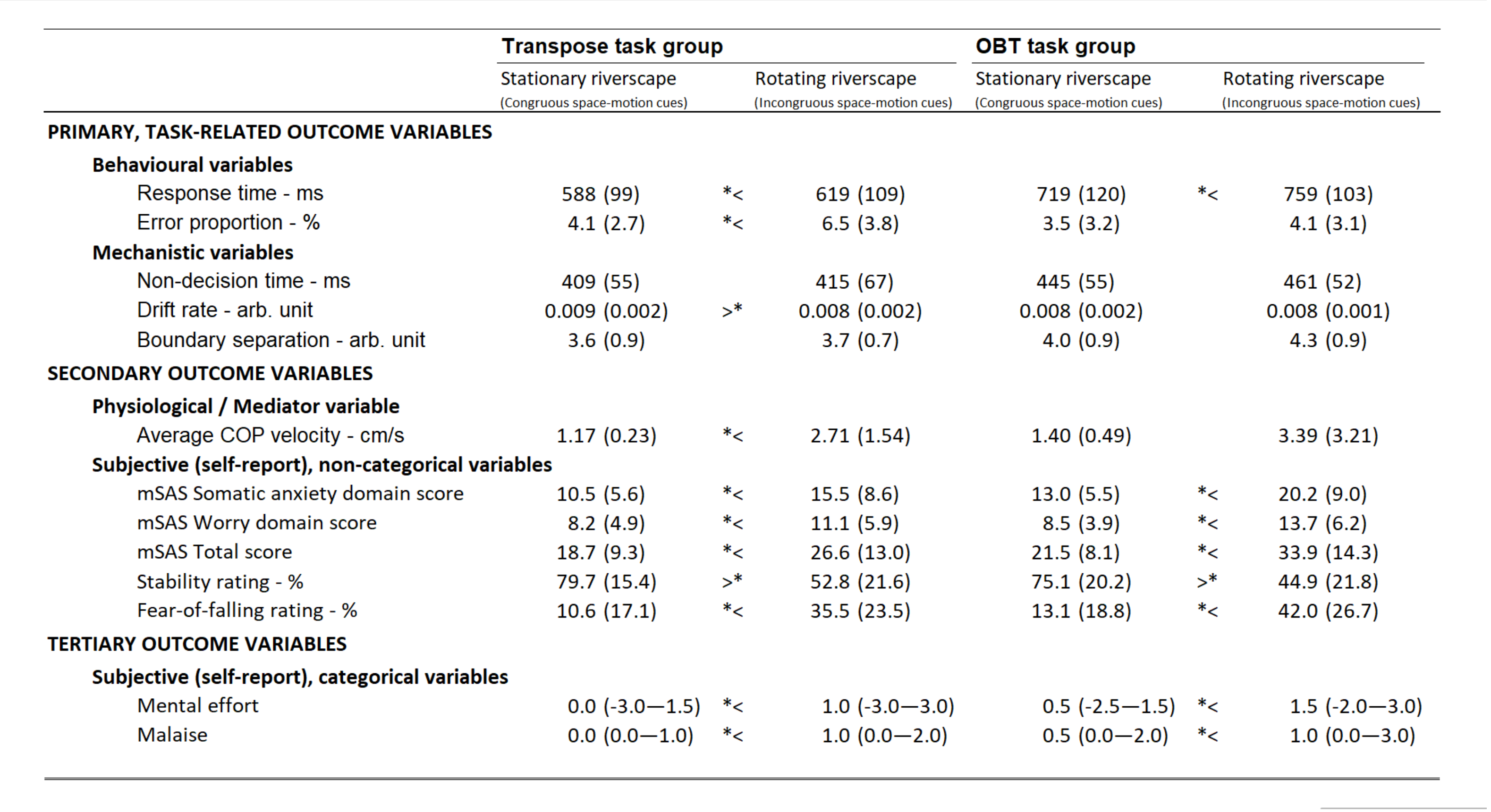
The mean age of the remaining 45 participants was 20 years (*SD* = 2.5 years). There were 22 female participants, 12 of whom had been allocated to the OBT task group. Nine of the participants were left-handed, and six of these completed the OBT task. Independent samples t-tests revealed there were no between-group differences in the heights (*M* = 169.90 cm; *SD* = 8.35 cm) and weights (*M* = 66.72 kg; *SD* = 15.02 kg) of participants in the two groups. According to scores on the STICSA (see section 3.6.1), 17 and 11 of all of the participants had possible and probable anxiety disorders, respectively. Furthermore, 13 had a probable cognitive anxiety component, and 18 had a probable somatic anxiety component. There were no between-group differences in STICSA subscale and total scores. Ten participants in the OBT task group were highly susceptible to visual vertigo since their normalised scores on the SVQ (see section 3.6.2) exceeded 0.7. The scores for only four participants in the Transpose task group exceeded this benchmark. Overall, participants in the two groups did not have significantly different SVQ scores when the data were subjected to an independent samples t-test. The mean balance confidence ratings for the whole sample were 78% for lower postural threat conditions and 53% for higher postural threat conditions. As for the other trait measures, there were no between-group differences in reported balance confidence.

4.4.2 General descriptives

The data for all of the dependent variables, except task strategy (see section 4.3.13), were amalgamated according to task and whether they derived from trial blocks performed during exposure to congruous or incongruous space-motion cues. Averages were then computed and inspected. These data are given in table 4.1 which appears to indicate that OKS, by way of the large, rotating riverscape image, had an effect on several primary, secondary and tertiary outcome variables derived from both tasks. However, some of the data, particularly for the secondary outcome variables, appear to be dispersed according to the relatively large standard deviation values. Not shown in table 4.1 is that participants in the OBT and Transpose task groups completed a similar number of trials throughout experimentation, averaging 132 and 137 trials, respectively. Most participants (86%) in the OBT task group experienced the vection illusion, as did most (78%) in the Transpose task group. However, 79% of participants in the former group reported that the illusion was sustained rather than brief, compared to just 39% of participants in the latter group. Indeed, the median vection duration scores for the OBT and Transpose task groups were 1 (sustained) and 0 (brief), respectively. A similar proportion of participants in both groups reported the illusion had been ‘moderate’ in its strength; 53% of OBT task group members, and 56% of Transpose task group members.

Table 4.1: Data obtained in Study 1 for primary, secondary and tertiary outcome variables categorised according to task and space-motion cue congruity.

All data are mean values with standard deviations in parentheses, except for mental effort and malaise (medians with minimum and maximum values in parentheses). Arrows with stars denote significant differences as revealed by simple effects analyses (see section 3.14.3).



	Transpose task group			**OBT task group**		
	Stationary riverscape (Congruous space-motion cues)		Rotating riverscape (Incongruous space-motion cues)	Stationary riverscape (Congruous space-motion cues)		Rotating riverscape (Incongruous space-motion cues)
PRIMARY, TASK-RELATED OUTCOME VARIABLES						
Behavioural variables						
Response time - ms	588 (99)	*<	619 (109)	719 (120)	*<	759 (103)
Error proportion - %	4.1 (2.7)	*<	6.5 (3.8)	3.5 (3.2)		4.1 (3.1)
Mechanistic variables						
Non-decision time - ms	409 (55)		415 (67)	445 (55)		461 (52)
Drift rate - arb. unit	0.009 (0.002)	>*	0.008 (0.002)	0.008 (0.002)		0.008 (0.001)
Boundary separation - arb. unit	3.6 (0.9)		3.7 (0.7)	4.0 (0.9)		4.3 (0.9)
SECONDARY OUTCOME VARIABLES						
Physiological / Mediator variable						
Average COP velocity - cm/s	1.17 (0.23)	*<	2.71 (1.54)	1.40 (0.49)		3.39 (3.21)
Subjective (self-report), non-categorical variables						
mSAS Somatic anxiety domain score	10.5 (5.6)	*<	15.5 (8.6)	13.0 (5.5)	*<	20.2 (9.0)
mSAS Worry domain score	8.2 (4.9)	*<	11.1 (5.9)	8.5 (3.9)	*<	13.7 (6.2)
mSAS Total score	18.7 (9.3)	*<	26.6 (13.0)	21.5 (8.1)	*<	33.9 (14.3)
Stability rating - %	79.7 (15.4)	>*	52.8 (21.6)	75.1 (20.2)	>*	44.9 (21.8)
Fear-of-falling rating - %	10.6 (17.1)	*<	35.5 (23.5)	13.1 (18.8)	*<	42.0 (26.7)
TERTIARY OUTCOME VARIABLES						
Subjective (self-report), categorical variables						
Mental effort	0.0 (-3.0—1.5)	*<	1.0 (-3.0—3.0)	0.5 (-2.5—1.5)	*<	1.5 (-2.0—3.0)
Malaise	0.0 (0.0—1.0)	*<	1.0 (0.0—2.0)	0.5 (0.0—2.0)	*<	1.0 (0.0—3.0)

In the OBT task group, only two (9%) of the 22 members reported having always or usually adopted the mental self-translocation strategy and, therefore, were classifiable as 'high self-translocators'. 19 (86%) members were classifiable as 'high transposers'. 43% of those reported that they had learned the rote strategy of flipping left and right, whenever confronted with front-facing avatars, during the practice trial. In the Transpose task group, only three (13%) of the 23 group members had attributed some meaning to the random array of facial features and buttons that were part of the 'cue-present' stimuli. More specifically, they reported that they had likened the array to the human form. Therefore, just these three participants may have adopted a mental self-translocation strategy during the Transpose task.

4.4.3 Hypothesis tests

Five participants in the OBT task group, but only one in the Transpose task group, achieved 100% accuracy on trials undertaken during exposures to both the static (i.e. congruous cues) and rotating (i.e. incongruous cues) riverscape image. It was not possible to calculate mechanistic variables (drift rate, boundary separation and non-decision time) for these six participants given the constraints of the EZ-diffusion model (see section 3.11.2.1.2). Hence, sets of mechanistic variable data for 15 participants in the OBT task group and 22 in the Transpose task group were subjected to the hypothesis tests. Regarding the behavioural variables (RT and error proportion), data from all 22 participants in the OBT task group and all 23 in the Transpose task group were subjected to the analyses.

4.4.3.1 Tests relating to null hypothesis 1

To test whether there were interaction effects of the independent variables (IVs; task and space-motion cue congruity) on any of the primary outcome variables, a series of two-way ANOVAs were conducted. There were no significant interactions between the IVs which affected either the two behavioural variables, $F < 2.7, p > 0.1, \eta_p^2 < 0.06$, or the three mechanistic variables, $F < 2.8, p > 0.1, \eta_p^2 < 0.08$. For the sake of completeness, there were main effects of space-motion cue congruity on RT, $F(1, 43) = 17.41, p < .001, \eta_p^2 = .288$, and error proportion, $F(1, 43) = 7.75, p = .007, \eta_p^2 = .153$, which indicate that OKS disrupted performance on the tasks. In-keeping with these results, a significant main effect of cue congruity on drift rate, $F(1, 35) = 12.72$, $p = .001$, $\eta_p^2 = .267$, indicates that OKS slowed the accumulation of information necessary for laterality judgements on the tasks. There was a significant main effect of task on RT, $F(1, 43) = 18.95$, $p < .001$, $\eta_p^2 = .306$, indicating that response times on the OBT task were longer than those on the Transpose task. The task factor had a borderline significant effect on both boundary separation, $F(1, 35) = 4.23$, $p = .047$, $\eta_p^2 = .108$, and non-decision time, $F(1, 35) = 5.19$, $p = .029$, $\eta_p^2 = .129$, which suggests that the slower response times on the OBT task were possibly underpinned by greater response caution and longer non-explicit decision processing during trials of that task.

Data pertaining to the secondary outcome variables (average COP velocity, total mSAS score, stability rating and fear-of-falling rating) were also subjected to the same two-way ANOVAs to test for task by cue congruity interaction effects. There were no significant interactions on any of these variables, nor were there any significant main effects of task. However, space-motion cue congruity had a significant effect on average COP velocity, $F(1, 43) = 28.06$, $p < .001$, $\eta_p^2 = .395$, indicating that OKS perturbed postural control across the task groups. Furthermore, there was a significant main effect of the cue congruity factor on total mSAS score, $F(1, 43) = 69.36$, $p < .001$, $\eta_p^2 = .617$, stability rating, $F(1, 43) = 97.59$, $p < .001$, $\eta_p^2 = .694$, and fear-of-falling rating, $F(1, 43) = 53.67$, $p < .001$, $\eta_p^2 = .555$. These results imply that OKS made participants more anxious about their well-being and less certain about their balance.

4.4.3.2 Tests relating to null hypothesis 2

To test whether there were within-subjects, simple effects of space-motion cue congruity on the primary outcome variables, a series of paired t-tests was conducted. These revealed that slower responses due to OKS occurred during trials of both the OBT task, $t(21) = 2.47$, $p = .020$, $r = .475$, and the Transpose task, $t(22) = 5.06$, $p = .001$, $r = .733$, as depicted in Figure 4.2A. Greater error was also caused by OKS but only on the Transpose task, $t(22) = 3.18$, $p = .006$, $r = .561$ (see Figure 4.2B). In terms of the mechanistic variables, there was only a significant simple effect of cue congruity on drift rates obtained from the Transpose task group, $t(21) = 4.65$, $p < .001$, $r = .713$ (see Figure 4.2C). Therefore, only on that task was OKS found to slow the accumulation of decision-related information.

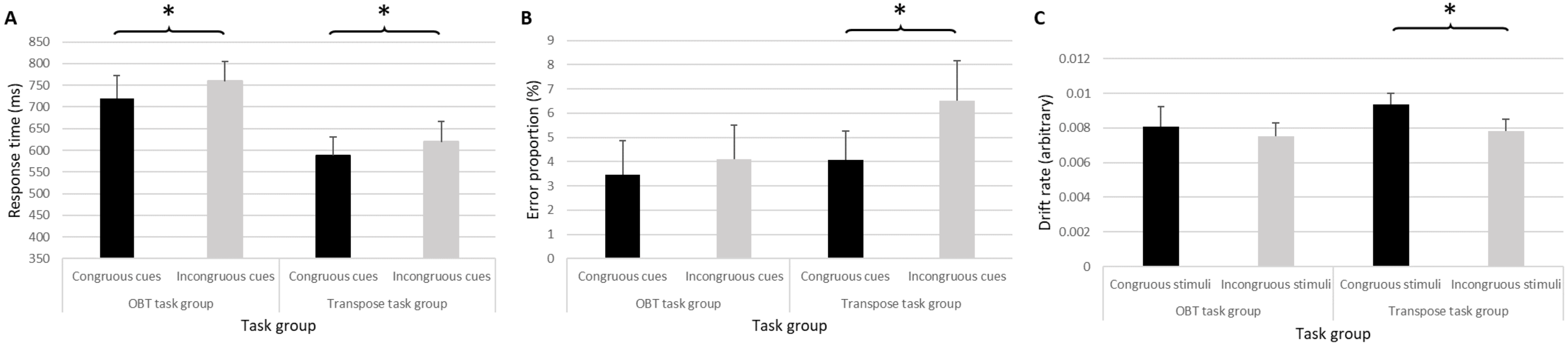


Figure 4.2: Bar charts showing mean response time [A], error proportion [B] and drift rate [C] segregated by task group (OBT versus Transpose) and by space-motion cue congruity (congruous [stationary backdrop] versus incongruous [rotating backdrop] cues).

Error bars represent 95% confidence intervals.

All of the data pertaining to the primary outcome variables were re-tested for simple effects of the space-motion cue congruity factor using the path-analytic method of mediation analysis, which controlled for the effect on cognitive performance of average COP velocity. The analyses revealed no significant direct effects of cue congruity on the behavioural or mechanistic variables. That is, with average COP velocity controlled, all of the significant effects detailed above were abolished, $t < .9$, $p > .3$. While this might indicate that average COP velocity mediated the disruptive effects of OKS on task performance, there were no significant indirect effects of this physiological variable on any of the task-related variables. More specifically, bias-corrected bootstrap confidence intervals (2000 bootstrap samples) straddled zero for the indirect effects of space-motion cue congruity, via COP velocity, on each primary outcome variable. No additional simple effects of OKS on task performance variables were revealed by the mediation analyses.

4.4.4 Supplementary analyses

To supplement the tests relating to null hypothesis 2, the secondary outcome variables were similarly subjected to paired samples t-tests, but mediation analyses were not undertaken. There was a significant effect of space-motion cue congruity on average COP velocity, but only for respective data obtained from the Transpose task group, $t(22) = 5.12$, $p = .008$, $r = .737$ (OBT task group, $t(21) = 3.29$, $p = .116$). These results indicate that OKS disrupted the balance of those participants in the Transpose but not the OBT task groups. With regard to total mSAS scores, stability ratings and fear-of-falling ratings, pairwise comparisons imply that, during OKS, participants in both groups felt more anxious (OBT task group, $t(21) = 6.49$, $p < .001$, $r = .817$; Transpose task group, $t(22) = 5.16$, $p < .001$, $r = .740$), unstable (OBT task group, $t(21) = 7.95$, $p < .001$, $r = .866$; Transpose task group, $t(22) = 6.21$, $p < .001$, $r = .798$), and fearful (OBT task group, $t(21) = 5.38$, $p < .001$, $r = .761$; Transpose task group, $t(22) = 4.96$, $p < .001$, $r = .727$).

Between-task comparisons of the tertiary outcome variables, specifically the malaise, mental effort, vection duration and vection strength scores, also constituted supplementary analyses. These analyses, with the space-motion cue congruity factor collapsed, were carried out by way of Mann-Whitney U tests. There was a borderline significant effect of task only on vection duration, $U = 239.50$, $z = 2.447$, $p = .036$, $r = .402$. This suggests that the episodes of illusory self-motion experienced by participants in the OBT task group may have been more sustained than those episodes experienced within the Transpose task group (see section 4.4.2 for median vection duration scores, and for the differing proportions of participants who experienced sustained vection).

Finally, Wilcoxon signed-rank tests were employed to analyse the within-subjects effects of space-motion cue congruity on ordinal data pertaining to malaise and mental effort. Reported levels of the latter were raised across both groups during OKS (OBT task group, $z = 3.84$, $p < .001$, $r = .580$; Transpose task group, $z = 3.83$, $p < .001$, $r = .564$). Reported levels of malaise were also higher during OKS (OBT task group, $z = 3.79$, $p < .001$, $r = .572$; Transpose task group, $z = 3.50$, $p < .001$, $r = .516$).

4.5 Discussion

4.5.1 Summary of the results

The present experiment investigated whether balance disorders can directly affect higher cognition by examining the effect of aberrant space-motion information associated with optokinetic stimulation (OKS) on the performance of two tasks hypothesised to have different susceptibilities to such misinformation: the Own Body Transformation (OBT) and Transpose tasks. OKS disrupted performance on both tasks according to simple effects analyses. Response times recorded during both were longer with than without OKS. More errors were made on the Transpose task during exposure to the incongruous space-motion cues brought about by the rotary motion of the visual backdrop. Pairwise comparisons of mechanistic variables calculated by the EZ-diffusion model indicated that the disturbance of performance on the Transpose task during OKS was underpinned by a decrease in drift rate; that is, by a reduction in the rate at which decision-related information was accumulated. No clear cognitive mechanism accounted for the longer response times on the OBT task, possibly because less data from that group could be subjected to the EZ-diffusion model and then to the hypothesis tests. In consequence, there may have been too little data to determine an effect of OKS on OBT task-related drift rate or other mechanistic variables.

Importantly, no difference was found between the OBT and Transpose tasks, in terms of the degree of disruption by OKS, for response time, error proportion and drift rate. This can be inferred from the non-significant task by space-motion cue congruity interaction effects yielded by the factorial ANOVAs. There were also no task-related differential effects of the aberrant space-motion stimulation on the remaining primary outcome variables (boundary separation and non-decision time) and on all of the secondary outcome variables. In both the OBT and Transpose task groups, participants' subjective and physiological states were degraded by OKS according to simple effects analyses.

4.5.2 Primary inferences about the direct effect of aberrant space-motion information on cognition

The lack of a differential disruption of OBT versus Transpose task performance indicates either that a direct effect of aberrant space-motion information cannot occur or that it is simply indiscernible from the design of this study and its results. There are several plausible reasons why OKS unexpectedly disrupted performance on the tasks to similar extents, thus obscuring interpretations about the direct effect of misinformation. Firstly, it is possible that the theoretical perspective on mental self-translocation (MS-TL), presented in Chapter 1 (see section 1.6 in particular), is flawed. More specifically, MS-TL may not have a particular dependence on veridical space-motion information. Therefore, it may not be preferentially vulnerable to aberrance of this information. In turn, OBT task performance, which is supposedly underpinned by MS-TL, would not have been disproportionately susceptible to the experimentally-induced balance disorder that manifested from the OKS.

As discussed in section 1.6.3, the dependence of MS-TL on space-motion information refers to the notion that the cognitive process may benefit from an accurate space-motion context just prior to its onset. More specifically, the integration of space-motion information during MS-TL may accumulate fewer errors following exposure to accurate visuo-vestibular referents, just like integration during angular path integration appears to be facilitated after such a veridical 'starting point' (Arthur, Philbeck, & Chichka, 2007, 2009; Israël, Bronstein, Kanayama, Faldon, & Gresty, 1996).

An alternate explanation for the failure to find differential effects is that the susceptibility of Transpose task performance to aberrant space-motion information was underestimated. More specifically, the cognitive processing underpinning that task actually might have been similar to the MS-TL evoked by the OBT task in terms of its requirement for accurate space-motion cues. The Transpose task is a spatial choice-reaction time task (Gardner et al., 2017) which is contingent on memory processes, particularly the recall of spatial mapping instructions. It is this contingency which may have made Transpose task performance unexpectedly susceptible to OKS. Performance on other tasks which rely on spatial memory has been shown to be disrupted in patients with chronic bilateral vestibular hypofunction, presumably due to their marked hippocampal atrophy (Brandt et al., 2005). Moreover, Dilda et al. (2012) found an increase in error rate when galvanic vestibular stimulation was administered to healthy participants while they performed a memory-contingent 'match-to-sample' task. The authors proposed that this was because the aberrant vestibular stimulation interfered with spatial memory processing in the hippocampus. However, it must be re-emphasised that the Transpose task does not depend on spatial memory, but simply on the recall of spatial mapping instructions. This makes extrapolations from Brandt and colleagues' (2005) and Dilda and colleagues' (2012) research less applicable, and a misinformation-related susceptibility of Transpose processes equivalent to that of MS-TL less plausible.

Perhaps the most likely reason for the lack of a differential disruption of OBT versus Transpose task performance relates to the low uptake of MS-TL by participants in the OBT task group. Only two of the 22 participants reported having imagined themselves taking the avatar's body position in order to make the necessary laterality judgements. That is, only 9% of the participants seemed to have engaged in MS-TL. Almost all of the others reported routinely adopting a rote strategy whereby they merely transposed or flipped left and right whenever confronted with front-facing avatars. This apparent rate of MS-TL evocation compares very unfavourably to two previous studies which employed the OBT task. In Gronholm and colleagues' (2012) study, 53% of 85 participants reported utilising MS-TL. In the study by Gardner et al. (2013), 40% of participants reported having adopted the MS-TL strategy, 59% adopted the rote strategy, and 38% declared that they had used both strategies. The unfavourable rate of reported MS-TL engagement in the present study was not clearly related to the study's methods, since the task-related instructions the participants were given were the same as those provided by Gronholm et al. (2012). Furthermore, strategy information was gleaned from the participants in the present study using the same questions employed by Gronholm et al. (2012).

Although participants' subjective reports about the cognitive processes or strategies they utilise during SPT tasks should be interpreted with caution (Candidi et al., 2013; Zacks &

Tversky, 2005), the self-report data from the present study seems to be compelling, and the possibility that participants treated the OBT task like a choice-reaction time task cannot be fully dismissed. It is possible that they did so as a consequence of a greater difficulty engaging in MS-TL under OKS. This could have been assessed by manipulating space-motion cue congruity as a between-subjects factor. However, this possibility seems less plausible given that 43% of the participants reported having adopted the rote strategy during the practice trial block, before they were even exposed to OKS. In effect, the data seems to indicate that the OBT task was not a valid means of engaging MS-TL. According to the internal model formulation of MS-TL, one way of assessing the validity of SPT tasks would be to examine the data they yield for a monotonic RT function (see section 1.7.1). It is not possible to assess the OBT task in this way since its stimulus set only comprises front- and rear-facing avatars. As such, it is difficult to separate differential performance costs genuinely associated with MS-TL from costs associated with stimulus response compatibility (May & Wendt, 2013; see section 4.2).

Responses times were longer on the OBT than the Transpose task. This unanticipated disparity was underpinned by borderline longer non-decision processing and borderline greater response caution on the OBT task. While this might have meant the Transpose task was not an ideal control task, the absence of task-related differential effects of OKS on primary outcome variables implies that the disparity in the tasks' inherent cognitive loads was relatively inconsequential.

4.5.3 Additional inferences about the mediation of disrupted cognitive task performance

The mediation analyses removed the significant simple effects of OKS on primary outcome variables yielded from both the OBT and Transpose tasks. While this suggests that task disruption by aberrant stimulation was mediated by one or more intervening factors, average COP velocity - the surrogate for postural (in)stability - was not clearly the sole factor. This can be inferred from the non-significant indirect effect of average COP velocity on the primary outcome variables. A larger sample may have been needed to show a significant indirect effect given that the mediation analyses employed were regression-based (see Montoya & Hayes, 2017). COP velocity was increased by OKS, indicating that postural instability was amplified, which may have distracted participants from their laterality judgements and, therefore, disrupted their task performance. This significant effect was only found in data from the Transpose task group possibly because the data from the OBT task group was more dispersed (see *SD* values in parentheses in Table 4.1). The greater dispersion attests to a less consistent destabilising effect of OKS on participants in the OBT task group. It is recognised that there are prominent individual differences in the way healthy persons make use of vestibular and visual signals for postural control (Guerraz et al., 2001), as well as for self-orientation perception (Witkin, 1959). So-called 'field dependent' individuals have been shown to rely more on visual cues in order to maintain their stability (Isableu, Ohlmann, Crémieux, & Amblard, 1997). This is not an uncommon intrinsic sensorimotor strategy (Agarwal et al., 2012). Interestingly, a larger proportion of participants in the OBT task group were highly susceptible to visual vertigo according to their normalised scores on the SVQ. Hence, the proportions of field-dependent and -independent participants may have been more equal in that group than in the Transpose task group, which seems to have had an over-sized proportion of field-independent participants. The dual characteristic of the OBT task group may have underpinned the greater dispersion of OKS-associated changes in average COP velocity and, therefore, may have obscured the simple effects and possibly the mediation analyses.

Simply modelling COP velocity as the mediator variable most probably overlooked other potential mediator and/or moderator variables. Several measures of participants' subjective states were collected during experimentation and might also have been appropriate to include in the mediation analyses had there been a much larger sample. Pairwise comparisons showed that OKS increased participants' anxiety, malaise and uncertainty about their balance. All of these may have contributed to a diversion of participants' attention from, and/or reduced motivation for, the cognitive tasks. Indeed, a decrement in attention to the Transpose task is suggested by the drop in drift rate as revealed by the simple effects analysis of this primary outcome variable. As discussed in section 2.3, it is generally accepted that attentional diversion leads to a decrease in drift rate (O'Callaghan et al., 2017; Teichert, Ferrera, & Grinband, 2014; van Ravenzwaaij, Dutilh, & Wagenmakers, 2012). Interestingly, participants in the OBT and Transpose task groups reported having exerted more effort on the tasks during OKS, which might contradict the preceding interpretation of the drop in drift rate. However, more recent theories assert that effort and attention are actually separate constructs (e.g. Bruya & Tang, 2018; see section

2.3 for further details). It is possible that effort ratings obtained in the present study may have been a closer marker of the participants' levels of motivation for the tasks than of their levels of attention to them.

While the majority of participants in both groups reported having experienced the vection illusion during trial blocks undertaken with background OKS, measures of this form of dizziness were not collected during trial blocks performed with congruous space-motion cues (i.e. in the absence of OKS). Hence, no within-subjects analyses were possible. Moreover, it was not possible to include vection-related scores in the mediation analyses. The inadequacies of the mediation analyses had been anticipated, which is why these analyses were not the main or only ones employed in this or two of the other studies (see Studies 3 and 4; Chapters 6 and 7, respectively). As discussed in section 2.3, subjecting all of the primary and secondary outcome variables to factorial ANOVAs was a more inclusive analytical strategy than the mediation analyses. The ANOVAs should have indicated whether some of those variables, which could not be included in the mediation analyses for sample size reasons, were potential mediator variables. Therefore, the two analytical techniques were complementary.

4.5.4 Conclusions

Optokinetic stimulation (OKS), and the resultant experimentally-induced balance disorder, disrupted performance on the OBT and Transpose tasks - two tasks of spatial cognition selected on the basis that they had different susceptibilities to aberrant space-motion information. More specifically, under OKS, there were longer response times on both tasks, plus higher error and lower drift rates specifically on the Transpose task. Importantly, there was no difference between performance on the OBT and Transpose tasks in terms of the degree of disruption by OKS of primary, task-related outcome variables. The lack of a differential disruption of OBT versus Transpose task performance indicates that a direct effect of aberrant space-motion information cannot occur or that it is simply indiscernible from the design of this study and its results. The most likely cause of this absence of a difference relates to the low uptake of mental self-translocation (MS-TL) by participants in the OBT task group. The self-report data strongly suggests that the OBT task was not a valid means of engaging MS-TL. Therefore, performance on it was probably no more vulnerable to aberrant space-motion information than performance on the Transpose task. Additional mediation analyses did not reveal an indirect effect of the mediator variable - COP velocity - on cognitive task performance, possibly due to an inadequate sample size. An important next step for this research is to identify or develop spatial perspective-taking and comparison tasks with clearer differences in demands for MS-TL and, thus, for space-motion information.

Chapter 5. Study 2:
The validation of a new spatial perspective-taking task

5.1 Abstract

Purpose:

The limitations of the OBT and Transpose tasks mean that these are unsuitable for inclusion in further research to determine whether balance disorders, and the aberrant space-motion information they entail, can directly affect higher cognition. New spatial perspective-taking (the 'Single Avatar Stimulus Set' [SASS] task) and control (the 'Single Object Stimulus Set' [SOSS] task and the 'Double Avatar Stimulus Set' [DASS] task) tasks were developed. The primary objectives of this study were to determine the validity of the SASS task as a means of evoking mental self-translocation (MS-TL), and to establish whether the SOSS and DASS tasks might have a comparable cognitive load, without evoking MS-TL.

Methods:

Fifty healthy participants were randomised into independent task groups. All three cognitive tasks were administered in two-minute trial blocks, four times in a row, without exposure to aberrant space-motion stimulation. The seated participants completed baseline measures of cognitive style and processing speed prior to the trial blocks. Afterwards, they performed established paper-and-pencil tests of mental self-translocation and mental object rotation.

Results:

Data pertaining to stimuli rotated by 90º to the right and left were excluded from analyses due to response inconsistencies during the SOSS task. On the SASS and SOSS tasks, there was an increase in participants' response times as the orientation of the tasks' stimuli increased from 45 to 135º. Only on the SASS task was there a further increase in response latency as the angular disparity increased again to 180º. The SASS task was associated

with reports of a mental self-translocation strategy, whereas the SOSS task was linked to reports of a rote strategy. On the DASS task, performance monotonicity was observed across larger orientation disparities. This was more challenging than the SASS and SOSS tasks.

Discussion:
Differing performance patterns on the SASS and SOSS tasks indicate that the response time monotonicity obtained from the former may be a signature of mental self-translocation, which makes the SASS task a valid spatial perspective-taking (SPT) task for the purposes of this research project. The three tasks appear to be underpinned by dissimilar cognitive processes, which may mean comparisons between the tasks when performed during aberrant stimulation may be informative. As such, they are suitable for inclusion in the ongoing research.

5.2 Introduction

The potential for further research to determine whether balance disorders, and the aberrant space-motion information they entail, can directly affect higher cognition rested on identifying or developing alternate spatial perspective-taking (SPT) and comparison tasks. Moreover, performance of these tasks would ideally vary by degree of susceptibility to aberrant information about the temporo-spatial activity of the whole body. To augment such variability, the new SPT task would need to evoke mental self-translocation (MS-TL) more consistently than the OBT task appears to have done in Study 1. That is, the new SPT task would need to be a valid means of eliciting MS-TL. Theoretically, SPT tasks with three-dimensional (3-D) avatars rotated incrementally in yaw have relatively strong validity (see section 1.7.1.3). According to the internal model formulation, MS-TL is instigated when an observer conceives a new position to mentally adopt (see section 1.6.2). The newly visualised position represents a goal state. It is compared with the observer's current state (i.e. a mental representation of his or her of self-location), and the sensorimotor circuitry for whole-body movement is activated if there is a discrepancy. Compared to the OBT and similar 2-D tasks, 3-D SPT tasks likely engender many more goal states because the on-screen orientation of the avatar is more varied. The more goal states a task engenders, the greater the uptake of MS-TL might be by participants seeking to optimise the efficiency and accuracy of their laterality judgements. Relatedly, greater variation of the on-screen orientation of the avatar may deter participants from identifying and/or adopting a rote strategy such as the ‘flipping’ tactic declared by many participants in the OBT task group (see sections 4.4.2 and 4.5.2). Imagining taking the perspectives of conspecifics in various angles of turn is commonplace for humans (Gardner, Stent, Mohr, & Golding, 2017). Hence, the numerous yawing goal states probably inherent in 3-D SPT tasks may also be advantageous in terms of the tasks’ ecological validity. In addition, the stronger humanoid aesthetic that 3-D avatars typically have might facilitate MS-TL engagement.

A variety of 3-D SPT tasks have been employed in published research (see Kessler & Thomson, 2010; Michelon & Zacks, 2006; Surtees, Apperly, & Samson, 2013; Tadi, Overney, & Blanke, 2009; van Elk & Blanke, 2014). However, no spatial control tasks, with equivalent stimulus-response compatibility, are conspicuous in this literature. As such, a new 3-D SPT task (the ‘Single Avatar Stimulus Set’ or SASS task) and a new version of the Transpose task (the ‘Single Object Stimulus Set’ or SOSS task) were developed. The design process and the detail of the new tasks’ stimulus material are described in Appendix B. To guard against the possibility that choice-reaction time tasks, like the Transpose and SOSS tasks, are susceptible to aberrant space-motion information (see section 4.5.2), a new mental object rotation (MOR) task was also developed. As discussed in section 1.8.2, MOR is hypothesised to be less dependent than MS-TL on space-motion information. On that basis, performance on the new MOR task, hereafter referred to as the ‘Double Avatar Stimulus Set’ or DASS task (see Appendix B), is predicted to be less vulnerable to misinformation than performance on the SASS and possibly the SOSS tasks.

One of the primary objectives of the present study was to validate the SASS task; that is, to determine whether it might be underpinned by MS-TL and not just by non-transformational cognitive processes. A related objective was to establish whether the SOSS and DASS tasks might elicit different cognitive processes with varying susceptibilities to aberrant space-motion information and, thereby, serve as useful comparison tasks in future research. In line with the results of previous studies, which employed 3-D SPT tasks (e.g. Kessler & Thomson, 2010; Surtees et al., 2013; Tadi et al., 2009; van Elk & Blanke, 2014), it was predicted that the SASS task would yield a monotonic RT function. Based on the theoretical perspective adopted throughout this thesis and conspicuous in the first paragraph of this section, response monotonicity would be a signature of MS-TL and, therefore, would validate the SASS task. However, there are other accounts for what the monotonic RT function might imply about the underlying cognitive process(es).

According to May and Wendt's (2013) 'spatial compatibility' account, the performance monotonicity associated with 3-D tasks, which display avatars in incremental yawing orientations, may be due to "graded compatibility effects" (May & Wendt, 2013, p. 2). That is, progressively large disparities between the avatar's and observer's orientations do not engender longer mental self-rotation times. Rather, they simply incur systematically greater non-transformational costs associated with changing spatial compatibility (see section 1.7.2). If this is the case, one would predict monotonic response times on the SOSS task, as well as on the SASS task. The present study was the first to test this prediction empirically. Just a single increase in RT on the SOSS task, as the on-screen stimulus (i.e. the measuring scale - see Appendix B and section 5.3.2) transitioned from rear- to front-facing, would suggest that response monotonicity on the SASS task is dissociable from spatial compatibility costs.

The 'mental object rotation' or 'MOR' account by May and Wendt (2013) implies that monotonic RT functions on 3-D SPT tasks could stem from imaginary manipulations of the avatar's rather than the observer's orientation. This account might be distinguishable from the 'standard' account, on which this thesis is largely based (i.e. the MS-TL-based account of response monotonicity), by the degrees to which the SASS and DASS tasks are disrupted during aberrant space-motion stimulation in future studies. It is generally accepted that MOR tasks, like the DASS task, elicit imaginary transformations of the target stimulus, and that performance monotonicity on these tasks is not underpinned by spatial compatibility or other non-transformational costs (e.g. Kessler & Thomson, 2010). Indeed, the DASS task was expected to yield a monotonic RT function across all of the contiguous angular disparities between the two on-screen avatars (see section 1.8.3 for further rationale).

With reference to the objectives documented above, the present study was designed:

- To determine the relative monotonicity of response times and error proportions on the new cognitive tasks,

- To ascertain whether the particular task that was performed influenced the type of cognitive strategy that was adopted,
- To correlate task performance variables with outcomes on measures with established dependences on MS-TL and MOR, and,
- To compare the cognitive loads of the new tasks.

Participants were not exposed to aberrant space-motion stimulation in this study, so that performance on the tasks could be evaluated and compared under stable sensory conditions.

5.3 Methods

5.3.1 Ethical considerations and recruitment

Full details of the ethical considerations and recruitment procedures are given in section 3.3. The eligibility criteria were altered for this study, mainly given that participants were not at risk of imbalance. Specifically, pregnancy was not an exclusion criterion. However, participants who were aware that they were colour blind were not eligible, because of the need to judge the colours of the scale pans depicted in the three new tasks.

The aim had been to recruit at least sixteen participants per task group. This number was based on the sample sizes of the studies by Tadi et al. (2009) ($N = 14$) and van Elk and Blanke (2014) ($N = 18$). Both of these studies specifically looked at patterns of performance on 3-D SPT tasks, and both obtained monotonic RT functions from their samples.

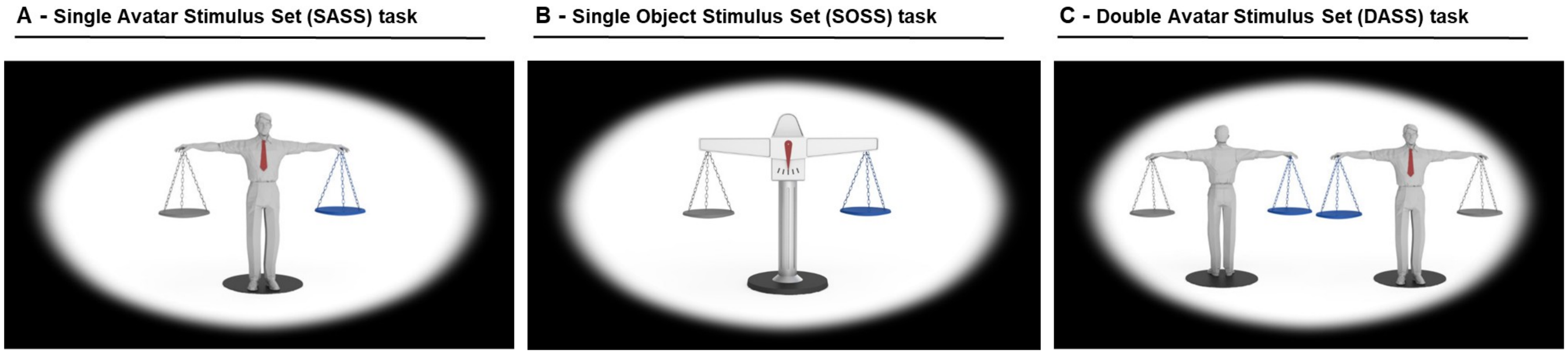
5.3.2 Cognitive tasks

Participants were randomly allocated to undertake either the SASS, SOSS or DASS tasks. All of the tasks were implemented using the E-Prime 2.0 experiment generator software (Schneider, Eschman, & Zuccolotto, 2002), running in the Windows 7 environment (Microsoft, Redmond, WA, USA) on a desktop computer (Dell, Round Rock, TX, USA). Participants were seated so that their eyes were 60 cm away from, but centrally aligned with, the computer's 22 inch screen. The response devices were two computer mice (see section 3.5), which the participants rested on their laps. While they undertook their allocated tasks, the lights in the windowless laboratory were turned off.

During the SASS task, the participants were recurrently presented with a single, 3-D, male avatar. As described in Appendix B, the avatar was completely grey in colour except for the red tie draped over its chest. It was always in an erect pose with its arms abducted. A grey and a blue scale pan dangled from its hands. The avatar appeared at random in any one of eight orientations in yaw (0º [rear-facing], 180º [front-facing], or turned by 45, 90 or 135º to the right or left). The blue scale pan was either in its left or right hand. Therefore, there were 16 permutations of the avatar's on-screen appearance. The participants randomised to undertake the SASS task were instructed to imagine themselves in the avatar's body position each time it appeared, in order to judge whether it held the blue pan in its left or right hand. Participants had to register their laterality judgements by tapping the mouse button with their corresponding index finger (see section 3.5). As with the OBT task, the correct response was ipsilateral (i.e. compatible) with the on-screen location of the blue scale pan when the avatar was fully or partially rear-facing, but contralateral (i.e. incompatible) with the location of the blue pan for fully or partially front-facing stimuli. When the avatar appeared side-on (i.e. turned to the right or left by 90º) there was not such a clear spatial mapping between the blue pan and the correct response.

The stimulus material presented during trials of the SOSS task comprised a measuring scale (see Appendix B for details). The on-screen dimensions of the scale were very similar to those of the male avatar presented during trials of the SASS task. It had a roughly cylindrical, vertical supporting strut and a cross beam which corresponded with the male avatar's abducted arms. The grey colouration of the measuring scale matched the avatar's. In place of the red tie was a red pointer at the upper aspect of the vertical strut. This helped to dissociate the front from the rear of the measuring scale. As with the male avatar, a grey and a blue scale pan dangled from each end of the scale's cross beam. The measuring scale was recurrently shown in any one of eight yawing orientations (0º [rear-facing], 180º [front-facing], or turned by 45, 90 or 135º to the right or left). The blue scale pan was suspended from either the left or right tip of the measuring scale's cross-beam. This made for 16 permutations of the scale's on-screen appearance. Participants allotted to the SOSS task group were instructed to click ipsilaterally to the on-screen location of the blue pan whenever the measuring scale was rear-facing; that is, when its red pointer was not showing. However, for front-facing stimuli, which were conspicuous due to the red pointer, participants were instructed to transpose or cross their response and, thereby, click contralaterally to the location of the blue pan. Hence, the spatial mappings of the SOSS task were of equivalent compatibility to those of the SASS task, but the participants who undertook the former did not need to engage in MS-TL. When the measuring scale appeared side-on (i.e. turned to the right or left by 90º), the instructions participants were given became inapplicable. They were simply told to develop their own solution to the laterality problem in these instances.

During the DASS task, the participants repeatedly viewed two male avatars shown side-by-side. As described in Appendix B, the position of the left avatar was invariant from trial-to-trial. The avatar on the right was rendered in eight yawing increments from 0º (rear-facing) to 180º (front-facing), through 45, 90 and 135º turns to the right and left, just as the avatar in the SASS task and the measuring scale in the SOSS task were. The blue scale pan was held either in its left or right hand. Again, there were 16 permutations of the stimulus material for this task. The participants randomly allocated to perform the DASS task were instructed to imagine rotating one of the avatars into the other's position, if their positions were different when they appeared on-screen, in order to judge whether they held the blue pan in the same or different hand. Participants had to click with their right and left index fingers if they judged that the avatars held the blue pan in the same or different hand, respectively. Although the spatial mappings of the DASS task were similar to those of the SASS and SOSS tasks, it was expected that the DASS task would be the most challenging. Mental object rotation tasks have been consistently reported to be more difficult, denoted by participants' slower responses and lesser accuracy, than SPT tasks (Creem-Regehr & Kunz, 2010; Kessler & Thomson, 2010; Preuss, Harris, & Mast, 2013; see section 1.8.4). Figure 5.1 presents sample stimulus material from the SASS, SOSS and DASS tasks.



'Left' - necessitating a left mouse click

'Left' - necessitating a left mouse click

'Same' - necessitating a left mouse click

Figure 5.1: Sample stimuli presented during the Single Avatar Stimulus Set (SASS) task [A], the Single Object Stimulus Set (SOSS) task [B] and the Double Avatar Stimulus Set (DASS) task [C].

Appropriate responses are shown beneath each stimulus. More complete sets of stimuli, plus ‘right’ responses, are given in Figure B.1 in Appendix B.

For all tasks, each trial commenced with the presentation of a black fixation cross, followed by the stimulus, and then visual feedback about whether the response was correct or incorrect. The durations of each of these trial elements are given in section 4.3.3. All elements were centred within an oval, white surround. The perimeter of this surround was smudged into a black outer border. Examples of correct responses for the tasks' stimuli are shown in Figure B.1 in Appendix B. Further details about the number of trial blocks completed by the participants can be found in the Experimental Procedure below (see section 5.3.6).

5.3.3 Cognitive style and processing speed measures

Before undertaking their allotted tasks, participants' cognitive style and ability were evaluated by way of two measures. At the end of study recruitment, scores on these measures were compared across task groups in order to check that they comprised participants with a similar distribution of baseline cognitive functioning.

5.3.3.1 Object-Spatial Imagery and Verbal Questionnaire (OSIVQ)

The OSIVQ is a self-report measure that was developed by Blazhenkova and Kozhevnikov (2008) to assess individual differences in information processing, based on the object-spatial-verbal theoretical model of cognitive style (Kozhevnikov, Kosslyn, & Shephard, 2005). Accordingly, object visualizers (or imagers) are individuals who prefer to construct vivid images of individual objects and to rely on visual-object strategies. In contrast, spatial visualizers favour schematic representations of the spatial relations of objects, and tend to adopt visual-spatial strategies. There are also verbalizers, who do not use imagery quite as much when performing cognitive tasks. Instead, they prefer to process and represent information verbally, and tend to rely on non-visual strategies. The OSIVQ comprises 45 items which are divided equally between object, spatial and verbal scales. Respondents rate each item on a five-point Likert scale ranging from 1 (totally disagree) to 5 (totally agree). Individual scale scores are found by averaging the scores on the corresponding 15 items.

The object, spatial and verbal scales have all demonstrated acceptable internal consistency (Cronbach's alpha coefficients greater than .74 for all three scales) and three-week test-retest reliability (correlation coefficients greater than .73 for the scales) (Blazhenkova &

Kozhevnikov, 2008). The developers of the OSIVQ suggest the following cut-offs: scores between 3 and 4.2 on the object scale indicate an average preference for object imagery; scores between 2 and 3.2 on the spatial scale suggest an average tendency for spatial imagery, and; scores between 2.4 and 3.3 on the verbal scale imply an average preference for verbal information processing. Scores above or below these cut-offs indicate that respondents have high or low preferences for the respective cognitive styles (Blazhenkova and Kozhevnikov, 2008).

5.3.3.2 Zahlenverbindungstest (ZVT)

Participants' cognitive processing speed was assessed using the ZVT or Number Connection Test (Oswald & Roth, 1978). This paper and pencil test comprises a ten by nine matrix filled with the numbers 1 to 90, which are arranged in a pseudo-random order. Based on one of the methods employed by Vernon (1993), participants in the present study were given 45 s to connect the numbers in ascending order. Their scores were the highest correct number that they were able to reach in that time. The three-day test-retest reliability of this form of the ZVT has been shown to be very good ($r = .86$). It has also been found to share almost 50% of the variance in Intelligence Quotient scores (Vernon, 1993). The participants practised on a smaller, five by six number matrix with no time limit, before completing the ZVT proper.

5.3.4 Strategy measure

Once participants had completed all four blocks of their cognitive task, they were asked about the strategies they had used in order to make the necessary laterality judgements. Based on van Elk and Blanke's (2014) method of ascertaining strategy-related information, the participants in the present study were asked to declare which of the following three strategies they used the most: I imagined rotating my body when judging the positions of the blue pan, I imagined rotating the figure/image when judging the positions of the blue pan, or, I used a transposing strategy, and switched which mouse I pressed when certain features were on screen. If participants were uncertain about how to respond, they were asked for further free text comments about their strategies. Descriptive data relating to the strategies the participants adopted will be presented as part of the construct validity analyses (see sections 5.3.11.1.2 and 5.4.3.2).

5.3.5 Criterion measures

In order to be able to test the convergent and divergent validity of the SASS task primarily, participants were administered with two paper and pencil tests at the end of the experimental schedule. These criterion measures are similar to those employed by Zacks et al. (2002) for the purpose of validating a SPT task comprising avatars tilted in roll.

5.3.5.1 Modified Mental Rotations Test (mMRT)

In line with Blazhenkova and Kozhevnikov (2008), a 10-item version of the Mental Rotations Test (Vandenberg & Kuse, 1978) was given to all participants. Each of the items on the mMRT comprises a row of five line-drawn shapes. More specifically, the 2-D drawings are of 3-D polygons composed of 10 joined-up cubes. The shape on the very left-hand-side of each row serves as the ‘standard’ or target. Participants have to decide whether each of the ‘comparison’ shapes to the right is the same as, or different to, the target. Essentially, participants must work out whether the target and comparison shapes have rotational symmetry, in which case they are the same, or mirror symmetry, in which case they are different. Two of the comparison shapes on each row are always rotated versions of the target shape, while the other two comparison shapes are rotated mirror images of the target. Participants are only requested to highlight the former on the test sheet. In the present study, participants were given five minutes to complete all 10 items. Two credits were awarded per item if both of the rotated versions of the target shape had been correctly identified. One credit was awarded if only one comparison shape had been chosen, and it was correct. To control for guessing, no credits were awarded if two shapes had been highlighted but only one was correct. The total mMRT score was calculated by summing all of the credits. Vandenberg and Kuse (1978) found that the MRT displayed very good internal consistency (Kuder-Richardson 20 = .88) and test-retest reliability (r = .83).

5.3.5.2 Modified Standardized Road-Map Test of Direction Sense (mSRMTDS)

In Money and colleagues’ (1965) SRMTDS, participants trace along a dotted line with a pencil. The dotted line comprises straight sections interspersed by a mixture of acute, right-angled and obtuse turns. The dotted line zigzags through geometric shapes and, therefore, bears some resemblance to a pathway through a grid-based city. Participants are instructed to imagine that they are following the pathway through the city as they are tracing along the dotted line. They have to state the direction taken at each turn. Therefore, the test requires participants to continually update their imagined egocentric perspective (Vingerhoets, Lannoo, & Bauwens, 1996; Zacks et al., 2002). In the present study, participants were given 20 s to trace as far along the dotted line as they could. Zacks et al. (2002) claim that making the test speeded in this manner increases its sensitivity to the perspective-taking abilities of healthy adults. There are, however, no available psychometric data on this modified version of the test. The mSRMTDS score was calculated in the present study by summing the total number of correct turns each participant specified. The test was preceded by a demonstration, during which the researcher traced along a shorter pathway in the corner of the grid.

5.3.6 Experimental procedure

The experimental procedure was based on that detailed in section 3.10. Once participants had provided their written consent and specified their dominant upper limb, they completed the OSIVQ and the ZVT (see section 5.3.3). They were then randomly allocated to undertake either the SASS, SOSS or DASS task. They received a slide-based briefing on the task and subsequently practised it. The practice block comprised two presentations of each of the SASS, SOSS or DASS tasks' 16 stimuli (see section 5.3.2). Participants were under instruction to respond as quickly but as accurately as possible. Following the practice block, the participants undertook four, two-minute experimental blocks. Each block was separated by a one-minute rest break, during which the laboratory lights were turned on.

Once all of the experimental blocks had been completed, participants answered the strategy question (see section 5.3.4), and then undertook the mMRT (see section 5.3.5.1). After a short break, they embarked on the mSRMTDS (see section 5.3.5.2). In total, the procedure took approximately 45 minutes.

5.3.7 Variables

The variables incorporated into this study are similar to those listed in section 3.11. However, some clarifications are required as follows.

5.3.7.1 Independent variables

The independent variables (IVs) varied by analytical procedure and, therefore, will be covered in the section detailing the statistical analyses below (see section 5.3.11).

5.3.7.2 Dependent variables

DVs were categorised as primary or secondary outcome variables.

5.3.7.2.1 Primary, task-related outcome variables

As detailed in section 3.11.2.1.

5.3.7.2.2 Secondary outcome variables

The secondary outcome variables derived from the range of self-report and performance-based instruments that were employed in this study. They included strategy responses, and mMRT and mSRMTDS scores.

5.3.8 Reduction of bias

As detailed in section 3.13.

5.3.9 Comparisons of baseline characteristics

Scores on the OSIVQ and ZVT were compared across the three groups by subjecting respective data to one-way ANOVAs, where 'task' was the between-subjects factor.

5.3.10 General descriptives

Means were calculated for data representing the primary, task-related variables to aid preliminary data inspection. Further details are given in section 5.4.2.

5.3.11 Principal statistical analyses

The principal inferential treatments of the data were distinguishable as either construct validity analyses, criterion validity analyses or complexity analyses. The former analytical procedures were the most important, in view of the primary objectives that were set for this study (see section 5.2). Each group of procedures are detailed in turn below.

To protect against Type I error, the chances of which may have otherwise been heightened by the multiple analytical procedures, Bonferroni correction was applied by dividing the alpha level (.05) by three. This number was selected on the basis that there were three principle groupings of inferential treatments of the data (validity analyses, criterion validity analyses and complexity analyses). Hence, the alpha was adjusted to $p \leq .017$. Values from .017 up to and including .025 were considered to be borderline significant. Probability values greater than .025 were deemed to be non-significant.

5.3.11.1 Construct validity analyses

There is no accepted procedure for establishing the construct validity of SPT or other mental spatial transformation tasks. The theoretical perspective adopted throughout this thesis implies that the evocation of a monotonic RT function is an important prediction of the internal model formulation of MS-TL (see sections 1.7 and 5.2) and, therefore, SPT tasks must yield this function to be valid. In Study 1, a monotonic RT function was not discernible because the OBT task only presents its avatar in two orientations. It was not possible, therefore, to discern the linearity of the relationship between avatar orientation and response variables, and this compounded doubts about whether the OBT task was valid. Those doubts were raised by the low rate of engagement in MS-TL reported by participants who undertook the OBT task. It follows that the construct validity of the SASS task should be based on whether it yields monotonic response functions and induces the majority of participants to engage in MS-TL then report that they did so. Analyses of performance monotonicity and strategy were conducted accordingly. Data from the SOSS and DASS tasks were also subjected to these analyses for reference and comparison.

5.3.11.1.1 Analyses of performance monotonicity

Establishing whether performance on the tasks had monotonic characteristics required two stages of analyses, which only incorporated the behavioural variables (response time and error proportion; see section 3.11.2.1.1). Initially, data representing these variables from all tasks were binned according to whether the on-screen stimulus had been turned to the right or left by 45, 90 or 135°. Paired t-tests were employed to investigate the effect of the 'direction of rotation' factor on data for corresponding angles of stimulus rotation to the right and left. This stage of the analyses checked if the SASS and DASS tasks had evoked imaginary rotations along the shortest possible path, and if the spatial mappings required by the SOSS task were consistent.

After screening for a direction of rotation effect, it was possible to collapse this factor, and analyse whether monotonic values for the behavioural variables had been obtained as the angular disparity between the observer and on-screen image (as for the SASS and SOSS tasks), or between the two avatars (as for the DASS task), had incrementally increased from 0 to 180º. A one-way repeated measures ANOVA, where angular disparity (0 vs 45 vs 135 vs 180º) was the within-subject factor, was conducted based on data from all three task groups (i.e. three ANOVAs in total). The reason why 90º was not included as a category or level for this factor will be explained in the Results (see section 5.4.3.1). The ANOVAs were followed-up initially by repeated contrasts so that each level of the angular disparity factor (except 0º) was compared to the previous level. More than one significant contrast, between data points relating to response time or error proportion, would be necessary for a task to demonstrate monotonicity across at least a confined range of angular disparities. One significant contrast would be insufficient to imply monotonicity, since this could simply relate to greater costs associated with incompatible versus compatible responses (see section 5.2 for clarification). The repeated measures ANOVAs were also followed-up by three, mixed two-way ANOVAs. For each of these, task (SASS vs SOSS task) was the between-subjects factor. Contiguous angular disparities constituted the within-subjects factors (ANOVA 1: 0 vs 45º, ANOVA 2: 45 vs 135º, ANOVA 3:135 vs 180º). A significant interaction between task and contiguous angular disparity would imply a task-related difference in performance monotonicity and, therefore, might dissociate transformational performance costs associated with MS-TL from spatial compatibility costs.

5.3.11.1.2 Analyses of performance strategy

Descriptive data relating to the strategies the participants adopted were calculated. More specifically, the number of participants, who reported using one of the three listed strategies (see section 5.3.4), was converted to a percentage of the total number of participants in the respective group. These data were then subjected to a Pearson's chi-square test to determine whether the task, which the participants performed, influenced the type of cognitive strategy they adopted.

5.3.11.2 Criterion validity analyses

The convergent and divergent validities of the SASS task were evaluated, in line with the methods of Zacks et al. (2002) and Blazhenkova and Kozhevnikov (2008), by correlating data for behavioural (response time and error proportion) and mechanistic (drift rate, boundary separation and non-decision time) variables against scores on the mSRMTDS and mMRT. Bivariate correlations were also calculated in a similar manner using data derived from the SOSS and DASS task groups. It was expected that the data from the SASS task would correlate with scores on the mSRMTDS but not with scores on the mMRT. In contrast, it was expected that performance on the DASS task would converge with ability on the mMRT but diverge with performance on the mSRMTDS. No correlations between SOSS task performance and scores on the two criterion measures were predicted. These contrasting patterns of predicted correlations were tested by comparing the coefficients from corresponding bivariate correlations using an on-line calculator based on the Fisher *r*-to-*z* transformation (Lowry, 2001).

5.3.11.3 Complexity analyses

The complexity of the SASS task was evaluated by way of two discrete sets of analyses as follows.

5.3.11.3.1 Comparisons of the three-dimensional tasks

The most important set of complexity analyses determined whether the SASS and SOSS tasks were equally challenging; that is, whether they yielded similar data for the behavioural and mechanistic variables. The data for the five variables were subjected to separate one-way ANOVAs, where task was the between-subject factor with three levels (SASS task vs SOSS task vs DASS task) and the angular disparity factor was collapsed. The Bonferroni post hoc procedure was selected for pairwise comparisons.

5.3.11.3.2 Comparisons of the spatial perspective-taking tasks

The complexity of the SASS task was also compared to that of the OBT task; the SPT task employed in Study 1. This was done in case of contrasting effects of optokinetic stimulation on SASS task performance in a future empirical study. Data pertaining to each of the primary, task-related variables obtained during the practice trial block for both cognitive tasks were individually subjected to independent t-tests.

5.4 Results

5.4.1 Participants and comparisons of their baseline characteristics

In total, 50 participants took part in this study, having met the eligibility criteria and provided written informed consent. Sixteen participants were randomly allocated to the SASS task group, and 17 were randomised to both the SOSS and DASS task groups. The proportion of errors participants in the three groups made across all four experimental blocks was low *(M* = 6.87%, *SD* = 6.16%). However, one participant in each group demonstrated particularly high cumulative error compared to other members of their groups. More specifically, their error proportions were more than 1.96 standard deviations greater than the mean proportions for their groups. All data for these three participants were excluded from the analyses given that their task performance was atypical, and in the attempt to reduce bias (see section 3.13.1). Therefore, the data that were analysed related to 15 SASS task group participants, 16 SOSS task group members and 16 participants in the DASS task group.

The mean age of the 47 remaining participants was 20.8 years (*SD* = 3.9 years). There were no between-group differences in age according to a one-way ANOVA. There were 36 (76.6%) female participants, 10 of whom had been allocated to the SASS task group. Thirteen females were in both the SOSS and DASS task groups. Eight (17.0%) of the participants were left-handed. Three completed the SASS task and two undertook the SOSS task. The remaining three left-handed participants were in the DASS task group. All participants were psychology students; three were postgraduate students and the remainder undergraduates. Two of the postgraduate students had been randomly allocated to the DASS task group. The other completed the SOSS task. Sample mean scores on the object, spatial and verbal scales of the OSIVQ were 3.5 (*SD* = 0.6), 3.2 (*SD* = 0.5) and 2.8 (*SD* = 0.5), respectively. These scores indicate that the sample comprised participants who were ‘average object visualisers’, ‘high spatial visualisers’ and ‘average verbalisers’. One-way ANOVAs indicated there were no between-group differences in scores on any of the OSIVQ scales. The mean ZVT score for all participants was 61.1 (*SD* = 12.8). As for data pertaining to demographics and cognitive styles, there was no between-group difference in ZVT score, implying that participants in the three task groups had similar distributions of cognitive processing speeds.

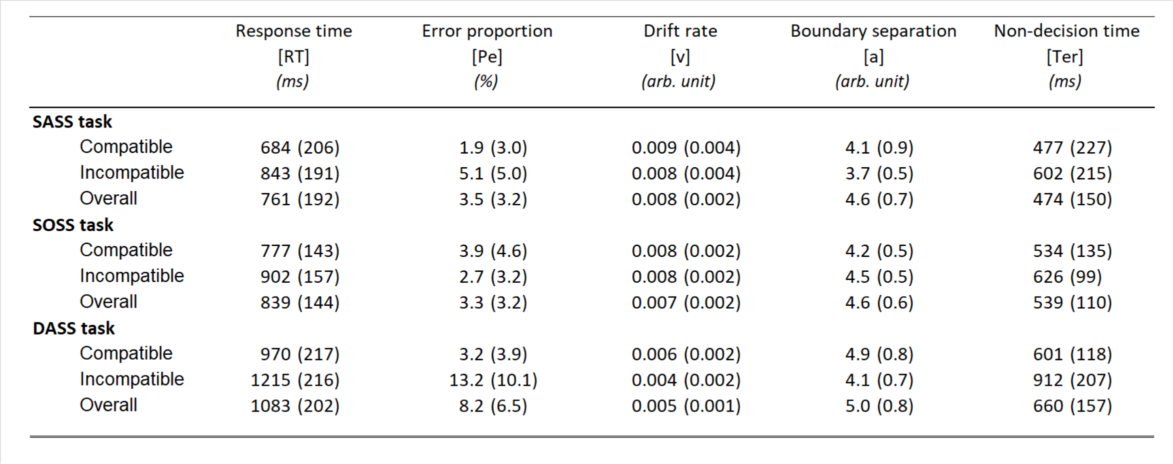
5.4.2 General descriptives

The data for behavioural (RT and error proportion) and mechanistic variables (drift rate, boundary separation and non-decision time) were binned according to task and whether they derived from trials which had required a spatially compatible (i.e. ipsilateral) or incompatible (i.e. contralateral) manual response. This meant excluding data pertaining to stimuli wherein the avatar or object was turned by 90º. Means were computed and inspected. These data are summarised in Table 5.1, which appears to indicate responses of similar efficiency were made during the SASS and SOSS tasks. As expected, the DASS task appears to have been the most challenging. Spatially incompatible responses on all three tasks seem to have been less efficient than compatible responses made during the respective tasks, which was also a predicted pattern of performance.

Table 5.1: Data for behavioural (RT and P_e) and mechanistic (v, a and Ter) variables categorised according to task and compatibility of the stimulus-response mapping.

Overall data values are also given (i.e. with the compatibility factor collapsed). All data are mean values with standard deviations in parentheses.

SASS - Single Avatar Stimulus Set task; SOSS - Single Object Stimulus Set task; DASS - Double Avatar Stimulus Set task



	Response time [RT] *(ms)*	Error proportion [Pe] *(%)*	Drift rate [v] *(arb. unit)*	Boundary separation [a] *(arb. unit)*	Non-decision time [Ter] *(ms)*
SASS task					
Compatible	684 (206)	1.9 (3.0)	0.009 (0.004)	4.1 (0.9)	477 (227)
Incompatible	843 (191)	5.1 (5.0)	0.008 (0.004)	3.7 (0.5)	602 (215)
Overall	761 (192)	3.5 (3.2)	0.008 (0.002)	4.6 (0.7)	474 (150)
SOSS task					
Compatible	777 (143)	3.9 (4.6)	0.008 (0.002)	4.2 (0.5)	534 (135)
Incompatible	902 (157)	2.7 (3.2)	0.008 (0.002)	4.5 (0.5)	626 (99)
Overall	839 (144)	3.3 (3.2)	0.007 (0.002)	4.6 (0.6)	539 (110)
DASS task					
Compatible	970 (217)	3.2 (3.9)	0.006 (0.002)	4.9 (0.8)	601 (118)
Incompatible	1215 (216)	13.2 (10.1)	0.004 (0.002)	4.1 (0.7)	912 (207)
Overall	1083 (202)	8.2 (6.5)	0.005 (0.001)	5.0 (0.8)	660 (157)

Across the four experimental trial blocks, participants in the SASS and SOSS task groups completed 130.7 (*SD* = 7.2) and 126.0 (*SD* = 6.5) trials, respectively. Those in the DASS task group undertook an average of 118.3 (*SD* = 8.0) trials. A one-way ANOVA, where task was the between-subjects factor, revealed a significant effect of task on total number of trials completed, *F(*2, 46) = 11.79, *p* < .001. The Bonferroni post hoc procedure detected significant pairwise differences between the DASS and SASS task groups (95% CI; -18.96 to -6.00) and between the DASS and SOSS task groups (95% CI; -14.12 to -1.38). These findings complement the data presented in Table 5.1 in that they imply the DASS task led to slower responses than the other tasks.

5.4.3 Construct validity analyses

5.4.3.1 Analyses of performance monotonicity

RT and error proportion data were resegregated according to the two levels of the ‘direction of rotation’ factor (leftward vs rightward stimulus rotations) and the following three levels of stimulus rotation: 45, 90 and 135°. These resegregated data are presented in figure 5.2.

Due to a software issue during experimentation, there were some missing response data for one participant in the SOSS task group, which is reflected in the degrees of freedom in the relevant t-test outputs. There was no effect of the direction of rotation factor on data obtained from the SASS and DASS tasks. However, for the SOSS task, RTs were significantly shorter when the measuring scale was turned by 90° to the right *(M* = 975 ms, *SD* = 281 ms) than to the left *(M* = 1066 ms, *SD* = 289 ms), *t*(14) = 3.36, *p* = .006, *r* = .668. The significant effect of the direction of rotation factor on these response data probably relates to the fact that participants in the SOSS task group were unable to apply the task’s spatial mapping instructions whenever the measuring scale was turned by 90° (see section 5.3.2). These data from the SOSS task, and equivalent data from the SASS and DASS tasks, were excluded from further analyses, as they might have confounded the interpretation of performance monotonicity. Consistent performance on all three tasks, when stimuli were presented with angular disparities of 45 and 135°, no matter the direction in which the stimuli were turned, meant it was possible to collapse the ‘direction of rotation’ factor following the data exclusion. RTs and error proportions for each task were then subjected to a one-way repeated measures ANOVA, where angular disparity (0 vs 45 vs 135 vs 180º) was the within-subject factor. Greenhouse-Geisser correction was applied in many instances, as is evident from some of the degrees of freedom reported below, due to problems with sphericity.

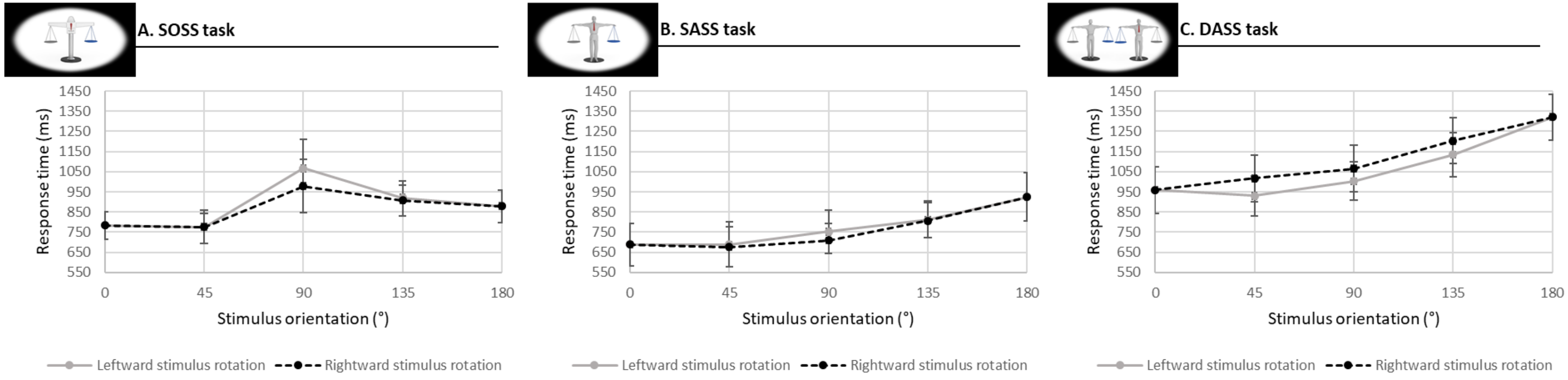


Figure 5.2: The relationship between stimulus orientation and response time as a function of the direction in which the stimulus was orientated.

Data are shown separately for the three cognitive tasks - SOSS [A], SASS [B] and DASS [C] tasks. Stimulus orientation refers to the disparity between task stimulus and the referent, which is the target stimulus in the case of the DASS task, but the participant's own orientation in the case of the SASS and SOSS tasks.

Regarding the SASS task, there was a significant effect of angular disparity on RT, *F*(1.8, 24.9) = 33.49, $p < .001$, η_p^2 = .705, and on error proportion, *F*(1.8, 25.6) = 5.74, $p = .010$, η_p^2 = .291. For RT, there were significant contrasts between two sets of contiguous angular disparities: 45 vs 135º, *F*(1, 14) = 22.43, $p < .001$, η_p^2 = .616, and; 135 vs 180º, *F*(1, 14) = 15.36, $p = .002$, η_p^2 = .523. There was no significant contrast between the remaining set of contiguous angular disparities: 0 vs 45º, *F*(1, 14) = .38, $p = .549$, η_p^2 = .026. For error proportion, there were no significant contrasts between sets of contiguous disparities. The RT results indicate that responses on the SASS task became progressively slower as the disparity between the participants and the avatar increased from 45 to 135 to 180º. This pattern of results is depicted in Figure 5.3.

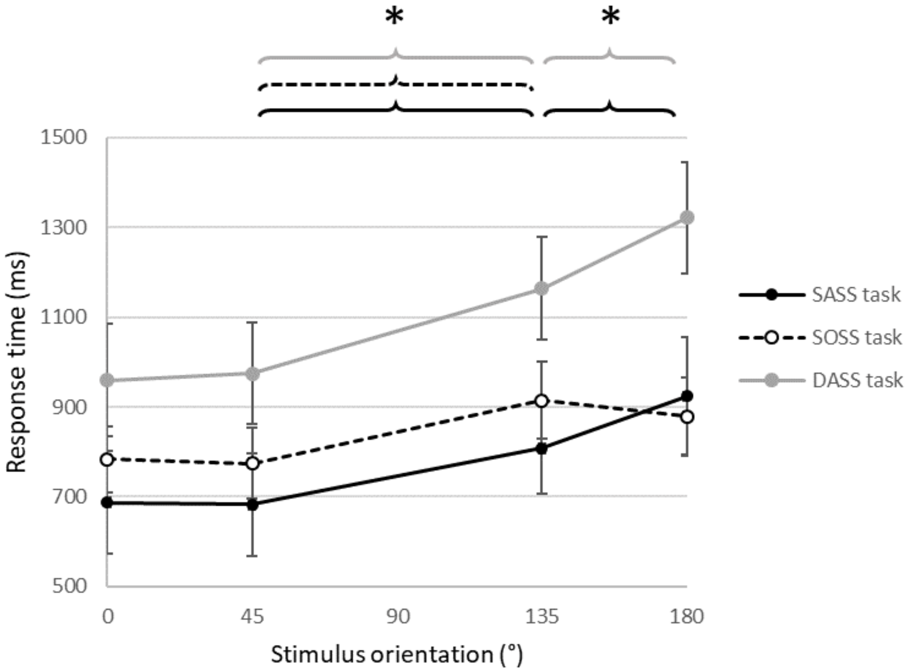


Figure 5.3: The relationship between stimulus orientation and response time as a function of cognitive task (SOSS, SASS or DASS task), with direction of stimulus rotation collapsed.

Regarding the SOSS task, there was a significant effect of angular disparity on RT, *F*(2.1, 31.5) = 17.97, $p < .001$, η_p^2 = .545, but not on error proportion. For RT, there was a significant contrast between one set of contiguous angular disparities: 45 vs 135º, *F*(1, 15) = 44.79, $p < .001$, η_p^2 = .749. There were no significant contrasts between the two other sets of contiguous angular disparities: 0 vs 45º, *F*(1, 15) = .47, $p = .504$, η_p^2 = .030, and;

135 vs 180º, $F(1, 15) = 2.34$, $p = .146$, $\eta_p^2 = .135$. For error proportion, there were no significant contrasts between sets of contiguous disparities. The one significant contrast within the RT data indicates that there was a single drop in response efficiency on the SOSS task as the disparity between the participants and the measuring scale increased from 45 to 135º (see Figure 5.3).

Finally, in relation to the DASS task, there was a significant effect of angular disparity on RT, $F(1.57, 23.5) = 52.56$, $p < .001$, $\eta_p^2 = .778$, and on error proportion, $F(3, 45) = 10.86$, $p < .001$, $\eta_p^2 = .420$. For RT, there were significant contrasts between two sets of contiguous angular disparities: 45 vs 135º, $F(1, 15) = 40.44$, $p < .001$, $\eta_p^2 = .729$, and; 135 vs 180º, $F(1, 15) = 45.89$, $p < .001$, $\eta_p^2 = .754$. There was no significant contrast between the remaining set of contiguous angular disparities: 0 vs 45º, $F(1, 15) = .53$, $p = .479$, $\eta_p^2 = .034$. For error proportion, there was only a significant contrast between one set of contiguous disparities: 45 vs 135º, $F(1, 15) =22.75$, $p < .001$, $\eta_p^2 = .603$. The results for this task indicate that responses on it became progressively less efficient as the angular disparity between the two avatars increased from 45 to 135 to 180º (see Figure 5.3).

A significant interaction was found in one of the three ANOVAs in which contiguous angular disparity and task (SASS task vs SOSS task) were the factors. This was on RT for the largest pair of angular disparities (135 vs 180º), $F(1, 29) = 16.58$, $p < .001$, $\eta_p^2 = .364$. This indicates that RT on the SASS task lengthened as the disparity between the participants and the on-screen stimulus increased from 135 to 180º, but RT on the SOSS task did not.

5.4.3.2 Analyses of performance strategy

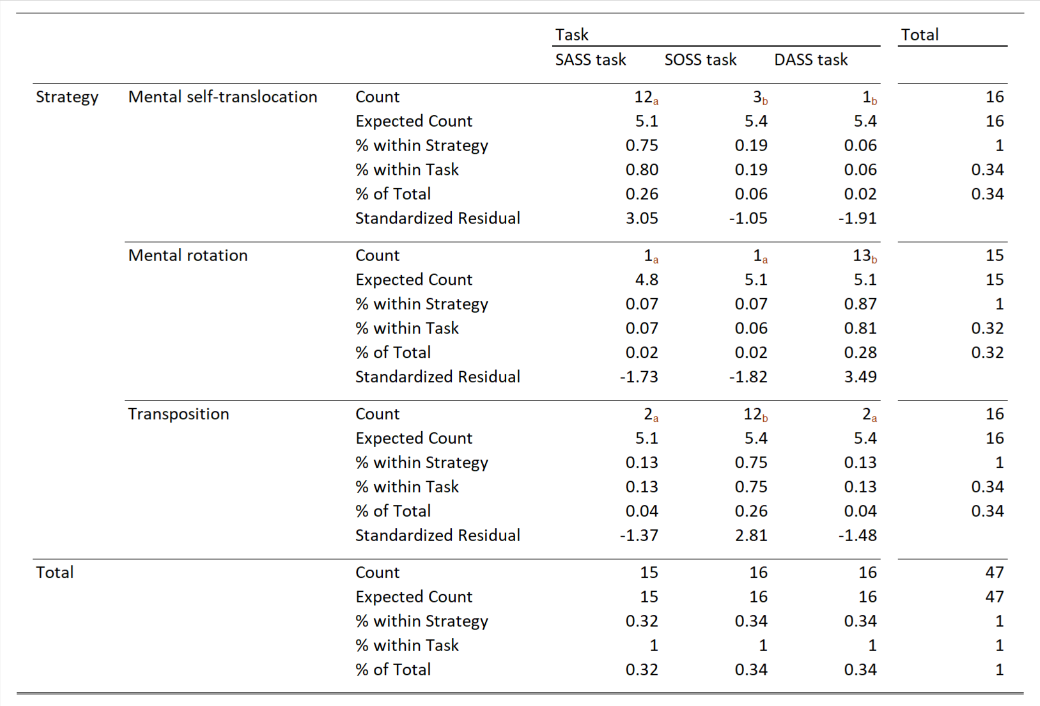
In the SASS task group, 12 (80%) of the 15 participants reported having solved the task by way of mental self-translocation (MS-TL). One participant indicated that she had imagined rotating the avatar into a more conducive position, rather than rotating her own perspective, in order to make the laterality judgements. That is, she adopted a mental rotation strategy. The two remaining participants stated that they had used the transposing strategy whereby they flipped left and right whenever the avatar was front-facing.

In the SOSS task group, 12 (75%) of the 16 participants reported having adopted the transposing strategy. Three (18.75%) of the group members reported that they had imagined themselves taking the measuring scale’s position before making their judgements. That is, they engaged in MS-TL. The remaining participant declared that she had mentally rotated the measuring scale.

Thirteen (81.25%) of the 16 participants in the DASS task group said that they adopted the mental rotation strategy. One reported having engaged in MS-TL, while the remaining two participants indicated that they had developed a transposing strategy, in order to make the same-different responses. All of these data are tabulated in Table 5.2.

Table 5.2: Contingency table showing how many members of each task group adopted each of the three cognitive strategies in order to make the required laterality judgements.

Adjacent columns with different subscripts indicate significantly different column proportions based on *z*-tests with Bonferroni correction. For example, the subscripts on the 'Mental self-translocation' strategy row indicate that the proportion of participants in the SASS task group who adopted that strategy was significantly different from the proportions who adopted the other strategies.



			Task			Total
			SASS task	SOSS task	DASS task	
Strategy	Mental self-translocation	Count	12_a	3_b	1_b	16
		Expected Count	5.1	5.4	5.4	16
		% within Strategy	0.75	0.19	0.06	1
		% within Task	0.80	0.19	0.06	0.34
		% of Total	0.26	0.06	0.02	0.34
		Standardized Residual	3.05	-1.05	-1.91	
	Mental rotation	Count	1_a	1_a	13_b	15
		Expected Count	4.8	5.1	5.1	15
		% within Strategy	0.07	0.07	0.87	1
		% within Task	0.07	0.06	0.81	0.32
		% of Total	0.02	0.02	0.28	0.32
		Standardized Residual	-1.73	-1.82	3.49	
	Transposition	Count	2_a	12_b	2_a	16
		Expected Count	5.1	5.4	5.4	16
		% within Strategy	0.13	0.75	0.13	1
		% within Task	0.13	0.75	0.13	0.34
		% of Total	0.04	0.26	0.04	0.34
		Standardized Residual	-1.37	2.81	-1.48	
Total		Count	15	16	16	47
		Expected Count	15	16	16	47
		% within Strategy	0.32	0.34	0.34	1
		% within Task	1	1	1	1
		% of Total	0.32	0.34	0.34	1

According to the chi-square test, there was a significant association between the task participants performed and the type of strategy they adopted, $\chi^2(4) = 44.49$, $p < .001$, $V = .688$.

5.4.4 Criterion validity analyses

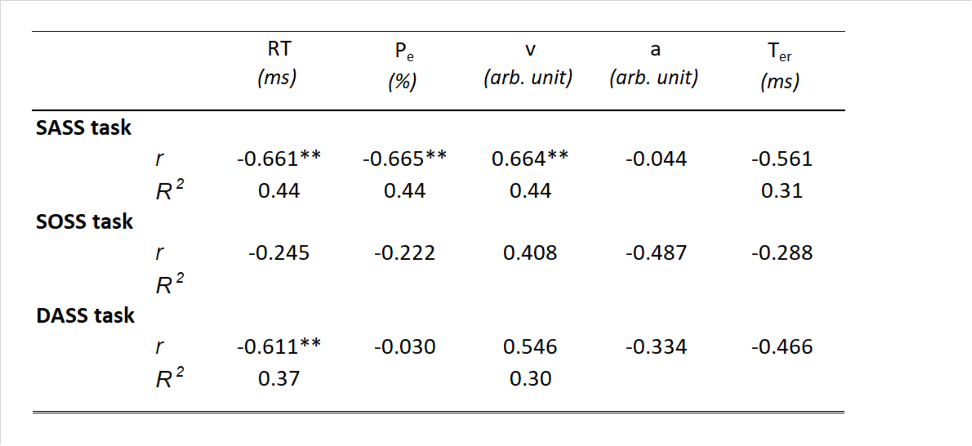
Criterion validity analyses incorporated data for the mechanistic variables (drift rate, boundary separation and non-decision time) as well as for the behavioural variables. Mechanistic variables were calculable for 41 of the 47 participants. The other six participants (one each in the SASS and DASS task groups, and four members of the SOSS task group) had maintained 100% accuracy throughout the experimental blocks, so their data could not be subjected to the EZ-diffusion model. All the data were entirely unsegregated for the criterion and complexity analyses (see section 5.4.5); that is, all factors included in the preceding analyses were collapsed. Those data for task stimuli turned by 90º to the left or right were still excluded.

Bivariate correlations showed that scores on the mSRMTDS, a test that requires participants to continually update their imaginary self-location, were significantly related to several performance variables derived from the SASS task, including RT, $p = .007$, error proportion, $p = .007$, and drift rate, $p = .010$. Correlation coefficients and coefficients of determination are given in Table 5.3, and the relationships between mSRMTDS scores and RTs are depicted graphically in Figure 5.4. These data indicate that higher achievement on the mSRMTDS was associated with better performance on the SASS task. There were no significant relationships between mMRT scores and SASS task performance variables.

Table 5.3: Correlation coefficients (r) and coefficients of determination (R^2) for bivariate correlations between scores on the modified Standardized Road-Map Test of Direction Sense and performance on the three cognitive tasks, according to behavioural (RT and P_e) and mechanistic (v, a and T_{er}) variables.

Note that R^2 values are only given for correlations with significant ($p \leq .017$) or borderline significant ($p \leq .025$) t-statistics.

* - Correlation is significant at the .025 level (2-tailed); ** - Correlation is significant at the .017 level (2-tailed); SASS - Single Avatar Stimulus Set task; SOSS - Single Object Stimulus Set task; DASS - Double Avatar Stimulus Set task; RT - Reponse time; P_e - Error proportion; v - Drift rate; a - Boundary separation; T_{er} - Non-decision time



		RT *(ms)*	P_e *(%)*	v *(arb. unit)*	a *(arb. unit)*	T_{er} *(ms)*
SASS task						
	r	-0.661**	-0.665**	0.664**	-0.044	-0.561
	R^2	0.44	0.44	0.44		0.31
SOSS task						
	r	-0.245	-0.222	0.408	-0.487	-0.288
	R^2					
DASS task						
	r	-0.611**	-0.030	0.546	-0.334	-0.466
	R^2	0.37		0.30		

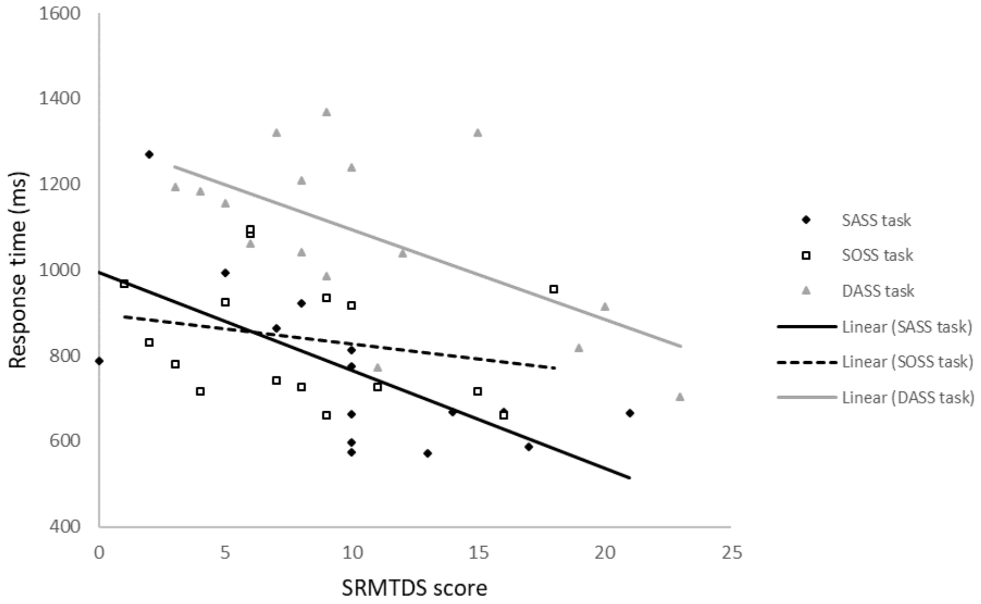


Figure 5.4: Scatterplot showing the relationships between scores on the modified Standardized Road-Map Test of Direction Sense and response times as a function of cognitive task.

There were no significant correlations between mSRMTDS or mMRT scores and outcomes on the SOSS task. With regard to the DASS task, scores on the mSRMTDS were significantly related only to RT, $p = .012$ (see Table 5.3 for correlation coefficients and Figure 5.4 for graphical depictions). There were no significant relationships between mMRT scores and DASS task performance variables.

According to calculations based on the Fisher *r*-*z* transformation, there were no significant differences between corresponding correlation coefficients. More specifically, coefficients obtained by correlating SASS task-related primary outcome variables individually with mSRMTDS and mMRT scores did not differ from respective coefficients obtained by correlating the SOSS or DASS task-related variables with the criterion measure scores. This indicates that performance on the SASS task is not associated with self-location updating (as measured by the mSRMTDS) or mental rotation ability (as measured by the mMRT) any differently than performance on the SOSS or DASS tasks is.

5.4.5 Complexity analyses

5.4.5.1 Comparisons of the three-dimensional tasks

Unsegregated data (see section 5.4.4) for the behavioural and mechanistic variables were analysed in order to determine the relative complexity of the new cognitive tasks. One-way ANOVAs, where task was the between-subjects factor with three levels (SASS task vs SOSS task vs DASS task), revealed a significant effect of task on RT, $F(2, 46) = 13.47$, $p < .001$, error proportion, $F(2, 46) = 5.75$, $p = .006$, drift rate, $F(2, 40) = 8.84$, $p < .001$, and non-decision time, $F(2, 40) = 6.77$, $p = .003$. The Bonferroni post hoc procedure detected no significant differences, in terms of any of the variables, between performance on the SASS and SOSS tasks (see Table 5.1 for mean group data for all variables). However, there were significant differences between the SASS and DASS tasks in terms of RT (95% CI; 160 to 484), drift rate (95% CI; -0.004 to -0.001), and non-decision time (95% CI; 57 to 315). Similarly, there were significant differences between the SOSS and DASS tasks for RT (95% CI; 84 to 403), error proportion (95% CI; 0.84 to 8.93), and drift rate (95% CI; -0.004 to -0.001). The results of the post hoc procedures indicate that the DASS task was more challenging than the other tasks. The SASS and SOSS tasks did not differ in terms of behavioural or mechanistic complexity.

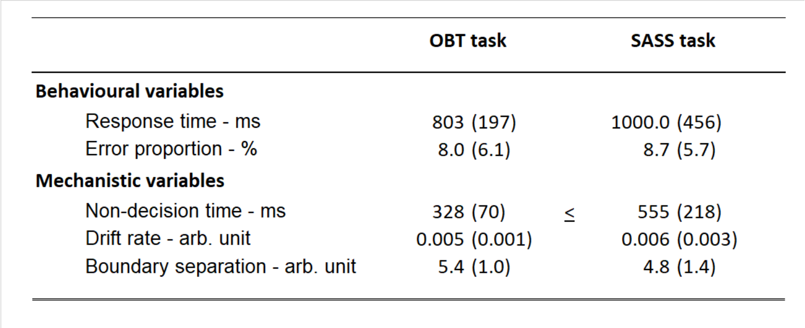
5.4.5.2 Comparisons of the spatial perspective-taking tasks

During the practice block, 21 and 11 participants in the OBT and SASS task groups, respectively, did not achieve 100% accuracy. Their data could be subjected to the EZ-diffusion model in order to calculate the unobserved variables. Independent t-tests revealed that there was only a borderline significant difference between non-decision time on the OBT task ($M = 328$ ms, $SD = 70$ ms) and non-decision time on the SASS task ($M = 555$ ms, $SD = 218$), $t(11.10) = 3.37$, $p = .020$, $r = .711$ (corrected for unequal variances). This result indicates that the SASS task may demand a longer period of non-explicit decision processing, but is otherwise similar to the established OBT task (see Table 5.4 for comparative data).

Table 5.4: Summary data for behavioural and mechanistic variables yielded during practice trials of the OBT and SASS tasks.

All data are mean values with standard deviations in parentheses.

SASS task - Single Avatar Stimulus Set task; OBT task - Own Body Transformation task



	OBT task		SASS task
Behavioural variables			
Response time - ms	803 (197)		1000.0 (456)
Error proportion - %	8.0 (6.1)		8.7 (5.7)
Mechanistic variables			
Non-decision time - ms	328 (70)	≤	555 (218)
Drift rate - arb. unit	0.005 (0.001)		0.006 (0.003)
Boundary separation - arb. unit	5.4 (1.0)		4.8 (1.4)

5.5 Discussion

The present experiment examined the validity, utility and complexity of three new spatial cognitive tasks which had been created to overcome the limitations of pre-existing tasks and, therefore, to facilitate research into the direct effect of aberrant space-motion information on higher cognition. The sample that was recruited was well-suited to the objectives of this study, since the mean scores on an imagery questionnaire, the OSIVQ, indicated that the participants had an imagery preference for schematic or spatial visualisations over vivid, object-based ones. Comparisons of their baseline characteristics indicated that participants with similar cognitive styles and processing speeds had been randomly allocated to the three independent task groups.

5.5.1 Primary inferences about the new experimental (SASS) and control (SOSS) tasks

The new Single Avatar Stimulus Set (SASS) task yielded a monotonic change in performance with angular disparity. More specifically, there were progressive increases in the participants' response latencies as the disparity between their own orientation and the avatar's position increased from 45 to 135 to 180º. These was no such increase in RT from 0 to 45º of avatar rotation. This confinement of the monotonic response function to larger angular disparities was not unexpected. The same pattern of monotonicity has previously been shown in another study, which employed a SPT task comprising 3-D avatars incrementally turned in yaw (Kessler & Thomson, 2010; see section 1.7.1.3), and in studies that used SPT tasks with avatars tilted through 360º in the roll plane (Kaltner, Riecke, & Jansen, 2014; Kessler & Thomson, 2010; Michelon & Zacks, 2006; Preuss et al., 2013). Kessler and Thomson (2010) suggested that participants are able to make a direct visual classification of the laterality of the avatar's limb, or other demarcated entity, for smaller angular disparities (of approximately 50º or less). That is, for smaller disparities between the observer and avatar, mental self-translocation (MS-TL) is simply not necessary (Kessler & Thomson, 2010; Surtees et al., 2013).

There was no monotonicity of errors on the SASS task in the present study, which implies that the progressive increase in RT was not simply a strategy to optimise accuracy as the avatar's position became more disparate from the participants' own positions. Moreover, a monotonic RT function across the larger angular disparities was not yielded by the SOSS task. The data obtained from that task showed there was an increase in RT from 45 to 135º of measuring scale rotation, but not from 135 to 180º. In addition, there was a significant interaction effect (task by contiguous angular disparity [135 vs 180º]) indicating that response latencies were increased on the SASS task, but not on the SOSS task, as the orientation of the on-screen stimulus increased from 135 to 180º. The pattern of performance observed on the SOSS task goes against May and Wendt's (2013) proposal that progressively larger orientations of the on-screen stimulus incur systematically greater costs associated with stimulus-response (in)compatibility. The present study is the first to show that those costs are confined to the juncture between front- and rear-facing stimuli rather than staggered across the spectrum of angular disparities. In turn, it provides new evidence supporting the notion that monotonic RT functions on SPT tasks, such as the SASS task, may represent the evocation of MS-TL. The present study was not designed to dissociate the MS-TL account of performance monotonicity from the mental object rotation (MOR) account. As outlined in section 5.2, these explanations might be distinguishable by the degrees to which performances of SPT and MOR tasks are disrupted during aberrant space-motion stimulation. Pending such research, the results of the present study appear to indicate that the SASS task is valid for the purposes of this project; that is, the performance monotonicity it yields may be indicative of MS-TL and, therefore, task performance may be dependent on space-motion information (see sections 1.6 and 1.7).

A difference between the SASS and SOSS tasks, in terms of cognitive processing, is further supported by their associations with distinct cognitive strategies reported by participants, according to the results of a Pearson chi-square test. In the SASS task group, 80% of the participants reported having solved the task by engaging in MS-TL. This compares very favourably to the rate of reported MS-TL uptake associated with the OBT task in Study 1 (9%). The majority (75%) of participants who completed the SOSS task, in the present study, declared that they had transposed the laterality of their responses whenever the measuring scale was front-facing. That is, the majority seem not to have engaged in MS-TL to make their left-right judgements.

Both behavioural (RT and error proportion) and mechanistic (drift rate) variables for the SASS task were correlated with scores on the modified Standardized Road-Map Test of Direction Sense (mSRMTDS). Higher achievement on the mSRMTDS was strongly associated with better performance outcomes on the SASS task. Since it is accepted that the former requires participants to update their perceptions of self-location (Vingerhoets et al., 1996; Zacks et al., 2002), the correlation coefficients imply that the SASS task has good convergent validity. In contrast, performance on the SOSS task and mSRMTDS did not correlate, in line with predictions. This implies that the SOSS task has good divergent validity. Despite these contrasting results, there was no selective association between the SASS task and mSRMTDS according to calculations based on the Fisher *r-z* transformation. It is possible that the null results for the comparisons of the correlation coefficients stemmed from issues with the size and distributions of the data tested (Zimmerman, 1986).

Despite their differences, the SASS and SOSS tasks are well-matched for difficulty or complexity of cognitive processing. The results of Study 1 showed there were marginal differences between the OBT and Transpose tasks in terms of non-decision time and boundary separation. However, the duration of non-explicit decision processing and the cautiousness of responses on the SASS and SOSS tasks were not different. The contrasting cognitive processes that appear to underpin performance on the SASS and SOSS tasks, according to differences in monotonicity and strategy, but the similar complexities of those processes, make these suitable spatial perspective-taking (i.e. experimental) and choice-reaction time (i.e. control) tasks, respectively.

5.5.2 Supplementary inferences about the additional control (DASS) task

The pattern of performance on the DASS task was similar to that on the SASS task. There were progressive decrements in the participants' response efficiency as the disparity between the orientations of the two avatars increased from 45 to 135 to 180º. The lack of such performance monotonicity across smaller disparities (i.e. between 0 and 45º discrepancies between the avatars' orientations) was unexpected. In previous studies, which have employed MOR tasks with stimulus sets comprising two misaligned figures, a consistent monotonic RT function has been recorded across the entire range of angular disparities (e.g. Falconer & Mast, 2012; Grabherr et al., 2007; Kaltner et al., 2014; Preuss et al., 2013). However, those studies manipulated the figures in the roll plane, whereas the avatars are misaligned in yaw in the DASS task. As with the SASS task, it may well be that participants are able to make a direct visual comparison of the laterality of the scale pans when the avatars' orientations differ by 45º. That is, there is no necessity to mentally rotate one of the avatars when there is such a small angular disparity between them.

There was compelling evidence to indicate that the DASS task was more challenging than both the SASS and SOSS tasks. In fact, this helps support the notion that the DASS task is a candidate MOR task. Such tasks have been consistently shown to be more effortful, denoted by participants' slower responses and lesser accuracy, than SPT tasks (Creem-Regehr & Kunz, 2010; Kessler & Thomson, 2010; Preuss et al., 2013; Zacks & Tversky, 2005). However, in previous studies (e.g. Zacks & Tversky, 2005) the added difficulty of the MOR tasks may have been partly due to the fact that their stimulus sets were larger than the SPT tasks' stimulus sets. Therefore, participants would have been slower to encounter and learn about the greater array of stimuli presented during the MOR tasks. In the present study, there were 16 permutations of all of the tasks' stimuli. Hence, the extra complexity of the DASS task was not clearly related to stimulus set size. The greater complexity of the DASS task relative to the SASS task is also advantageous in that it should help to clarify whether the vulnerability of higher cognitions to aberrant space-motion stimulation is dependent on their difficulty. The results of Study 1 suggest that this is not the case (see section 4.5.2 for clarification).

It was surprising that there were no correlations between DASS task and mMRT outcomes. This may have stemmed from the fact that the latter did not require speeded judgements, unlike all of the other tasks. The lack of a pressing time period within which to complete the mMRT may have diminished performance variability across the sample. The correlations between performance on the DASS task and mSRMTDS was also unexpected. It is possible that the perceptual processing entrained during MOR is not entirely related to upper limb action, as argued in section 1.8.2, but may make some reference to the state of the body as a whole. This may be the case particularly when the stimulus material comprises two complete body forms as with the DASS task. If MOR does not operate completely independently of space-motion information, it would explain why RT on the DASS task was associated with the ability to update imaginary self-location perception as indexed by the mSRMTDS. Overall, the results of the present study indicate that the DASS task is a candidate MOR task and, therefore, is a suitable additional spatial control task for future studies.

5.5.3 Limitations

The direction in which the measuring scale was rotated had an unexpected effect on response times on the SOSS task, albeit this effect was limited to trials when the scale was orientated by 90º. As discussed in section 5.4.3.1, the effect probably relates to the fact that participants were unable to apply the SOSS task's spatial mapping instructions whenever the measuring scale was turned side-on (see section 5.3.2). Hence, the participants made less consistent laterality judgements. With hindsight, the new tasks should have incorporated stimuli with angular disparities of 0º (rear-facing), 60º to the left and right, 120º to the left and right, and 180º (front-facing). No matter, even with 90º orientations of the stimuli removed, the new tasks in their current form still comprise six unique stimulus orientations. Therefore, the stimulus material of the SASS task should still deter participants from adopting a rote strategy.

Because of the low number of errors on all three tasks, it was not possible to subject the data, when it was segregated by angular disparity, to the EZ-diffusion model. Therefore, it was not possible to analyse the monotonicity of data pertaining to the mechanistic variables. This may have provided useful insights into variations in cognitive processing across the spectrum of stimulus orientations. It would appear that only one study to date (Molenaar, Tuerlinckx, & van der Maas, 2015) has completed such an analysis based on data derived from a MOR task. The main finding was a progressive lengthening of non-decision time as the angular disparity between the target and comparison shapes increased (see section 3.11.2.1.2).

Another limitation of the present study was that the questions posed to participants, in order to determine what strategies they adopted while performing their allotted cognitive tasks, may have been overly simplistic. They did not glean sufficient information from the participants as to whether their strategies varied according to stimulus orientation (van Elk & Blanke, 2014) or task familiarity. Finally, the response options on the DASS task were unconventional. Participants were required to click on the right response button when the two avatars shared rotational symmetry and on the left button when they did not. While this is logical, given that the 'same' response and the 'right' button press both have a positive polarity (e.g. Proctor & Vu, 2006), in most related studies (e.g. Kaltner et al., 2014; Zacks & Tversky, 2005), same-different judgements are implemented by left-right responses. This is a more intuitive response format in the sense that the 'same-different' idiom is more common than the 'different-same' idiom, and the former equates to 'left-right' on a spatial dimension.

5.5.4 Conclusions

For the Single Avatar Stimulus Set (SASS) task, performance monotonicity occurred across the appropriate series of avatar orientations. In contrast, for the Single Object Stimulus Set (SASS) task, a different, non-monotonic pattern of performance was observed as the angular disparity between the participants' and the measuring scale's orientations increased from 135 to 180°. This interaction between task and angular disparity indicates that the cognitive processes, which underpin SASS task performance, are dissociable from the processing of spatially incompatible stimuli. The monotonic response time (RT) function obtained from the SASS task may, therefore, be a signature of mental self-translocation (MS-TL), which makes the SASS task a valid spatial perspective-taking (SPT) task for the purposes of this research project. As further evidence for this, participants reported having adopted different strategies on the SASS and SOSS tasks. However, there was no selective association between performance on the SASS task and outcomes on an established paper-and-pencil test of MS-TL.

The new Double Avatar Stimulus Set (DASS) task also yielded a partial monotonic RT function. It was more challenging than the SASS and SOSS tasks. Both of these outcomes indicate that the DASS task is a candidate mental object rotation (MOR) task. Overall, it would appear that the SASS task is an appropriate experimental task for future studies, and the SOSS and DASS tasks are appropriate controls. The differences in their cognitive processing may mean these new tasks have differential susceptibilities to aberrant space-motion information and, therefore, they have the potential to facilitate research into whether balance disorders can have a direct, unmediated effect on higher cognition.

Chapter 6. Study 3:
The effect of optokinetic stimulation on spatial perspective-taking and comparison tasks with 3-D task stimuli

6.1 Abstract

Purpose:

To investigate whether balance disorders, and the aberrant space-motion information they entail, can directly affect higher cognition, this study examined the effect of optokinetic stimulation (OKS) on the performance of three new tasks shown to be underpinned by differentiable cognitive processes in the preceding study. Roll-plane OKS was retained as the means of inducing a balance disorder in healthy participants, in order to minimise the potential for nystagmus to mediate disruptions of cognition.

Methods:

Forty-eight healthy participants were randomised into independent groups to undertake the 'Single Avatar Stimulus Set' (SASS) task, invoking mental self-translocation, the 'Single Object Stimulus Set' (SOSS) task, requiring rote-learned stimulus-response mappings, or the 'Double Avatar Stimulus Set' (DASS) task, eliciting mental object rotation. All cognitive tasks were administered in two-minute trial blocks, four times in a row, with alternating exposure to static and rotating visual surrounds. Participants stood feet together atop a force platform during experimentation and, afterwards, completed several self-report measures.

Results:

During OKS, there were less cautious responses on the SASS task as indicated by a reduction in boundary separation. There was also longer non-explicit decision processing and a marginal increase in error propensity on the SASS task. Importantly, factorial ANOVAs showed there was no difference between performance on the SASS and control (SOSS and DASS) tasks in terms of the degree of disruption by OKS of the primary, task-

related outcome variables. A post hoc power analysis indicated that more than double the number of participants in each task group would have been needed in order to have confirmed a selective disruption of SASS task performance. The aberrant stimulation had wide-ranging but inconsistent simple effects on participants' physiological and subjective states.

Discussion:
The lack of a differential disruption of SASS versus control task performance means that it is not possible to draw firm conclusions as to whether aberrant space-motion information can have a direct, unmediated effect on cognition. However, an inadequate sample size contributed to the null results of the factorial ANOVAs. The wide-ranging yet idiosyncratic effects of OKS on participants' physiological and subjective states may confound interpretation of the analyses around which this research has been designed. An important next step for this research is to address the inadequacies of this study's sample size and employ an alternate form of aberrant stimulation which provides compelling but inaccurate space-motion information even when participants are seated.

6.2 Introduction

Commensurate with the overarching objective of this research programme, the main purpose of the present study was to determine whether the results of Study 1 would be replicated using the new tasks that were developed and validated in Study 2. Therefore, roll-plane optokinetic stimulation (OKS) was retained as the aberrant space-motion stimulation to which participants would be exposed during interleaving trial blocks. Employing three tasks instead of two might provide new insight into whether the effect of aberrant space-motion information on higher cognition can be direct. After all, if the results of Study 1 were reproduced; that is, if OKS disrupted performance on both the new experimental ('Single Avatar Stimulus Set' or SASS) and control ('Single Object Stimulus Set' or SOSS) tasks but selectively spared performance on the alternate control ('Double Avatar Stimulus Set' or DASS task), it would support the view that the cognitive process underpinning choice-reaction time tasks has an underestimated vulnerability to misinformation (see section 4.5.2 for further details). Moreover, it would suggest that balance disorders can directly affect cognition. The results of Study 1 would have to be re-interpreted accordingly - this inference having been hitherto put on hold simply because that study did not employ a suitable comparison task with lesser vulnerability to aberrant space-motion information than both the OBT and Transpose tasks.

However, if the DASS task were to be disrupted to the same extent as the SASS and SOSS tasks in the present study, this would support the notion that the theoretical perspective on mental self-translocation (MS-TL), presented in Chapter 1 (see section 1.6 in particular), is flawed (see section 4.5.2 for further details). More specifically, it would indicate that MS-TL does not have a selective dependence on veridical space-motion information. The same would also be true of the cognitive processes subserving performance on the SOSS and DASS tasks. If this were the outcome, an entirely new approach would be needed to try to isolate the direct effect of aberrant space-motion information on higher cognition.

A third pattern of results, which might emerge from the present study, would comprise a selective disruption of performance on just one of the tasks. If it were not the SASS task that were implicated, it might suggest that one of the cardinal manifestations of the experimentally-induced balance disorder was responsible. Therefore, a direct effect of aberrant space-motion information would seem unlikely or, at best, remain elusive. If, however, SASS task performance were preferentially disrupted, the preceding theoretical perspective on MS-TL would gain support. Moreover, an unmediated disruption of cognition by aberrant space-motion information would be implied[19]. This pattern of results would be further indication that the OBT task employed in Study 1 was not a valid means of evoking MS-TL.

The re-implementation of the experimental paradigm of Study 1, including the use of OKS as the aberrant stimulation, would help control for the potential mediating effects of nystagmus once again. To the researcher's best knowledge, this would be the first study of performance on a spatial perspective-taking task, comprising 3-D avatars displayed trial-on-trial in different yawing increments, under incongruous space-motion conditions.

As per Study 1, the present study was designed:

- To establish if OKS has any differential effects, between the independent task groups, on primary or secondary outcome variables, and,

---

[19] The assumption here is that OKS selectively disrupted performance on the SASS task without preferentially disturbing the respective participants' subjective or physiological states (see section 2.3 for clarification).

- To determine if OKS specifically causes disruption of primary outcomes derived from any of the cognitive tasks, and, if so,
- To ascertain if the disruptive effects may be accounted for indirectly by any of the consequences of the aberrant stimulation, in particular the disturbance of postural control.

6.3 Methods

6.3.1 Ethical considerations and recruitment

Full details of the ethical considerations and recruitment procedures are given in section 3.3. The sample size of this study was based on that of Study 2, given that monotonic response functions were discernible from the data collected from the 15-member SASS task group in that study.

6.3.2 Aberrant space-motion stimulation

As detailed in section 3.4.

6.3.3 Cognitive tasks

This study employed the SASS, SOSS and DASS tasks, which are described in section 5.3.2. A slight amendment was made to all of the tasks ahead of this study. Stimuli depicting the avatar (SASS and DASS tasks) or measuring scale (SOSS task) turned to the left or right by 90º were removed from the tasks' stimulus sets because of the inconsistent results these stimuli yielded in Study 2 (see sections 5.4.3.1 and 5.5.3 for clarifications). Therefore, all of the tasks had 12 unique stimuli rather than the 16 permutations they originally comprised (see section 5.3.2). In addition, the response options on the DASS task were switched so that they were more conventional in the present study. As such, participants were required to click on the left response button when the two avatars shared rotational symmetry (i.e. when they were the same) and on the right button when they did not (i.e. when the avatars were different; see section 5.5.3 for the limitations of the original response options). Participants in all groups viewed a small field projection of the tasks' visual elements. Further details about the projector set-up can be found in section 3.5.

6.3.4 Trait measures

As detailed in section 3.6.

6.3.5 State measures

As detailed in section 3.7.

6.3.6 Strategy measure

The method of ascertaining strategy-related information in Study 2 was enhanced in this study. All participants were presented with the following three strategy descriptions: ‘I imagined rotating my body when judging the positions of the blue pan’, ‘I imagined rotating the figure/image when judging the positions of the blue pan’, and, ‘I used a transposing strategy, and switched which mouse I pressed when certain features were on screen’. Rather than simply declaring which one of the three strategies they used the most, the participants in the present study had to rate how often they used each one (never = 1; rarely = 2; sometimes = 3; often = 4, or; always = 5). Scores for each strategy were totalled for each task. The average frequency with which participants in the same group adopted each strategy was then calculable as a percentage.

6.3.7 Space-motion misperception measures

As detailed in section 3.9.

6.3.8 Experimental procedure

The procedure for this study is given in detail in section 3.10. The only addendum is that participants in all three groups undertook 24 practice trials of their allocated task in a single block while sitting down. This meant that they had had two attempts at each one of the 12 unique stimuli before the experimental trial blocks got started.

6.3.9 Variables

The variables incorporated in this study are listed in section 3.11. The predictor variable ‘task’ had three levels in the present study: SASS task vs SOSS task vs DASS task.

6.3.10 Hypotheses

As detailed in section 3.12.

6.3.11 Reduction of bias

As detailed in section 3.13.

6.3.12 Comparisons of baseline characteristics

As detailed in section 3.14.1.

6.3.13 General descriptives

Details of the descriptive statistics calculated from the data are given in section 3.14.2. The treatment of the strategy responses obtained from the present study is described in section 6.3.6.

6.3.14 Hypothesis tests

As detailed in section 3.14.3.

6.3.15 Supplementary analyses

As detailed in section 3.14.4.

6.3.16 Exploratory analyses

Additional, unplanned analyses are described in section 6.4.5.

6.4 Results

6.4.1 Participants and comparisons of their baseline characteristics

In total, 48 student volunteers from the University of Westminster took part in this study, having met the eligibility criteria and provided written informed consent. The SASS, SOSS and DASS task groups all comprised 16 randomly-allocated participants. The mean proportion of errors across all of the participants was low at 10.8% (*SD* = 9.3%). However, four participants demonstrated particularly high cumulative error compared to other members of their groups. More specifically, their error proportions were more than 1.96 standard deviations greater than the mean proportions for their groups. Two of these participants had been in the SASS task group, one had been in the SOSS task group, and one had been a member of the DASS task group. All data for these four participants were excluded from the analyses given that their task performance was atypical, and in the attempt to reduce bias (see section 3.13.1). Therefore, the data that were analysed related to 14 SASS task group participants, 15 SOSS task group members and 15 participants in the DASS task group.

The mean age of the remaining 44 participants was 21.3 years (*SD* = 4.3 years). There were no between-group differences in age according to a one-way ANOVA. There were 31 (70.1%) female participants, 11 and 12 of whom had been allocated to the SASS and DASS task groups, respectively. Eight females were in the SOSS task group. Four (9.1%) of the participants were left-handed. Two completed the SASS task, and one left-handed participant was in both the SOSS and DASS task groups. The majority of the participants (39; 88.6%) were undergraduate psychology students, but there were also two postgraduate students and three physiotherapists. Both the SOSS and DASS task groups comprised one postgraduate. All of the physiotherapists had been randomly allocated to the DASS task group.

One-way ANOVAs revealed there were between-group differences in the heights (*M* = 164.79 cm; *SD* = 8.28 cm), *F*(2, 43) = 3.77, *p* = .031, but not the weights (*M* = 64.40 kg; *SD* = 12.88 kg) of participants in the three groups. The Bonferroni post hoc procedure showed that participants in the SASS task group were significantly taller than those in the SOSS task group (95% CI for the size of the between-group difference; 0.65 to 15.11 cm).

According to scores on the STICSA (see section 3.6.1), three of the participants had possible anxiety disorders and five had probable anxiety disorders. Furthermore, three had a probable cognitive anxiety component, and 10 had a probable somatic anxiety component. There were no between-group differences in STICSA subscale and total scores. Four participants in both the SOSS and DASS task groups were highly susceptible to visual vertigo since their normalised scores on the SVQ (see section 3.6.2) exceeded 0.7. The scores for none of the participants in the SASS task group exceeded this benchmark. Overall, participants in the three groups did not have significantly different SVQ scores when the data were subjected to a one-way ANOVA. The mean balance confidence ratings for the whole sample were 81.4% for lower postural threat conditions and 58.8% for higher postural threat conditions. As for the other trait measures, there were no between-group differences in reported balance confidence.

6.4.2 General descriptives

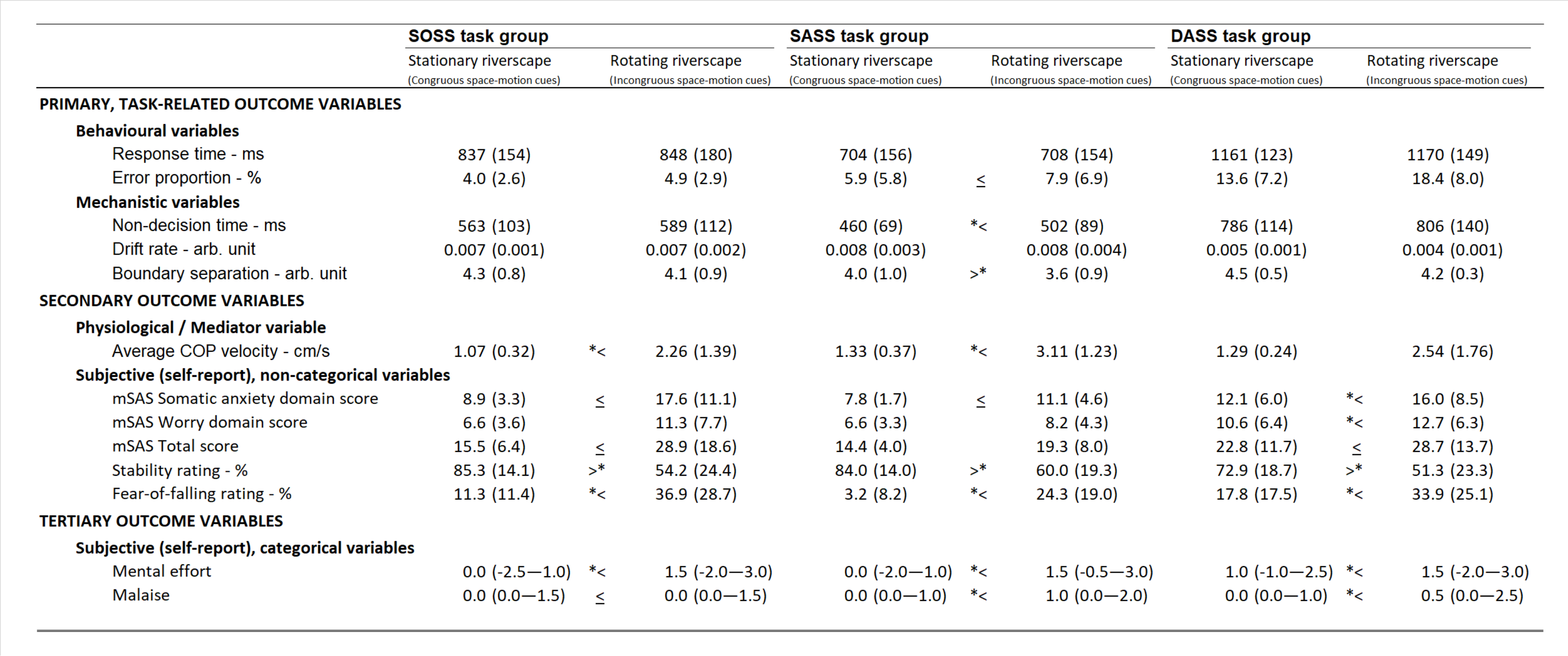
The data for all of the dependent variables, except task strategy (see section 6.3.6), were amalgamated according to task and whether they derived from trial blocks performed during exposure to congruous or incongruous space-motion cues. Averages were then computed and inspected. These data are given in table 6.1 which appears to indicate that OKS, by way of the large, rotating riverscape image, had an effect on several primary, secondary and tertiary outcome variables derived from all three tasks. However, some of the data, particularly for error proportion and the non-categorical variables, appear to be dispersed according to the relatively large standard deviation values.

Across the four experimental blocks, participants in the SASS and SOSS task groups completed a mean of 133.5 (*SD* = 6.2) and 128.9 (*SD* = 5.4) trials, respectively. As had been the case in Study 2, significantly fewer trials (*M* = 117.9; *SD* = 4.1) were undertaken by those in the DASS task group, $F(2, 43) = 33.91$, $p < .001$. Most participants (71%) in the SASS task group experienced the vection illusion, as did most in the SOSS (80%) and DASS (60%) task groups. 33% of participants in the latter group reported that the illusion was sustained rather than brief, compared to just 8% of participants in the SOSS task group and 0% in the SASS task group. That is, all of the participants, who completed the SASS task, felt that vection only occurred in brief bouts. Despite these apparent between-group differences in the frequency of reported vection duration, the median vection duration score for all groups was 1 (brief). The proportions of participants in the three groups, who reported the illusion had been ‘moderate’ in its strength, were as follows: 40% of SASS task group members, 75% of SOSS task group members, and 56% of participants in the DASS task group. The median vection strength scores were as follows: SASS task group = 1.5 (weak-moderate), SOSS task group = 2 (moderate), DASS task group = 2 (moderate). The vection duration and strength scores are further analysed in section 6.4.4 below.

In the SASS task group, participants reported having engaged in mental self-translocation (MS-TL) during 39.7% of trials. They stated that they adopted a mental rotation strategy and a transposing strategy during 19.8% and 40.5% of the total trials, respectively. Those in the SOSS task group declared that they had completed 20.5% of trials using the MS-TL strategy, 22.2% of trials employing the mental rotation strategy, and 57.3% of trials using the transposing strategy. Finally, members of the DASS task group appeared to have relied most heavily on the mental rotation strategy; they reported having used it in 55.8% of trials. They stated that they had utilised MS-TL and the transposing strategy during 15.0% and 29.2% of all trials, respectively.

Table 6.1: Data obtained in Study 3 for primary, secondary and tertiary outcome variables categorised according to task and space-motion cue congruity.

All data are mean values with standard deviations in parentheses, except for mental effort and malaise (medians with minimum and maximum values in parentheses). Arrows with stars denote significant differences as revealed by simple effects analyses. Underlined arrows indicate borderline significant differences (see section 3.14.3).



	SOSS task group			**SASS task group**			**DASS task group**		
	Stationary riverscape (Congruous space-motion cues)		Rotating riverscape (Incongruous space-motion cues)	Stationary riverscape (Congruous space-motion cues)		Rotating riverscape (Incongruous space-motion cues)	Stationary riverscape (Congruous space-motion cues)		Rotating riverscape (Incongruous space-motion cues)
PRIMARY, TASK-RELATED OUTCOME VARIABLES									
Behavioural variables									
Response time - ms	837 (154)		848 (180)	704 (156)		708 (154)	1161 (123)		1170 (149)
Error proportion - %	4.0 (2.6)		4.9 (2.9)	5.9 (5.8)	≤	7.9 (6.9)	13.6 (7.2)		18.4 (8.0)
Mechanistic variables									
Non-decision time - ms	563 (103)		589 (112)	460 (69)	*<	502 (89)	786 (114)		806 (140)
Drift rate - arb. unit	0.007 (0.001)		0.007 (0.002)	0.008 (0.003)		0.008 (0.004)	0.005 (0.001)		0.004 (0.001)
Boundary separation - arb. unit	4.3 (0.8)		4.1 (0.9)	4.0 (1.0)	>*	3.6 (0.9)	4.5 (0.5)		4.2 (0.3)
SECONDARY OUTCOME VARIABLES									
Physiological / Mediator variable									
Average COP velocity - cm/s	1.07 (0.32)	*<	2.26 (1.39)	1.33 (0.37)	*<	3.11 (1.23)	1.29 (0.24)		2.54 (1.76)
Subjective (self-report), non-categorical variables									
mSAS Somatic anxiety domain score	8.9 (3.3)	≤	17.6 (11.1)	7.8 (1.7)	≤	11.1 (4.6)	12.1 (6.0)	*<	16.0 (8.5)
mSAS Worry domain score	6.6 (3.6)		11.3 (7.7)	6.6 (3.3)		8.2 (4.3)	10.6 (6.4)	*<	12.7 (6.3)
mSAS Total score	15.5 (6.4)	≤	28.9 (18.6)	14.4 (4.0)		19.3 (8.0)	22.8 (11.7)	≤	28.7 (13.7)
Stability rating - %	85.3 (14.1)	>*	54.2 (24.4)	84.0 (14.0)	>*	60.0 (19.3)	72.9 (18.7)	>*	51.3 (23.3)
Fear-of-falling rating - %	11.3 (11.4)	*<	36.9 (28.7)	3.2 (8.2)	*<	24.3 (19.0)	17.8 (17.5)	*<	33.9 (25.1)
TERTIARY OUTCOME VARIABLES									
Subjective (self-report), categorical variables									
Mental effort	0.0 (-2.5—1.0)	*<	1.5 (-2.0—3.0)	0.0 (-2.0—1.0)	*<	1.5 (-0.5—3.0)	1.0 (-1.0—2.5)	*<	1.5 (-2.0—3.0)
Malaise	0.0 (0.0—1.5)	≤	0.0 (0.0—1.5)	0.0 (0.0—1.0)	*<	1.0 (0.0—2.0)	0.0 (0.0—1.0)	*<	0.5 (0.0—2.5)

6.4.3 Hypothesis tests

Two participants in both the SASS and SOSS task groups (but none in the DASS task group) achieved 100% accuracy on trials undertaken during exposures to both the static (i.e. congruous cues) and rotating (i.e. incongruous cues) riverscape image. It was not possible to calculate mechanistic variables (drift rate, boundary separation and non-decision time) for these four participants, given the constraints of the EZ-diffusion model (see section 3.11.2.1.2). Hence, sets of mechanistic variable data for 12 participants in the SASS task group, 13 in the SOSS task group and 15 in the DASS task group were subjected to the hypothesis tests. Regarding the behavioural variables (RT and error proportion), data from all 14 participants in the SASS task group and all 15 in the SOSS and DASS task groups were subjected to the analyses.

6.4.3.1 Tests relating to null hypothesis 1

To test whether there were interaction effects of the independent variables (IVs; task and space-motion cue congruity) on any of the primary outcome variables, a series of two-way ANOVAs were conducted. There were no significant interactions between the IVs which affected either the two behavioural variables, $F < 2.1, p > 0.1, \eta_p^2 < 0.95$, or the three mechanistic variables, $F < 1.4, p > 0.2, \eta_p^2 < 0.07$. For the sake of completeness, there was a main effect of space-motion cue congruity on error proportion, $F(1, 41) = 9.70, p = .003, \eta_p^2 = .191$, which indicates that OKS tended to disrupt performance on the tasks. In-keeping with this result, a significant main effect of cue congruity on boundary separation, $F(1, 37) = 12.91, p = .001, \eta_p^2 = .259$, indicates that OKS reduced the cautiousness with which participants made their laterality judgements. In addition, there was a borderline effect of cue congruity on non-decision time, $F(1, 37) = 4.88, p = .033, \eta_p^2 = .116$, which suggests that OKS may have prolonged the duration of non-explicit decision processing during trials of the tasks. There was a significant main effect of task on both RT, $F(2, 41) = 37.11, p < .001, \eta_p^2 = .644$, and error proportion, $F(2, 41) = 19.56, p < .001, \eta_p^2 = .488$. Furthermore, the task factor significantly affected drift rate, $F(2, 37) = 13.81, p < .001, \eta_p^2 = .428$, and boundary separation, $F(2, 37) = 35.44, p < .001, \eta_p^2 = .657$. The Bonferroni post hoc procedure indicated that responses on the DASS task were significantly less efficient than responses on the SASS task in terms of RT (95% CI for the size of the between-group difference; 322 to 597 ms), error proportion (95% CI; 4.5 to

14.0%), drift rate (95% CI; -0.005 to -0.002 arb. unit), and non-decision time (95% CI; 217 to 412 ms). Compared to responses on the SOSS task, those made during the DASS task were also less efficient (CI for difference in RT: 188 to 458 ms, CI for difference in error proportion: 6.7 to 16.4%, CI for difference in drift rate: -0.005 to -0.001 arb. unit, CI for difference in non-decision time: 125 to 316 ms).

Data pertaining to the secondary outcome variables (average COP velocity, total mSAS score, stability rating and fear-of-falling rating) were also subjected to the same two-way ANOVAs to test for task by cue congruity interaction effects. There were no significant interactions on any of these variables, nor were there any significant main effects of task. However, space-motion cue congruity had a significant effect on average COP velocity, $F(1, 41) = 50.47$, $p < .001$, $\eta_p^2 = .552$, indicating that OKS perturbed postural control across the task groups. Furthermore, there was a significant main effect of the cue congruity factor on total mSAS score, $F(1, 41) = 23.61$, $p < .001$, $\eta_p^2 = .365$, stability rating, $F(1, 41) = 97.50$, $p < .001$, $\eta_p^2 = .704$, and fear-of-falling rating, $F(1, 41) = 51.99$, $p < .001$, $\eta_p^2 = .559$. These results imply that OKS made participants more anxious about their well-being and less certain about their balance.

6.4.3.2 Tests relating to null hypothesis 2

To test whether there were within-subjects, simple effects of space-motion cue congruity on the primary outcome variables, a series of paired t-tests was conducted. These revealed that OKS caused a borderline significant increase in error only on the SASS task, $t(13) = 2.53$, $p = .033$, $r = .576$, as depicted in Figure 6.1A. However, it significantly reduced boundary separation (i.e. the cautiousness of responses) on the SASS task, $t(11) = 3.18$, $p = .017$, $r = .692$ (see Figure 6.1B), and increased non-decision time (i.e. non-explicit decision processing) on that task, $t(11) = 3.09$, $p = .017$, $r = .681$ (see Figure 6.1C). There were no other simple effects of the cue congruity factor on any other primary DVs for any of the tasks.

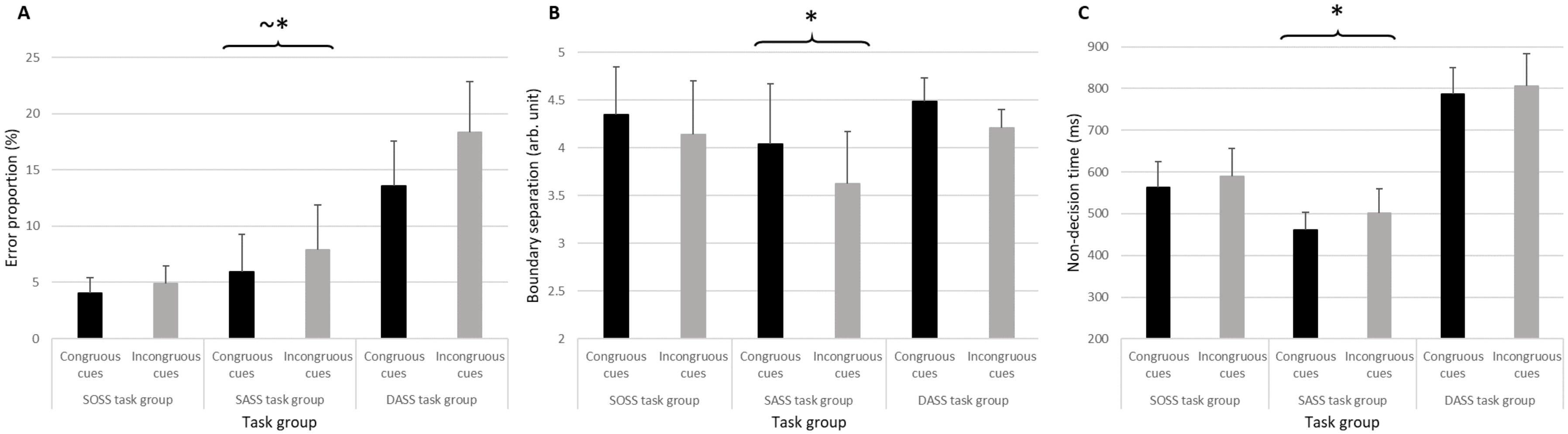


Figure 6.1: Bar charts showing mean error proportion [A], boundary separation [B] and non-decision time [C] segregated by task group (SASS task versus SOSS task versus DASS task) and by space-motion cue congruity (congruous [stationary backdrop] versus incongruous [rotating backdrop] cues).

Error bars represent 95% confidence intervals. Asterisks denote significant differences as revealed by simple effects analyses. The asterisk preceded by a swung dash indicates a borderline significant difference (see section 3.14.3).

All of the data pertaining to the primary outcome variables were re-tested for simple effects of the space-motion cue congruity factor using the path-analytic method of mediation analysis, which controlled for the effect on cognitive performance of average COP velocity. The analyses revealed no significant direct effects of cue congruity on the behavioural or mechanistic variables. That is, with average COP velocity controlled, all of the significant effects detailed above were abolished, $t < .3$, $p > .3$. While this might indicate that average COP velocity mediated the disruptive effects of OKS on task performance, there were no significant indirect effects of this physiological variable on any of the task-related variables. More specifically, bias-corrected bootstrap confidence intervals (2000 bootstrap samples) straddled zero for the indirect effects of space-motion cue congruity, via COP velocity, on each primary outcome variable. No additional simple effects of OKS on task performance variables were revealed by the mediation analyses.

6.4.4 Supplementary analyses

To supplement the tests relating to null hypothesis 2, the secondary outcome variables were similarly subjected to paired samples t-tests, but mediation analyses were not undertaken. There was a significant effect of space-motion cue congruity on average COP velocity, but only for data from the SASS task group, $t(13) = 5.82$, $p = .001$, $r = .850$, and the SOSS task group, $t(14) = 4.02$, $p = .024$, $r = .732$. Pertaining to the DASS task group, the effect of cue congruity on average COP velocity was non-significant, $t(14) = 3.06$, $p = .123$. These results indicate that OKS disrupted the balance of those participants in the SASS and SOSS task groups but not of those in the DASS task group. With regard to stability and fear-of-falling ratings, pairwise comparisons imply that, during OKS, participants in all three groups felt more unstable (SASS task group, $t(13) = 8.14$, $p < .001$, $r = .914$; SOSS task group, $t(14) = 5.03$, $p = .001$, $r = .803$; DASS task group, $t(14) = 6.28$, $p < .001$, $r = .859$), and fearful (SASS task group, $t(13) = 4.40$, $p = .002$, $r = .773$; SOSS task group, $t(14) = 4.65$, $p = .003$, $r = .779$; DASS task group, $t(14) = 3.43$, $p = .007$, $r = .676$). There was not such a uniform effect, across the groups, of space-motion cue congruity on total mSAS scores. There was no effect on scores obtained from the SASS task group, $t(13) = 2.97$, $p = .068$, a borderline effect on scores from the SOSS task group, $t(14) = 3.20$, $p = .037$, $r = .650$, but a significant effect on scores given by members of the DASS task group, $t(14) = 3.00$, $p = .019$, $r = .626$.

Between-task comparisons of the tertiary outcome variables, specifically the malaise, mental effort, vection duration and vection strength scores, also constituted supplementary analyses. These analyses, with the space-motion cue congruity factor collapsed, were carried out by way of Kruskal-Wallis tests (i.e. one-way ANOVAs on ranks). The results of all four tests were not statistically significant, indicating that there were no differences in the respective self-reports across the task groups. Median scores for malaise and mental effort can be found in Table 6.1, and for vection duration and strength in section 6.4.2.

Finally, Wilcoxon signed-rank tests were employed to analyse the within-subjects effects of space-motion cue congruity on ordinal data pertaining to malaise and mental effort. Reported levels of the latter were raised for participants in all three groups during OKS: SASS, $z = 2.95$, $p = .003$, $r = .558$; SOSS, $z = 2.56$, $p = .010$, $r = .468$; DASS, $z = 2.49$, $p = .013$, $r = .454$. Levels of malaise were also higher in two of the groups during OKS: SASS, $z = 2.59$, $p = .010$, $r = .489$; DASS, $z = 2.57$, $p = .010$, $r = .468$. There was a borderline effect of space-motion cue congruity on malaise ratings given by members of the SOSS task group, $z = 2.14$, $p = .033$, $r = .390$.

6.4.5 Exploratory analysis

A sample size calculation was conducted, by way of a post-hoc power analysis, to determine how many participants would have been needed in order to have found a significant task by space-motion cue congruity interaction effect in the present study. The calculation was performed using the G*Power program (version 3.1.9.2; Faul, Erdfelder, Lang, & Buchner, 2007) based on the outputs of the two-way ANOVA on the DV error proportion. The results of this particular test were selected for inclusion in the sample size calculation because it had yielded the highest *F* statistic and effect size value, as well as the lowest probability value, of all the related hypothesis tests (see section 6.4.3.1). The calculation was performed with the alpha and power levels set at .05 and .80, respectively, and with a non-sphericity correction of 1. The total sample size calculated from these figures was 102 participants, or 34 per task group.

6.5 Discussion

6.5.1 Summary of the results

The present experiment investigated whether balance disorders can directly affect higher cognition by examining the effect of aberrant space-motion information associated with optokinetic stimulation (OKS) on the performance of three new tasks - the Single Avatar Stimulus Set (SASS) task, the Single Object Stimulus Set (SOSS) task, and the Double Avatar Stimulus Set (DASS) task - which were shown to be underpinned by differentiable cognitive processes in Study 2. OKS disrupted two mechanistic aspects of performance on the experimental task - the SASS task - according to simple effects analyses. More specifically, participants were less cautious in making their laterality judgements while exposed to the rotary motion of the visual backdrop, as indicated by a reduction in boundary separation. They demonstrated longer non-explicit decision processing, as per an increase in non-decision time. In addition, OKS resulted in a borderline increase in error propensity on the SASS task. Hence, there was a marginal disruption by OKS of a behavioural aspect of SASS task performance as well.

Disruptions of neither the behavioural aspect nor the mechanistic aspects of performance were selective to the SASS task according to the non-significant task by space-motion cue congruity interaction effects yielded by the factorial ANOVAs for all primary, task-related outcome variables. Similarly, there were no task-specific preferential effects of the aberrant space-motion stimulation on any of the secondary outcome variables. Most of the subjective and physiological markers were disturbed by OKS right across the three task groups according to simple effects analyses of related data.

6.5.2 Primary inferences about the direct effect of aberrant space-motion information on cognition

The lack of a preferential disruption of performance on the SASS task, according to the factorial ANOVAs, means that it is not possible to draw firm conclusions as to whether there can be a direct, unmediated effect of the aberrant space-motion information inherent in balance disorders. Given that three tasks were employed, as opposed to two in Study 1, it seems unlikely that the absence of a differential effect of OKS on task-related variables was due to an underestimated vulnerability of the rote-learned cognitions that underpin choice-reaction time tasks such as the SOSS and Transpose tasks (see sections 4.5.2 and 6.2 for further discussions). Had this been the case, a relative immunity to disturbance of performance on the DASS task would still have been expected to result in significant task by space-motion cue congruity interaction effects. Moreover, simple effects analyses showed there was no disruption in performance on the SOSS task while it was undertaken during exposure to incongruous versus congruous space-motion cues, indicating that it is not particularly vulnerable to aberrant space-motion information.

It is possible that MS-TL was not evoked as repetitiously by the SASS task during this study as it had been during Study 2 and, therefore, the susceptibility to misinformation of performance on the task dropped to a level equivalent with the susceptibility of performance on the SOSS and DASS tasks. According to self-reports, there appears to have been a 39.7% uptake of MS-TL by the SASS task group in this study versus an 80.0% uptake by the respective group in Study 2. This might imply that OKS instigated a change in the way participants strategized during the SASS task, perhaps because it was too difficult to engage in MS-TL due to incongruous space-motion cues. Their increased preference for a rote-learned strategy may have meant the SASS task participants performed just as robustly under OKS as the control group participants did. However, it is important to note that strategy information was obtained using a revised survey in the present study (see section 6.3.6). It gauged the proportions of trials during which the MS-TL, mental object rotation (MOR) and rote-learned strategies were adopted for each of the three tasks, rather than participants' main preference for just one of those strategies, as the survey in Study 2 had done. This new approach was unconventional insomuch as it transformed ordinal response data into ratio data. However, proportioning task trials by strategy, as opposed to trichotomising the participants by strategy, is advantageous since participants may not have a fixed cognitive routine throughout trial blocks. On spatial perspective-taking (SPT) tasks, for example, the strategies participants adopt may vary with the orientations of the avatar (van Elk & Blanke, 2014). Due to the altered method of collecting strategy data, it is not possible to determine whether OKS did instigate a change in the way participants strategized. Even if participants were more disinclined to adopt MS-TL for the SASS task during OKS, that task still appears to have evoked the cognitive process more than the other tasks did, according to the self-report data in ratio form. Therefore, a preferential vulnerability of performance on the SASS task should have been preserved. The fact that it was not brings into question whether MS-TL even has a selective dependence on veridical space-motion information, as has been promoted throughout this thesis (see section 1.6 in particular).

As discussed in section 6.2, the absence of a selective effect of OKS is inconsistent with the internal model formulation of MS-TL. However, the formulation is based on theories of imagery which appear to be the most intuitive and accepted at present (see section 4.5.2). The results of this study may, in fact, provide weak support for the preferential vulnerability to aberrant space-motion information of MS-TL. After all, simple effects analyses only showed a disruption of performance on the SASS task, not on the control tasks. In view of the results of these analyses, perhaps the most likely reason for the null interaction effects, and the resultant lack of confirmation of a selective disruption of SASS task performance, relates to the size of the study sample. Indeed, the post hoc power analysis indicated that more than double the number of participants in each task group would have been needed in order to have found a significant task by space-motion cue congruity interaction effect in the present study. This was the first time the three new cognitive tasks had been employed in a study wherein participants were exposed to different levels of the space-motion cue congruity factor. The effect sizes of that factor were therefore unknown, so the study’s sample size had been set pragmatically. In the overview, it appears that the basis of this research programme remains valid, and a study that employs a similar protocol with the new tasks embedded may yet provide more conclusive evidence for a direct effect of balance disorders, so long as that study is adequately powered.

6.5.3 Additional inferences about the manifestations of optokinetic stimulation

For the secondary variable data, as with the primary variables, simple effects differed across the task groups. More specifically, pairwise comparisons showed that OKS increased average COP velocity in the SASS and SOSS task groups, but not in the DASS task group. Conversely, anxiety levels were raised by OKS in the DASS task group, but were only marginally elevated in the SOSS task group, and were not affected at all in the SASS task group. This pattern of results does not clearly relate to the proportions of field independent and dependent individuals in each group (see section 4.5.3 for clarification of terms). The SVQ responses of four participants in both the SOSS and DASS task groups indicated that they were field dependent, yet increased postural perturbations were only recorded from the former group under OKS, and heightened anxiety was only reported by the latter group with stimulation.

One possible explanation for these seemingly inconsistent results is that an increase in COP velocity may not always represent a deterioration in postural control. Ehrenfried and colleagues (2003) recorded increases in the COP displacements of their participants as the velocity of the planar, large field visual motion to which they were exposed, was increased. Rather than interpreting this as a deterioration in postural control, the research group proposed that the "…sway enhancement could be exploratory 'testing of the ground' movements to check for self motion" (Ehrenfried et al., 2003, p. 140). Therefore, participants in the SASS and SOSS task groups, who showed increased COP velocity, may actually have had more adaptive postural control during OKS than those in the DASS task group, who did not show an increase in COP velocity. Ehrenfried and colleagues' (2003) proposal is, however, controversial (Forbes, Chien, & Blouin, 2018). It still seems likely that the changes in COP velocity and subjective states recorded in the present study were highly idiosyncratic and variably interactive, possibly due in part to the fact that the participants were unpractised at maintaining balance during roll-plane OKS. Some participants may have reacted to the novel stimulus by stiffening their postures, while others swayed more, because of unique and emergent influences of their ontogenetics plus psychological and physiological states.

If the data for many of the secondary outcome variables were dependent on individual differences, interpretation of the factorial ANOVAs and mediation analyses might be problematic. Removing the postural imperative and, thereby, reducing the idiosyncrasies of postural responses and their interactions with subjective state, might improve the interpretability of the data obtained in future research. Although it would have been possible to expose seated participants to OKS in the present study and in Study 1, it was reasoned that this approach might have implicitly down-graded participants' reliance on visual signals and, thereby, nullified the aberrant space-motion information generated by the OKS (see section 3.4). To progress the current research project, an alternate form of aberrant stimulation is required which provides compelling but inaccurate self-motion velocity or other space-motion information even when participants are seated.

6.5.4 Potential methodological limitations

This study did not show a differential disruption of task performance and, therefore, a clear unmediated effect of aberrant space-motion information, probably because of the inadequacy of the sample size. If that inadequacy were addressed in a future study, and a selective effect of aberrant stimulation on the SASS task were demonstrated, it is possible that other methodological limitations might still preclude firm conclusions about the directness of the effect. So far only categorical data has been collected regarding participants' levels of dizziness, therefore it has not been possible to test the data for task by space-motion cue congruity interaction effects, which could be confounding.

Uneven proportions of male and female participants in the task groups, as was the case in the present study, might also hamper the interpretation of otherwise insightful results. It is well-recognised that gender affects mental rotation ability. Voyer and colleagues' (1995) meta-analysis of sex differences in spatial abilities, found that the average difference (using Cohen's $d = (M1 - M2) / SD$) between men and women on the Mental Rotations Test (see section 5.3.5.1) was 0.94. This large effect indicates that men perform nearly one standard deviation above the average performance of women (Parsons et al., 2004). The magnitude of the gender effect has been shown to vary with task-related instructions, design and response format (e.g. Debelak, Gittler, & Arendasy, 2014; Moè, 2009). Compared with investigations into gender differences in mental rotation, there has been far less research into the effect of gender on perspective-taking ability (Kaiser et al., 2008). No matter, a larger proportion of males in the DASS task group than in the SASS task group could lead to a preferential disruption of SASS task performance if the inherent male advantage leads to greater performance resilience during aberrant stimulation.

Finally, the external validity of future research may also be problematic if the recruitment procedure is unchanged. In the present and preceding studies, convenience samples largely comprising undergraduate psychology students were recruited. The use of such samples in psychology research remains a contentious issue (Peterson & Merunka, 2014). Some researchers have argued that undergraduate students are appropriate study participants when the research emphasis is on basic cognitive processes, as it is in this project (Lucas, 2003). However, other researchers have challenged the recruitment of undergraduate students even for cognitive science research given that, compared with older adults, they tend to have stronger cognitive skills and more compliant behaviour (Sears, 1986). To improve the generalizability of this project’s findings about the directness of the effect of aberrant space-motion information, an alternative recruitment procedure may need to be adopted in the next study.

6.5.5 Conclusions

Optokinetic stimulation (OKS), and the resultant experimentally-induced balance disorder, disrupted mechanistic aspects of performance on the SASS task - a new spatial perspective-taking task. More specifically, under OKS, participants were less cautious in making their laterality judgements and showed longer non-explicit decision processing on the SASS task. Of greater relevance, factorial ANOVAs revealed there was no difference between performance on the SASS and control (SOSS and DASS) tasks in terms of the degree of disruption by OKS of primary, task-related outcome variables. The lack of a differential disruption of task performance means that it is not possible to draw firm conclusions as to whether balance disorders, and the aberrant space-motion information they entail, can directly affect higher cognition. The inadequate sample size most likely accounts for the null results of the factorial ANOVAs. A post hoc power analysis indicated that more than double the number of participants in each task group would have been needed in order to have found a significant task by space-motion cue congruity interaction effect. Supplementary, pairwise comparisons of data pertaining to the participants’ subjective and physiological states revealed inconsistent patterns of results. The wide-ranging yet idiosyncratic effects of OKS on postural control and subjective states appear to confound interpretation of the analyses around which this research has been designed. Important next steps for this research are to: address the inadequacies of this study’s sample size, employ an alternate form of aberrant stimulation which provides compelling but inaccurate space-motion information even when participants are seated, incorporate a non-categorical measure of dizziness, and adapt the recruitment and randomisation procedures.

Chapter 7. Study 4:

The effect of impulse stimulation on spatial perspective-taking and comparison tasks with 3-D task stimuli

7.1 Abstract

Purpose:

To investigate further whether balance disorders, and the aberrant space-motion information they entail, can directly affect higher cognition, this study examined the effect of an alternate form of visuo-vestibular stimulation on the performance of the three spatial tasks employed in the preceding studies. Two modes of passive whole-body rotation were selected as the basis for the experimental and control conditions. Impulse deceleration from constant velocity rotation constituted the aberrant stimulation in the experimental condition, whereas zero deceleration constituted the control condition. The new experimental paradigm was designed to reduce the idiosyncrasies of participants' postural and subjective responses by minimising the postural imperative.

Methods:

Seventy-eight healthy participants undertook either the 'Single Avatar Stimulus Set' (SASS) task, invoking mental self-translocation, the 'Single Object Stimulus Set' (SOSS) task, requiring rote-learned stimulus-response mappings, or the 'Double Avatar Stimulus Set' (DASS) task, eliciting mental object rotation. All spatial cognitive tasks were administered six times, in one-minute trial blocks, after one minute of constant angular velocity (90°/s). Halfway through alternating trial blocks, chair velocity reduced abruptly from 90 to 0°/s. Participants wore wireless heart rate monitors throughout so that anxiety could be inferred from the ratio of low to high frequency (LF/HF ratio) components of pulse trains. Several self-report measures were completed after each trial block to gauge participants' symptomatic and psychological states.

Results:

With impulse stimulation, responses on the SASS task were characterised by smaller boundary separations and longer non-decision times. There was also a marginal increase in error propensity on the SASS task. Mediation analyses showed that these simple effects of impulse stimulation were not secondary to its effect on LF/HF ratio. The decrement in boundary separation due to the aberrant stimulation was selective to the SASS task. There was also a selective decrease in motion symptoms during the experimental condition reported by the participants who undertook that task.

Discussion:

The selective disruption of an aspect of SASS task performance by impulse stimulation, in the absence of concurrent preferential disturbances of the physiological or subjective states of the participants in the SASS task group, suggests that the performance disruption was the direct effect of the aberrant space-motion information associated with the abrupt deceleration. The decrease in boundary separation plus the increase in non-decision time do not follow the predictions of the standard account of decision-making which implies that the former represents a reduction of response caution. These direct cognitive effects of aberrant space-motion information are considered further in the General Discussion.

7.2 Introduction

To minimise the balance imperative throughout the experimental procedure, and thereby reduce the idiosyncrasies of participants' postural and subjective responses, two modes of passive whole-body rotation were selected as the basis for the experimental and control conditions in the present study. More specifically, abrupt or impulse deceleration from constant velocity rotation constituted the aberrant stimulation, thus providing a basis for the experimental condition, while zero deceleration from constant velocity rotation constituted the control condition. Participants were seated during both modes of whole-body rotation. Therefore, the new experimental paradigm removes the need to measure COP velocity and permits a different mediation model to be tested in the present study.

Impulse deceleration or stimulation, including its mechanisms and consequences, is described chiefly in section 1.5.2. In brief, because the endolymphatic fluid encapsulated in the lateral semicircular canals of the vestibular organ has inertia, impulse stimulation causes the cupulae to be distorted in the direction opposite to that which they had been deflected during the acceleration to constant angular velocity. As a result, the person exposed to the abrupt deceleration (mis)perceives self-rotation in a direction opposite to his or her initial rotary motion (Baloh, Honrubia, & Kerber, 2011; Carpenter, 2003; Laurens & Angelaki, 2011), even after he or she has come to a stop as is faithfully signalled by the visual system. The misperception of self-rotation implies that impulse stimulation provides compelling but inaccurate space-motion information even though participants are seated.

Compared to cross-coupled stimulation (see section 2.4.5), an alternate form of aberrant stimulation of the vestibular system, nausea and other motion symptoms have been less frequently reported following impulse stimulation. Similarly, zero deceleration - uninterrupted passive rotation about the z-axis - does not typically produce motion sickness (Guedry, 1965). Moreover, zero deceleration is a suitable basis for a control condition because it may lead to similar levels of distraction or inattention as impulse stimulation, owing to the unusual experience of constant velocity rotation, even though it does not induce the stark misperception of self-rotation.

The potential disadvantage of exposing participants to passive whole-body rotation, and impulse stimulation in particular, is that nystagmus may occur. This may mediate disruptions of cognition making the direct effect of aberrant space-motion information indiscernible (see section 4.2). Loan equipment was acquired to enable the potential disruptive effects of nystagmus on cognition to be evaluated. The software was incompatible with the E-Prime experiment generator program which implemented the spatial tasks (see section 3.5). Therefore, the present study comprised preliminary and main investigations with separate purposes as described below.

The preliminary investigation was designed:

- To determine the likelihood that post-rotatory nystagmus would confound interpretation of a direct effect of aberrant space-motion information on cognition.

Similar to the first and third studies, the main investigation was designed:

- To establish if impulse stimulation has any differential effects, between the independent task groups, on primary or secondary outcome variables, and,
- To determine if impulse stimulation specifically causes disruption of primary outcomes derived from any of the cognitive tasks, and, if so,
- To ascertain if the disruptive effects may be accounted for indirectly by any of the consequences of the aberrant stimulation, in particular the disturbance of psychological state.

7.3 Study 4A: Preliminary investigation

7.3.1 Methods

7.3.1.1 Aberrant space-motion stimulation

Incongruous vestibular stimulation was by way of impulse deceleration, which was administered based on the methods of Okada et al. (1999) and Nigmatullina et al. (2015). It was intended to perturb participants' perceptions of self-motion. They sat upright and safely restrained in a motorised, indirect drive, low friction chair fitted with a footrest. The chair was originally designed and constructed at Royal Aircraft Establishment (RAE) Farnborough to rotate pilots about their cranio-caudal or z axes. A fabric cabin surrounded the chair. When closed, it excluded extraneous visual input. The inside of the cabin was always illuminated by the in-built light in order that participants had clear and fixed visual references to aid the suppression of their nystagmus. The researcher monitored the participants via a live video feed that was relayed from inside the cabin to the nearby external control unit. A portable computer rested on the participants' laps (see section 7.3.1.2 for further details), which encouraged the participants to tip their heads forwards by approximately 20 to 30º, thereby bringing their lateral semicircular canals into the Earth horizontal plane. Figure 7.1 shows a demonstrator positioned in the rotatory chair with one panel of the fabric cabin open.

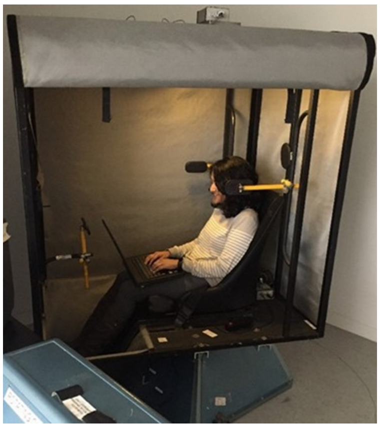


Figure 7.1: Motorised rotatory chair with demonstrator in situ.

Rightward chair rotation was initiated at a constant acceleration of 1º/s^2, bordering on the perceptual threshold for angular acceleration (see section 1.4.2.2.1). Once the chair reached 90º/s, it maintained that velocity for 60 s in order to allow for vestibular adaptation (see section 1.4.2.2.1). Thereafter, the computerised task was initiated for one minute (see section 7.3.1.2 for further details). Thirty seconds into the task, the chair decelerated abruptly at 20º/s^2, coming to a complete stop in 4.5 s. Participants continued with their allocated task until it timed out. The abrupt deceleration following constant velocity rotation constituted the impulse stimulus and evoked the post-rotatory self-motion illusion and nystagmus (see section 1.5.2).

7.3.1.2 Computerised tasks and experimental procedure

Six healthy postgraduate student volunteers took part in this study (*M* = 31.4 years of age, *SD* = 6.5 years; four females). Once they had provided written consent, they were randomly allocated to undertake either the ‘Single Avatar Stimulus Set’ (SASS) task, ‘Single Object Stimulus Set’ (SOSS) task or ‘Double Avatar Stimulus Set’ (DASS) task, which are described in sections 6.3.3 and 5.3.2. Two participants completed each task. They all received a slide-based briefing on the task and subsequently completed a one-minute practice block before getting into the rotatory chair. Unique to this preliminary study, the tasks were implemented using the SMI BeGaze software (SensoMotoric Instruments, Teltow, Germany) running in the Windows 7 environment (Microsoft, Redmond, WA, USA), on a laptop (Dell, Round Rock, TX, USA) with a 15.6 inch screen. Other amendments were also made to the structure and response format of all three tasks specifically for the purposes of this preliminary study. Trials commenced with the presentation of a black fixation cross, which appeared on screen for a fixed period of 250 ms. This was followed immediately by a random task-related stimulus (one avatar-SASS; measuring scale-SOSS; two avatars-DASS), which terminated after a fixed period of 1750 ms. Participants had to enunciate their laterality judgements rather than click on mouse or keyboard buttons. The researcher noted down their judgements and, subsequently, cross-referenced these with the sequence of stimuli the participants had been presented with. Error proportions were calculated but no other behavioural variables could be obtained from the vocal response format. The feedback screen was removed as a visual element in all three tasks and no other feedback was provided to the participants during the one-minute block.

Following the practice block, the participants were assisted to climb in to the rotatory chair. A seatbelt was fastened around them, and the laptop was positioned on their laps. The participants loosely held it, and their eye movements were calibrated (see section 7.3.1.3). The fabric cabin was closed and chair rotation was initiated. The one-minute task block was implemented after 60 s of constant velocity rotation at 90°/s. As described in 7.3.1.1, the impulse stimulus was delivered halfway through the task block. Once the task block was complete, the fabric cabin of the stationary chair was opened, and the participants were given a two-minute rest period.

Participants were exposed to one additional period of chair rotation thereafter. However, instead of completing their allocated tasks during this period of rotation, this time participants simply stared at a full-screen, dynamic white noise video for one minute. The video was intended to ensure participants attended to the laptop screen but had no stable focal point. The overarching aim of this condition was to gain insight into the degree to which nystagmus was elicited by the impulse stimulation even when the participants were not focused on the tasks' stimuli. The participants were assisted to climb out of the rotatory chair once they felt the post-rotatory illusion had fully dissipated.

7.3.1.3 Eye tracking and data analyses

The SMI Redn-Scientific remote eye tracker (SensoMotoric Instruments, Teltow, Germany) captured the participants' eye movements at 60 Hz during both of the one-minute experimental blocks. The tracker was secured at the foot of the laptop's screen. Participants' eye movements were calibrated prior to the first experimental block using the default routine incorporated in the SMI BeGaze software. Only the data for right eye movements in the x-axis, which occurred during the 30 s immediately after the velocity steps, were processed. The data were exported from SMI BeGaze to Excel (version 2016; Microsoft, Redmond, WA, USA) for smoothing with a macro-based, fourth order, low-pass Butterworth filter (Van Wassenbergh, 2007). The cut-off frequency was set at 6.15 Hz after Duchowski et al. (2014). Slow phase velocities (SPVs) were calculated using trigonometry as per Singh et al. (2016). A fifth order polynomial trend line was then fitted to the SPV profiles. For each task group, the data for the participant, whose trend lines had the highest coefficients of determination, were selected for further inspection and analysis. By interpolation from the trend lines, SPVs at the 10-s mark following impulse stimulation - 'SPV_{10}' - were estimated for the three participants or, more specifically, for their eye movements while they were completing the task (experimental block 1) and while they were staring at the white noise video (experimental block 2). Visual inspection of the trend lines had indicated that SPVs were maximal approximately 10 s after the velocity step across all of the SPV profiles.

7.3.2 Results and discussion

The mean proportion of errors across all six participants was low at 8.9% (*SD* = 7.2%). Error proportions for each of the participants are given in Table 7.1. Those participants, who completed the DASS task, appear to have made the most errors. This may simply relate to the greater difficulty of the DASS task, as indicated by the results of Study 2 (see section 5.4.5.1), rather than due to a specific disruption, by the superimposition of post-rotatory nystagmus, of the more complex saccadic eye movements presumably required by the DASS task. The low error proportions give an initial indication that it is possible for participants to undertake the SASS, SOSS and DASS tasks following impulse stimulation.

Table 7.1: Error proportions, SPV_{10} values and R^2 values for all six participants.

SPV_{10} - interpolated slow phase velocity 10 s after impulse stimulation; R^2 - coefficient of determination for the polynomial trend lines fitted to each SPV profile

	Error proportion (%)	SPV_{10} (°/s)		R^2	
	Block 1 - Task	Block 1 - Task	Block 2 - Noise	Block 1 - Task	Block 2 - Noise
SASS task group member					
P01	10.0	3.4	8.1	0.3	0.7
P03	0.0	-	-	-	-
SOSS task group member					
P02	3.3	2.9	4.3	0.2	0.1
P05	6.7	-	-	-	-
DASS task group member					
P04	13.3	-	-	-	-
P06	20.0	3.4	4.2	0.6	0.6
Total	8.9				

Further evidence that post-rotatory nystagmus does not preclude completion of the cognitive tasks derives from the SPVs that were calculated from the outputs of the remote eye tracker. By interpolation from three participants' SPV profiles, SPV_{10} values during the SASS, SOSS and DASS tasks were 3.4, 2.9 and 3.4°/s, respectively (see Table 7.1 for further details). During oculographic clinical assessments, nystagmus is typically only considered significant if SPVs exceed 4°/s (Shepard, Janky, & Eggers, 2013). Therefore, the SPVs obtained following impulse stimulation in the present study were low, indicating that the post-rotatory nystagmus was weak. Figure 7.2 depicts the eye movement traces and SPV profiles with polynomial trend lines for the participants in the SASS and DASS task groups, whose trend lines had the highest coefficients of determination. The large saccadic eye movements, which were evident during the DASS task, do not appear to have been disrupted by nystagmus according to Figure 7.2D. It appears that only the participant in the SASS task group (P01) had stronger nystagmus while he was staring at the white noise video (Figure 7.2B) compared to when he was completing the SASS task (Figure 7.2A). Overall, the post-rotatory nystagmus was suppressed by the strong visual cues provided by the internal features of the rotating chair's well-lit cabin, even when participants were not fixating specifically on the tasks' stimulus material.

This was a small, preliminary investigation, so the data may misrepresent the true scale of the nystagmus that impulse stimulation generates, even in participants with rich visual inputs. Furthermore, collecting eye movement data using a remote eye tracker is an untested and unconventional method. Eye movements were calibrated but the entire set-up was not. Systematic errors may have led to the underestimation of nystagmus intensities. However, based on the low error proportions, the eye movement traces in Figure 7.2, and the low SPVs, there is a relatively low likelihood that nystagmus would be an intractable confound if a larger scale investigation were undertaken to ascertain the direct effect of the aberrant space-motion information associated with impulse stimulation on higher cognition. The main investigation was, therefore, carried out.

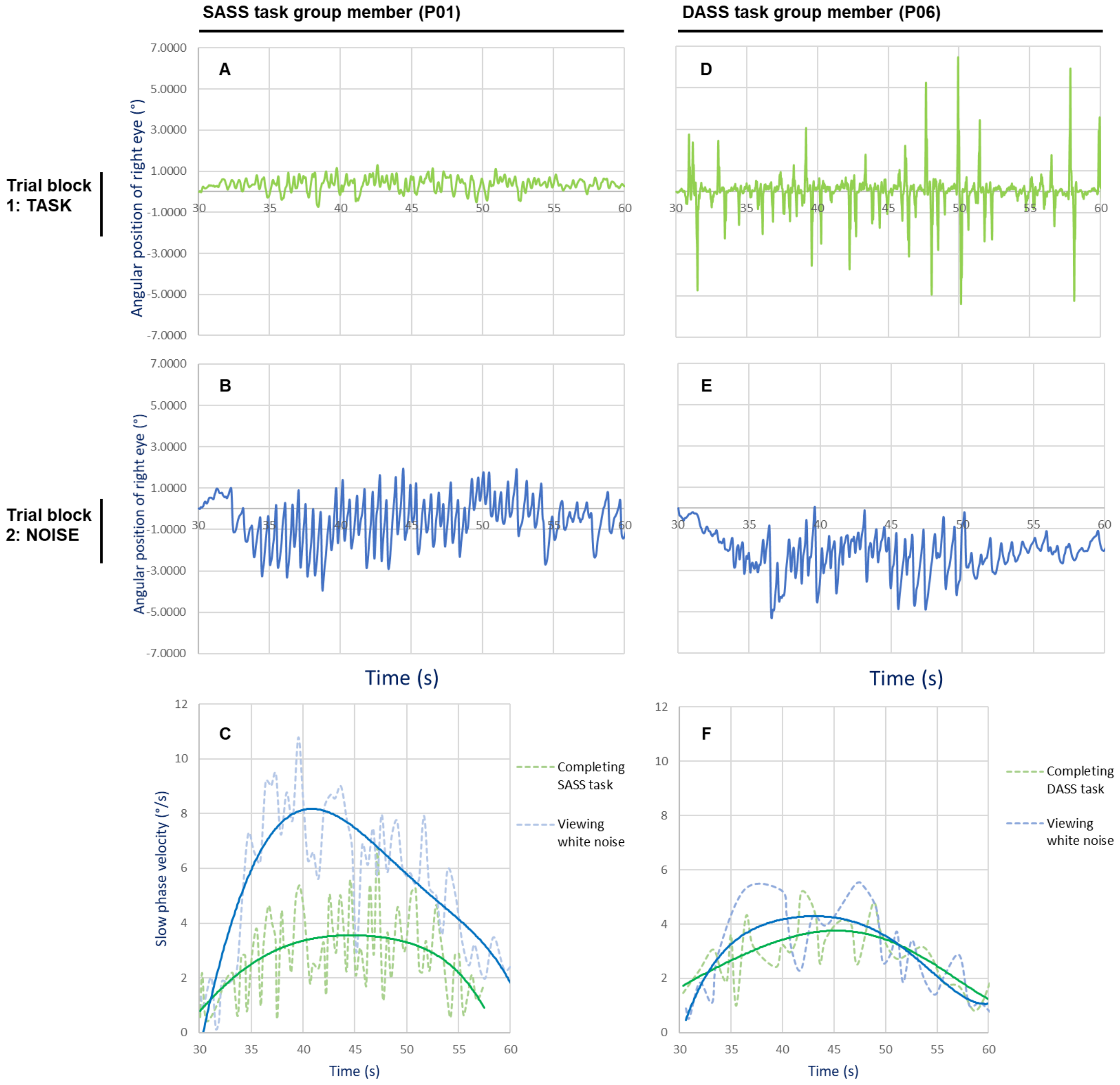


Figure 7.2: Graphs showing angular position of the right eye against time during trial blocks 1 (A and D) and 2 (B and E), plus respective slow phase velocities against time (C and F), for selected members of the SASS task and DASS task groups in the 30-s period after impulse stimulation.

SASS task = Single Avatar Stimulus Set task; DASS task = Double Avatar Stimulus Set task

7.4 Study 4B: Main investigation

7.4.1 Methods

7.4.1.1 Ethical considerations and recruitment

Full details of the ethical considerations are given in section 3.3. In view of the limitations associated with recruitment to the previous studies (see section 6.5.4), the recruitment procedure was adapted for this study. Three age strata were delineated to allow for stratified randomisation, which was mainly intended to raise the age of the sample, bringing it closer to the typical age of patients with balance disorders seen in secondary healthcare settings. 60 younger adults (18 to 39 years), 12 middle-aged adults (40 to 64 years) and 6 older adults (65 years and over) were sought. Within each age stratum, the intention was to study an equal number of male and female participants. The Psychology Department's Research Participant Scheme (RPS) was used once more to recruit some of the younger participants. But, the Participant Information Sheet for this study (see Appendix C) was also circulated outside the University of Westminster. More specifically, the researcher supplied it to friends and family, and to colleagues at Guy's and St Thomas' Hospitals. Local branches of the University of the Third Age were also contacted in search of older volunteers.

The power analysis conducted as part of Study 3 (see section 6.4.5) suggested that 34 participants per task group (102 participants in total) would have been needed in that study in order to have found a significant task by space-motion cue congruity interaction effect on error proportion at 80% power. Given the potential for impulse stimulation to yield a more persistent misperception of self-motion than roll-plane optokinetic stimulation (see sections 1.6.3 and 3.3), the aim was to recruit 26 rather than 34 participants to the three task groups (78 participants in total) in the present study.

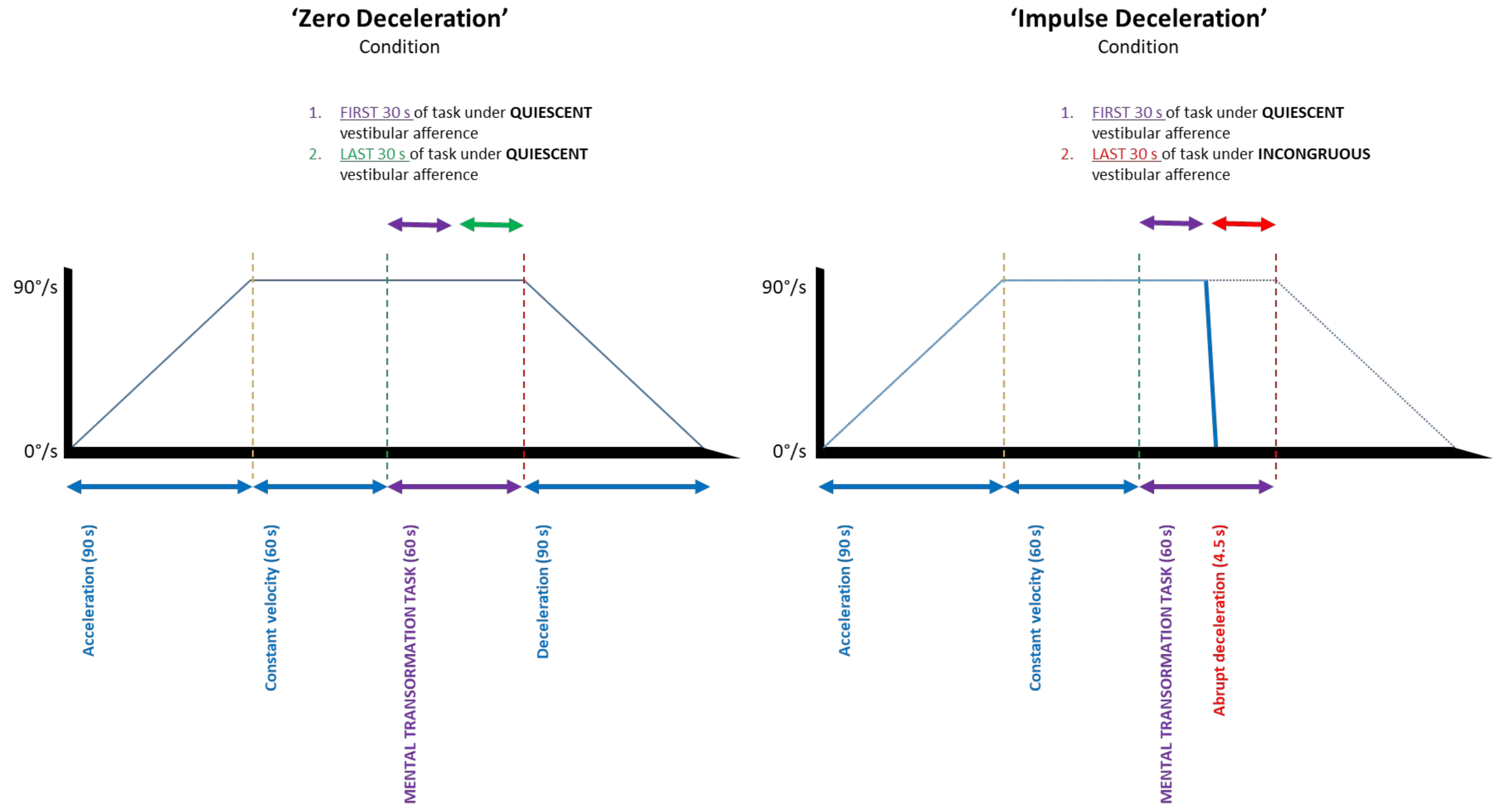
7.4.1.2 Aberrant space-motion stimulation

Aberrant space-motion information was generated in the present study by way of impulse stimulation (see section 7.3.1.1). As discussed in section 7.2, this causes incongruous vestibular activation. Delivering impulse stimulation halfway through trial blocks was intended to make the participants less able to anticipate it.

In the control condition, the chair did not abruptly decelerate when participants were midway through trial blocks. Instead, it continued to rotate at 90°/s until the one-minute blocks ended. Thereafter, it decelerated at $1°/s^2$ until it came to a standstill. The lack of a velocity step during the control condition meant there was no incongruous vestibular activation. More specifically, the participants' vestibular systems would have remained in an adapted state, so both vestibular and visual afference would have signalled stationarity during the latter half of the trial blocks. By gently decelerating the chair after the one-minute blocks in the control condition, the participants were not overly exposed to the velocity step so had less opportunity to habituate to it. The contrasting profiles of the chairs' rotational velocities during the experimental (incongruous) and control (congruous) conditions are depicted in Figure 7.3.

During both the experimental and control conditions, the direction of chair rotation was towards each participant's dominant side (see section 7.4.1.4.3). Stronger responses have been shown in cortical vestibular processing areas ipsilateral to the stimulated ear (Lopez & Blanke, 2011). Therefore, by adjusting the direction of chair rotation in accordance with limb dominance, each participant's dominant vestibular cortical hemisphere, which is contralateral to the dominant sensorimotor hemisphere (Dieterich & Brandt, 2015), was most active during steady acceleration of the chair, and until vestibular adaptation occurred. Then, every participant's non-dominant vestibular cortical hemisphere mediated the post-rotatory illusion following impulse stimulation.

To mask the sound of the chair's motor during both the experimental and control conditions, Brownian noise was played through the chair's in-built speaker positioned above the participants' heads (De Winkel, Katliar, & Bülthoff, 2015; Kaski et al., 2016; Nigmatullina et al., 2015). The researcher communicated with participants using a microphone which transmitted via the chair's speaker. The Brownian noise and wired communication ensured that participants' auditory location cues were impoverished (De Winkel et al., 2015).


‘Zero Deceleration’ Condition

1. FIRST 30 s of task under **QUIESCENT** vestibular afference
2. LAST 30 s of task under **QUIESCENT** vestibular afference

‘Impulse Deceleration’ Condition

1. FIRST 30 s of task under **QUIESCENT** vestibular afference
2. LAST 30 s of task under **INCONGRUOUS** vestibular afference

Figure 7.3: Rotational velocity profiles during the control (congruous; A) and experimental (incongruous; B) conditions.

7.4.1.3 Cognitive tasks

This study employed the SASS, SOSS and DASS tasks with those stimuli depicting the avatar (SASS and DASS tasks) or measuring scale (SOSS task) turned to the left or right by 90º omitted (see section 6.3.3). In contrast to the methods adopted in the preliminary study above (see section 7.3.1.2), the tasks were executed using the E-Prime experiment generator software on the Toshiba laptop once more (see section 3.5). Manual responses were also re-implemented. The response buttons were the laptop's ridged 'F' and 'J' keys. Respectively, these buttons corresponded with 'left' and 'right' responses on the SASS and SOSS tasks, and with 'same' and 'different' responses on the DASS task. Participants rested their index fingers on these buttons throughout experimentation.

All participants completed two discrete practice blocks before the experimental blocks (see section 7.4.1.8 for further details). During the first practice block, the durations of the tasks' stimulus elements were the same as they had been in Studies 1, 2 and 3. That is, each trial commenced with the presentation of a black fixation cross, which appeared for 1400 ms. This was followed immediately by the stimulus, which terminated after a response had been made, or after 2100 ms, whichever was sooner. Thereafter, visual feedback was displayed about whether the response was correct or incorrect. This feedback stayed on-screen for 1500 ms, and was followed by the fixation cross for the next trial. During the second practice block, the durations of the fixation cross and feedback screens were both reduced to 500 ms. These were reduced still further in the experimental blocks to 150 and 300 ms, respectively.

7.4.1.4 Trait measures

The participants' psychological traits and other general proclivities were assessed using three validated measures for reasons given in section 3.6. Blank copies of all three measures can be found in Appendix D, but their development and psychometric properties are described next.

7.4.1.4.1 State-Trait Inventory for Cognitive and Somatic Anxiety (STICSA)

As detailed in section 3.6.1.

7.4.1.4.2 Motion Sickness Susceptibility Questionnaire short-form (MSSQ-Short)

The MSSQ-Short was developed by Golding (2006) to facilitate the prediction of individual differences in motion sickness caused by motion stimuli. It lists nine modes of transport or amusement rides, against which the respondent must rate how often he or she felt sick or nauseated (not applicable-never travelled; never felt sick = 0; rarely felt sick = 1; sometimes felt sick = 2; frequently felt sick = 3) as a child and also as an adult. Motion sickness scores are calculated separately for childhood (‘MSA’) and adulthood (‘MSB’) experiences by summing the respective responses, multiplying the sum by nine, then dividing this figure by nine less the number of modes of transport never travelled. The MSSQ-Short raw score is found by adding MSA and MSB. Scores of 19 or greater would have been in the 75th percentile of scores obtained from a normal population (Golding, 2006), so indicate a relatively high susceptibility to motion sickness. The MSSQ-Short has demonstrated good internal consistency (Cronbach’s alpha coefficient .87) and test-retest reliability (correlation coefficient approximately .9; Golding, 2006).

7.4.1.4.3 Modified Edinburgh Handedness Questionnaire (mEHQ)

The original EHQ was developed by Oldfield (1971) to efficiently gauge hand laterality. It comprised 10 manual tasks or manipulanda against which respondents had to rate their preference for right- or left-handed use. Salmaso and Longo (1985) adapted the 10 items included in the EHQ, since some of the original tasks, such as writing, were shown to be subject to cultural pressure and were poorly representative of limb dominance, therefore. On their mEHQ (Salmaso & Longo, 1985), respondents specify hand preference on a five-point Likert scale (strongly left-handed = -2; left-handed = -1; indifferent = 0; right-handed = 1; strongly right-handed = 2). A laterality quotient is then calculated according to the formula given in Appendix D. Salmaso and Longo (1985) were able to show that handedness distributions depend on item selection, familial sinistrality and age.

7.4.1.5 State measures

A series of measures were collected during or immediately after every experimental block for reasons given in section 3.7. Blank copies of the self-report measures described below are provided in Appendix D.

7.4.1.5.1 Simulator Sickness Questionnaire (SSQ)

The SSQ was derived from pre-existing measures of 'real' motion sickness (Kennedy, Lane, Berbaum, & Lilienthal, 1993). In part, it was intended to identify simulators with problematic realism or fidelity. The SSQ lists 16 symptoms which are associated with incongruous motion environments, such as vertigo, nausea and difficulty concentrating. Following a simulator ride, respondents rate their level of each symptom on a four-point Likert scale (none = 0; slight = 1; moderate = 2; severe = 3). Factor analysis by Kennedy et al. (1993) identified three distinct symptom clusters which were labelled 'nausea', 'oculomotor' and 'disorientation'. Raw scores for each of these subscales are found by summing responses given to respective items. Weighted subscale scores are calculated by multiplying the raw scores by specific scaling factors. The total SSQ score is simply the sum of the three raw subscale scores. In Kennedy and colleagues' (2003) research, total scores above 10 for military aviation personnel indicated that a simulator caused significant symptoms. Scores exceeding 20 implied that a simulator was particularly problematic. Using a driving simulator, the SSQ was found to have good test-retest reliability; $r \sim .78$ (Kennedy et al., 2003).

7.4.1.5.2 Self-evaluation item (Y-6 item)

In order to efficiently record participants' state anxiety following periods of rotation in the chair, they were requested to complete the Y-6 item. This is a short-form of the State-Trait Anxiety Inventory (see section 3.6.1 for further details) developed by Marteau and Bekker (1992). Participants respond to three anxiety-present and three anxiety-absent items using a four-point Likert scale (not at all = 1; somewhat = 2; moderately = 3; very much = 4). Subsequently, scores for the anxiety-absent items are reversed, and all scores are then added together to give a raw total. The 'total STAI Y-6 item score' is found by multiplying the raw total by 20 and dividing by six. Marteau and Bekker (1992) obtained correlation coefficients greater than .9 using the Y-6 item, indicating it has good test-retest reliability. They also found that use of this measure produced scores which were similar to those obtained using the full-form STAI.

7.4.1.5.3 Mental effort scale

As described in section 3.7.4.

7.4.1.5.4 Perception of balance scale

As the objective was for participants to feel secure in the rotating chair, and minimally distracted by the imperative to maintain their sitting balance, they were asked to report their perception of stability on a custom two-item scale. This comprised both an imbalance-present and an imbalance-absent item. Participants responded to these using the four-point Likert scale of the Y-6 item (see section 7.4.1.5.2). The score on the imbalance-absent item was reversed before the 'total perception of balance score' was found by simple addition of the two scores. A higher total score indicated a stronger perception of imbalance while the chair was rotating.

7.4.1.5.5 Heart rate variability (HRV) measurement

Recordings of the participants' pulse were taken during all experimental trial blocks in order to gauge their autonomic balance in real-time. The recordings were collected by way of a wireless Polar T31 pulse transmitter (Polar Electro, Kempele, Finland), which was strapped to participants' chests just below the bra line in direct contact with their skin. To optimise conductance, electrically conductive gel was applied to the transmitter's inbuilt electrodes before it was fitted. The transmitter sampled electrical activity of the heart at 1000 Hz. Its receiver was attached to the stationary base of the rotating chair. This connected by wire to a PowerLab 4/20 unit (ADInstruments, Sydney, Australia), which, in turn, was connected to a laptop running LabChart Pro v8.0 (ADInstruments).

Following the acquisition of time-stamped heartbeats, frequency domain analysis, using the Lomb peridogram, was performed in the HRV 2.0 module of the LabChart program. This technique partitions the total variance of a continuous series of beats into its frequency components, most importantly into the low frequency (LF; 0.04-0.15 Hz) and high frequency (HF; 0.15-0.45 Hz) components (Billman, 2013). The HF component is widely believed to reflect vagal (i.e. parasympathetic) efference to the heart, whereas the LF component is assumed to relate to sympathetic outflow to the heart (Task Force of the European Society of Cardiology and the North American Society of Pacing and Electrophysiology, 1996). Based on these assumptions, the ratio of LF to HF (LF/HF ratio) has been used to infer autonomic balance in health and disease. According to Malliani et al. (1991, p. 482), "functional states likely to be accompanied by an increased sympathetic activity are characterized by a shift of the LF-HF balance in favor of the LF component; the opposite occurs during presumed increases in vagal activity". Although some researchers disagree with this premise (e.g. Billman, 2013), the LF/HF ratio has been used as a marker of mental stress (Salahuddin, Cho, Gi Jeong, & Kim, 2007). The present study followed suit; the LF/HF ratio was taken to be an indirect measure of anxiety. Time domain cardiovascular parameters have been used in previous investigations into the effect of acute dizziness on cognition as surrogates of participants' psychological states (Ambler & Guedry, 1972; Ehrenfried, Guerraz, Thilo, Yardley, & Gresty, 2003).

Data for every trial block were binned into the first and last 30 s of the respective block, and LF/HF ratios were calculated for the latter periods. It is debatable whether frequency domain analyses can be conducted on such short epochs of data. However, there is evidence that HRV parameters calculated for 30-s intervals are reliable and correlate well with parameters calculated for longer periods (Brisinda et al., 2013; Salahuddin et al., 2007). Furthermore, research has shown that Polar heart rate monitors provide short-term HRV data with no appreciable bias or additional random error in comparison to the outputs of well-established 12-lead ECG systems (Nunan et al., 2009).

7.4.1.6 Strategy measures

As detailed in section 6.3.6.

7.4.1.7 Space-motion misperception measures

Based on the method used to measure the vection illusion in Studies 1 and 3 (see section 3.9), participants in the present study were asked whether they had experienced the post-rotatory illusion during trial blocks, and, if so, how strong it had been. The specific questions, which the participants had to respond to at the end of experimentation about their experience of the illusion, are given in Appendix D. Accordingly, the strength of the post-rotatory illusion was rated as either weak, moderate or strong. These responses were converted to scores of 1, 2 and 3, respectively.

7.4.1.8 Experimental procedure

As detailed in section 3.10, every testing session began with a slide-based briefing on the study. Participants were asked to complete a health screening questionnaire and then provide written consent if they were content to do so. They were then requested to state their occupation and any pressing health issues which the health screening questionnaire had missed. Height and mass measurements were collected. Once participants had completed the STICSA, MSSQ-Short and mEHQ (see section 7.4.1.4), they were randomly allocated to undertake just one of the cognitive tasks.

Participants were assisted to climb in to the rotatory chair. Its seatbelt was fastened around them, and the laptop was positioned on their laps. They initially practised their allocated task while the chair was stationary and one panel of the fabric cabin was open so that they had orientation cues from the laboratory. During this first practice block, participants had one attempt at each of the 12 stimuli which comprised the tasks' stimulus sets. While still sat in the stationary chair, they were given a slide-based briefing about the second practice block, and how the chair would rotate during it. The fabric cabin was closed and chair rotation was initiated at a constant acceleration of $1^{o}/s^{2}$. Just for this practice block, the direction of chair rotation was towards participants' non-dominant upper limbs, and the velocity of the chair levelled off at 30 rather than $90^{o}/s$. After it did so, participants were requested to move their heads slightly in the coronal and sagittal planes so that they experienced the cross-coupled acceleration stimulation and its nauseating effects. This helped to emphasise to the participants that they should keep their heads as still as possible throughout testing. Brownian noise was played into the chair's cabin, and the cognitive task was initiated for one minute. The chair's angular velocity remained constant throughout. With prior warning, the chair decelerated abruptly and came to a standstill. Participants were asked if this caused any motion illusions, and they were requested to describe those illusions experienced. A final briefing was given about the experimental trial blocks and the chair motions involved.

The experiment proper comprised six blocks of trials of the allocated cognitive task. Each block had a fixed duration of one minute. In an interleaving manner, three of the blocks were conducted with zero deceleration of the chair (i.e. it maintained a constant angular velocity of $90^{o}/s$ – denoted 'congruous cues'), and three blocks with impulse deceleration halfway through them (denoted 'incongruous cues'). These two motion conditions constituted the two levels of the within-subject factor 'space-motion cue congruity'. Whether the first block comprised congruous or incongruous space-motion cues was counterbalanced between participants in the same task group. On all six occasions, Brownian noise started to play into the chair's cabin once its angular velocity levelled off at $90^{o}/s$. It continued to play throughout the subsequent one-minute period of constant velocity rotation and then during the one-minute period in which participants undertook their allocated task. Pulse recordings were only taken during the latter period.

The fabric cabin was opened as soon as the chair came to a standstill following the gentle deceleration, which featured in the control condition. The participants were then passed paper copies of the SSQ, Y-6 item, mental effort scale and perception of balance scale to complete (see section 7.1.4.5). To standardise the latency between termination of trial blocks and completion of the self-report scales across control and experimental conditions, the fabric cabin was only opened once 90 s had elapsed following the trial blocks in the latter condition. The chair was stationary throughout this period, having come to a standstill much sooner due to the velocity step. Completing the self-report measures following each block took over two minutes, and allowed for any after-effects of the rotatory motion to dissipate. After all of the experimental blocks had been completed, participants were asked about the strategies they had used in order to solve their allocated tasks (see section 7.4.1.6). Finally, they were asked whether they had experienced the post-rotatory illusion during experimentation, and, if so, how strong it had been (see section 7.4.1.7). Their levels of malaise were evaluated every 5 minutes at the very end of the experiment, in order to ensure that all participants returned to an asymptomatic baseline before departing the laboratory.

7.4.1.9 Variables

Details of most of the variables can be found in section 3.11, however, the following addenda apply. The predictor variable ‘task’ had three levels: SASS task vs SOSS task vs DASS task. LF/HF ratio served as a secondary, physiological outcome variable and as a mediator variable in the hypothesis tests (see section 7.4.1.14). The secondary, subjective outcome variables in this study included the SSQ total score and subscores (nausea, oculomotor and disorientation scores) and the total STAI Y-6 item score. Responses given by participants regarding their mental effort, perception of balance, task strategy and space-motion misperception served as tertiary outcome variables.

7.4.1.10 Hypotheses

As detailed in section 3.12.

7.4.1.11 Reduction of bias

The procedures that were used to reduce the impact of bias are described in section 3.13. In addition to these, LF/HF ratios were not calculated for those participants whose heart rates were greater or lesser than the mean heart rate for the sample by 1.96 standard deviations. This served to exclude HRV data for participants with heart rates below 44 and above 96 beats per minute. On inspection of the data, poor relay of the pulse signal from the wireless transmitter or the exclusion of numerous ectopic beats accounted for the very low heart rates that were recorded from a few individuals.

7.4.1.12 Comparisons of baseline characteristics

As detailed in section 3.14.1.

7.4.1.13 General descriptives

Details of the descriptive statistics calculated from the data are given in section 3.14.2. The treatment of the strategy responses obtained from the present study is described in section 6.3.6.

7.4.1.14 Hypothesis tests

As detailed in section 3.14.3.

7.4.1.15 Supplementary analyses

The basis of the supplementary analyses is described in section 3.14.4. To clarify, paired t-tests were carried out to infer the effects of space-motion cue congruity on secondary outcomes, that is, on LF/HF ratio, SSQ scores (total score and subscores) and total STAI Y-6 item score. In addition, between-task comparisons of all of the tertiary outcome variables, with the space-motion cue congruity factor collapsed, were carried out by way of Kruskal-Wallis tests. Within-subjects comparisons of just the mental effort and perception of balance scores, specifically between levels of the space-motion cue congruity factor, were carried out using Wilcoxon signed-rank tests.

7.4.2 Results

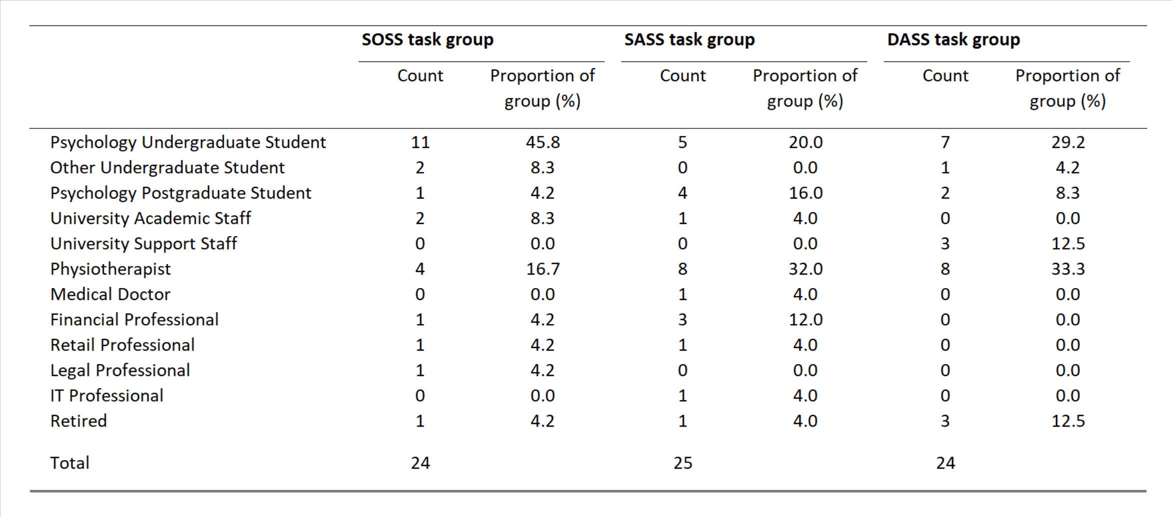
7.4.2.1 Participants and comparisons of their baseline characteristics

In total, 78 volunteers took part in this study, having met the eligibility criteria and provided written informed consent. The SASS, SOSS and DASS task groups all comprised 26 randomly-allocated participants. The mean proportion of errors across all of the participants was low at 5.7% (*SD* = 6.9%). However, five participants demonstrated particularly high cumulative error compared to other members of their groups. More specifically, their error proportions were more than 1.96 standard deviations greater than the mean proportions for their groups. One of these participants had been in the SASS task group, two had been in the SOSS task group, and another two had been members of the DASS task group. All data for these five participants were excluded from the analyses given that their task performance was atypical, and in the attempt to reduce bias (see section 3.13.1). Therefore, the data that were analysed related to 25 SASS task group participants, 24 SOSS task group members and 24 participants in the DASS task group. The LF/HF ratio data for one participant in the SOSS task group was excluded from relevant analyses because she was taking a medicine with a negative inotropic action (bisoprolol).

The mean age of the remaining 73 participants was 33.1 years (*SD* = 13.8 years). There were no between-group differences in age according to a one-way ANOVA. There were 38 (52.1%) female participants spread evenly among the task groups (SASS task group, *n* = 13; SOSS task group, *n* = 13; DASS task group, *n* = 12). Seven (9.6%) of the participants were left-handed and they, too, were evenly distributed amongst the groups (SASS task group, *n* = 3; SOSS task group, *n* = 2; DASS task group, *n* = 2). Within each of the groups, the participants had varied occupations as detailed in Table 7.2.

Table 7.2: Occupations of the participants in each of the task groups.

SASS task = Single Avatar Stimulus Set task; SOSS task = Single Object Stimulus Set task; DASS task = Double Avatar Stimulus Set task



	SOSS task group		**SASS task group**		**DASS task group**	
	Count	Proportion of group (%)	Count	Proportion of group (%)	Count	Proportion of group (%)
Psychology Undergraduate Student	11	45.8	5	20.0	7	29.2
Other Undergraduate Student	2	8.3	0	0.0	1	4.2
Psychology Postgraduate Student	1	4.2	4	16.0	2	8.3
University Academic Staff	2	8.3	1	4.0	0	0.0
University Support Staff	0	0.0	0	0.0	3	12.5
Physiotherapist	4	16.7	8	32.0	8	33.3
Medical Doctor	0	0.0	1	4.0	0	0.0
Financial Professional	1	4.2	3	12.0	0	0.0
Retail Professional	1	4.2	1	4.0	0	0.0
Legal Professional	1	4.2	0	0.0	0	0.0
IT Professional	0	0.0	1	4.0	0	0.0
Retired	1	4.2	1	4.0	3	12.5
Total	24		25		24	

One-way ANOVAs revealed there were no between-group differences in the heights (*M* = 169.45 cm; *SD* = 8.99 cm) and weights (*M* = 70.35 kg; *SD* = 11.53 kg) of participants in the three groups. According to scores on the STICSA, eleven and seven of all of the participants had possible and probable anxiety disorders, respectively. Furthermore, ten had a probable cognitive anxiety component, and nine had a probable somatic anxiety component. There were no between-group differences in STICSA subscale and total scores. Seven participants in the SASS task group, two members of the SOSS task group, and three in the DASS task group were highly susceptible to motion sickness according to their MSSQ-Short raw scores. Overall, participants in the three groups did not have significantly different motion sickness susceptibilities when MSSQ-Short raw scores were subjected to a one-way ANOVA.

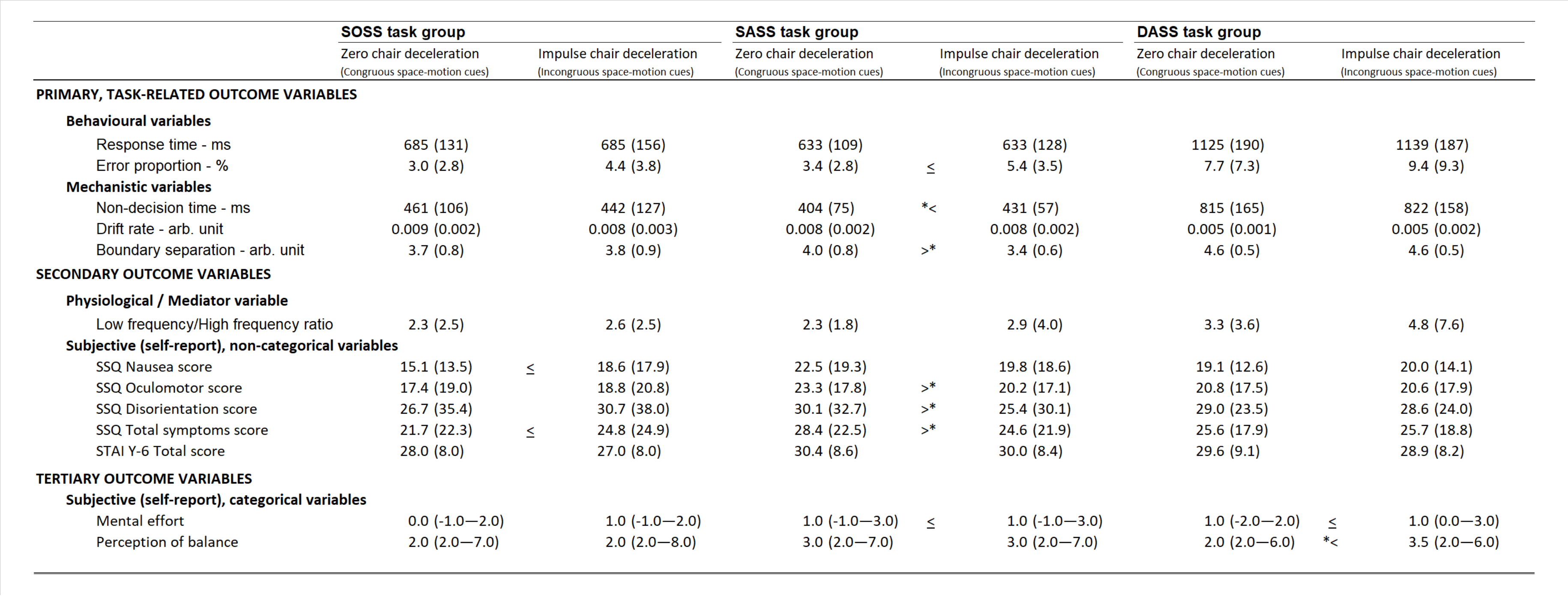
7.4.2.2 General descriptives

The data for all of the dependent variables, except task strategy and space-motion misperception, were amalgamated according to task and whether they derived from trial blocks performed during exposure to congruous or incongruous space-motion cues. Averages were then computed and inspected. These data are given in table 7.3, which appears to indicate that impulse stimulation, by way of the velocity steps from 90°/s, had relatively circumscribed effects on primary, secondary and tertiary outcome variables across the task groups. Some of the data, particularly related to the secondary outcome variables, appear to be dispersed according to the relatively large standard deviation values.

Across the six experimental blocks, participants in the SASS and SOSS task groups completed a mean of 293.6 (*SD* = 25.0) and 284.6 (*SD* = 29.0) trials, respectively. As had been shown in Studies 2 and 3, significantly fewer trials (*M* = 205.0; *SD* = 27.5) were undertaken by those in the DASS task group, $F(2, 72) = 78.05$, $p < .001$. Most participants (84%) in the SASS task group experienced the post-rotatory illusion, as did most in the SOSS (83%) and DASS (92%) task groups. 35% of participants in the DASS task group reported that the illusion was strong, as did 43% and 35% of participants in the SASS and SOSS task groups, respectively. The median score for the strength of the post-rotatory illusion in all of the groups was 2 (’moderate’).

Table 7.3: Data obtained in Study 4 for primary, secondary and tertiary outcome variables categorised according to task and space-motion cue congruity.

All data are mean values with standard deviations in parentheses, except for mental effort and perception of balance (medians with minimum and maximum values in parentheses). Arrows with stars denote significant differences as revealed by simple effects analyses. Underlined arrows indicate borderline significant differences (see section 3.14.3).



	SOSS task group			**SASS task group**			**DASS task group**		
	Zero chair deceleration (Congruous space-motion cues)		Impulse chair deceleration (Incongruous space-motion cues)	Zero chair deceleration (Congruous space-motion cues)		Impulse chair deceleration (Incongruous space-motion cues)	Zero chair deceleration (Congruous space-motion cues)		Impulse chair deceleration (Incongruous space-motion cues)
PRIMARY, TASK-RELATED OUTCOME VARIABLES									
Behavioural variables									
Response time - ms	685 (131)		685 (156)	633 (109)		633 (128)	1125 (190)		1139 (187)
Error proportion - %	3.0 (2.8)		4.4 (3.8)	3.4 (2.8)	≤	5.4 (3.5)	7.7 (7.3)		9.4 (9.3)
Mechanistic variables									
Non-decision time - ms	461 (106)		442 (127)	404 (75)	*<	431 (57)	815 (165)		822 (158)
Drift rate - arb. unit	0.009 (0.002)		0.008 (0.003)	0.008 (0.002)		0.008 (0.002)	0.005 (0.001)		0.005 (0.002)
Boundary separation - arb. unit	3.7 (0.8)		3.8 (0.9)	4.0 (0.8)	>*	3.4 (0.6)	4.6 (0.5)		4.6 (0.5)
SECONDARY OUTCOME VARIABLES									
Physiological / Mediator variable									
Low frequency/High frequency ratio	2.3 (2.5)		2.6 (2.5)	2.3 (1.8)		2.9 (4.0)	3.3 (3.6)		4.8 (7.6)
Subjective (self-report), non-categorical variables									
SSQ Nausea score	15.1 (13.5)	≤	18.6 (17.9)	22.5 (19.3)		19.8 (18.6)	19.1 (12.6)		20.0 (14.1)
SSQ Oculomotor score	17.4 (19.0)		18.8 (20.8)	23.3 (17.8)	>*	20.2 (17.1)	20.8 (17.5)		20.6 (17.9)
SSQ Disorientation score	26.7 (35.4)		30.7 (38.0)	30.1 (32.7)	>*	25.4 (30.1)	29.0 (23.5)		28.6 (24.0)
SSQ Total symptoms score	21.7 (22.3)	≤	24.8 (24.9)	28.4 (22.5)	>*	24.6 (21.9)	25.6 (17.9)		25.7 (18.8)
STAI Y-6 Total score	28.0 (8.0)		27.0 (8.0)	30.4 (8.6)		30.0 (8.4)	29.6 (9.1)		28.9 (8.2)
TERTIARY OUTCOME VARIABLES									
Subjective (self-report), categorical variables									
Mental effort	0.0 (-1.0—2.0)		1.0 (-1.0—2.0)	1.0 (-1.0—3.0)	≤	1.0 (-1.0—3.0)	1.0 (-2.0—2.0)	≤	1.0 (0.0—3.0)
Perception of balance	2.0 (2.0—7.0)		2.0 (2.0—8.0)	3.0 (2.0—7.0)		3.0 (2.0—7.0)	2.0 (2.0—6.0)	*<	3.5 (2.0—6.0)

In the SASS task group, participants reported having engaged in mental self-translocation (MS-TL) during 49.5% of trials. They stated that they adopted a mental rotation strategy and a transposing strategy during 19.3% and 31.3% of the remaining trials, respectively. Those in the SOSS task group declared that they had completed 16.8% of trials using the MS-TL strategy, 20.8% of trials employing the mental rotation strategy, and 62.4% of trials using the transposing strategy. Finally, members of the DASS task group appear to have relied most heavily on the mental rotation strategy; they reported having used it in 56.8% of trials. They stated that they had utilised MS-TL and the transposing strategy during 18.9% and 24.3% of the remaining trials, respectively.

7.4.2.3 Hypothesis tests

Eleven participants in the SOSS task group, ten in the SASS task group and nine in the DASS task group achieved 100% accuracy on trials undertaken during exposures to both zero (i.e. congruous cues) and impluse (i.e. incongruous cues) deceleration of the rotating chair. It was not possible to calculate mechanistic variables (drift rate, boundary separation and non-decision time) for these 30 participants given the constraints of the EZ-diffusion model (see section 3.11.2.1.2). Hence, sets of mechanistic variable data for 15 participants in the SASS task group, 13 in the SOSS task group and 15 in the DASS task group were subjected to the hypothesis tests. Regarding the behavioural variables (RT and error proportion), data from all 25 participants in the SASS task group and all 24 in the SOSS and DASS task groups were subjected to the analyses.

7.4.2.3.1 Tests relating to null hypothesis 1

To test whether there were interaction effects of the independent variables (IVs; task and space-motion cue congruity) on any of the primary outcome variables, a series of two-way ANOVAs were conducted. There was a significant interaction between the IVs affecting the mechanistic variable boundary separation, $F(2, 40) = 4.07$, $p = .025$, $\eta_p^2 = .169$, as depicted in Figure 7.4. According to the data presented in Table 7.3, it would appear that participants in the SASS task group may have been less cautious about their responses following impulse stimulation, whereas the response conservativeness of participants in the other groups did not differ. There were no other significant interaction effects on the remaining primary outcome variables; the effect on non-decision time being the next largest, $F(2, 40) = 2.39$, $p = .105$, $\eta_p^2 = .107$. For the sake of completeness, there was a main effect of space-motion cue congruity on error proportion, $F(1, 70) = 7.69$, $p = .007$, $\eta_p^2 = .099$, which indicates that impulse stimulation tended to disrupt performance on the tasks. There were no other main effects of the space-motion cue congruity factor.

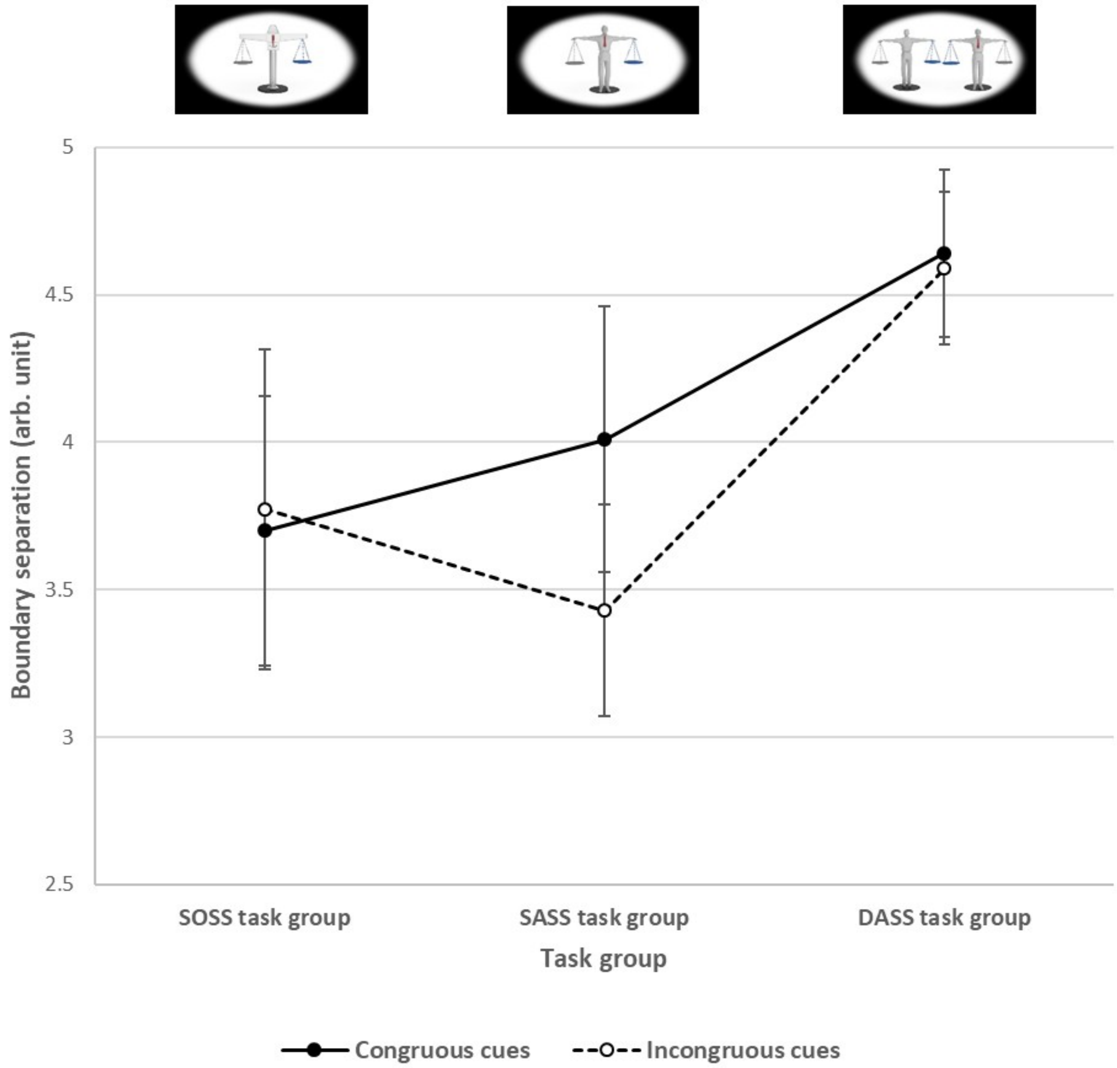


Figure 7.4: Line graph depicting the significant interaction effect (task by space-motion cue congruity) on the primary dependent variable, boundary separation.

Error bars represent 95% confidence intervals.

There was a significant main effect of task on all five primary outcome variables: RT, $F(2, 70) = 81.74$, $p < .001$, $\eta_p^2 = .700$; error proportion, $F(2, 70) = 7.00$, $p = .002$, $\eta_p^2 = .167$; drift rate, $F(2, 40) = 23.02$, $p < .001$, $\eta_p^2 = .535$; boundary separation, $F(2, 40) = 10.28$, $p < .001$, $\eta_p^2 = .339$; non-decision time, $F(2, 40) = 52.18$, $p < .001$, $\eta_p^2 = .723$. The Bonferroni post hoc procedure indicated that responses on the DASS task were significantly less efficient than responses on the SASS task in terms of RT (95% CI for the size of the between-group difference; 395 to 604 ms), error proportion (95% CI; 0.7 to 7.5%), drift rate (95% CI; -0.005 to -0.002 arb. unit), boundary separation (95% CI; 0.3 to 1.5% arb. unit) and non-decision time (95% CI; 293 to 509 ms). Compared to responses on the SOSS task, those made during the DASS task were also less efficient (CI for difference in RT: 342 to 554 ms, CI for difference in error proportion: 1.4 to 8.2%, CI for difference in drift rate: -0.005 to -0.002 arb. unit, CI for difference in boundary separation: 0.3 to 1.5 arb. unit, CI for difference in non-decision time: 255 to 479 ms).

Data pertaining to the secondary outcome variables (LF/HF ratio, SSQ total and subscores and total STAI Y-6 item score) were also subjected to the same two-way ANOVAs to test for task by cue congruity interaction effects. There were significant interactions which affected the SSQ nausea score, $F(2, 70) = 4.12, p = .020, \eta_p^2 = .105$, SSQ disorientation score, $F(2, 70) = 6.60, p = .002, \eta_p^2 = .159$, and SSQ total score, $F(2, 70) = 5.61, p = .006, \eta_p^2 = .138$. According to the data presented in Table 7.3, it would appear that participants in the SOSS task group may have experienced more simulator symptoms under incongruous conditions but, conversely and unexpectedly, participants in the SASS task group may have experienced more symptoms during congruous conditions. The significant interaction effect on SSQ total score is depicted in Figure 7.5. There were no main effects of task on the secondary outcome variables, and just one main effect of space-motion cue congruity. This related to the total STAI Y-6 item score, $F(1, 70) = 5.46, p = .022, \eta_p^2 = .072$. This main effect implies that there was a tendency for impulse stimulation to reduce reported anxiety levels across the task groups.

7.4.2.3.2 Tests relating to null hypothesis 2

To test whether there were within-subjects, simple effects of space-motion cue congruity on the primary outcome variables, a series of paired t-tests was conducted. These revealed that impulse stimulation caused a significant reduction in boundary separation (i.e. the cautiousness of responses), $t(14) = 2.89, p = .014, r = .612$ (see Figure 7.6A), and a significant increase in non-decision time (i.e. non-explicit decision processing), $t(14) = 2.90, p = .023, r = .613$ (see Figure 7.6B), only on the SASS task. There was also a borderline significant increase in error only on that task, $t(24) = 2.34, p = .033, r = .431$, as depicted in Figure 7.6C. There were no simple effects of the cue congruity factor on any primary DVs for the SOSS and DASS tasks. The largest effect was on error proportion for the SOSS task, *t*(23) = 0.09, *p* = .105, *r* = .346.

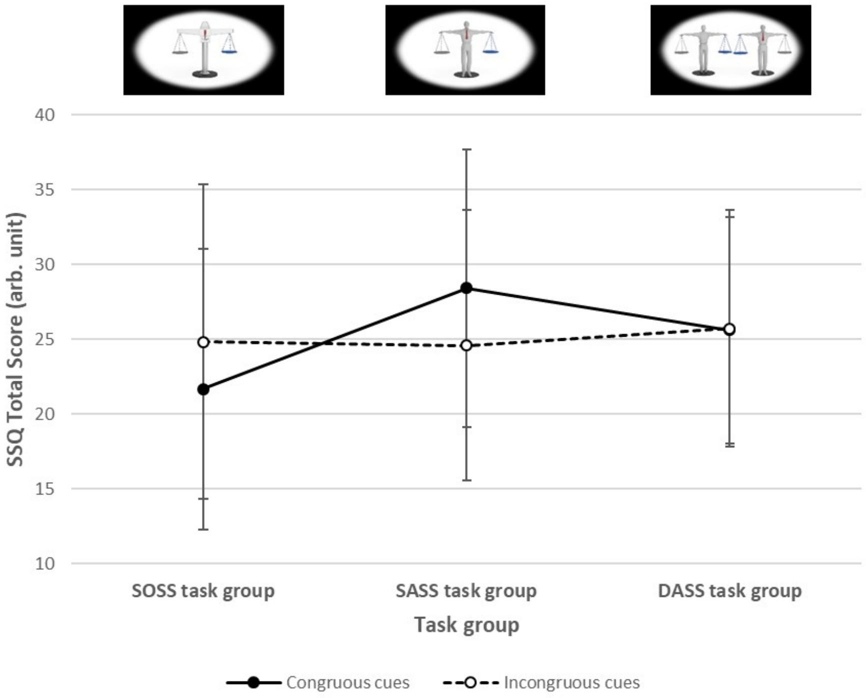


Figure 7.5: Line graph depicting the significant interaction effect (task by space-motion cue congruity) on SSQ total score, a secondary dependent variable.

Error bars represent 95% confidence intervals.

All of the data pertaining to the primary outcome variables were re-tested for simple effects of the space-motion cue congruity factor using the path-analytic method of mediation analysis, which controlled for the effect on cognitive performance of LF/HF ratio. These analyses revealed significant direct effects of cue congruity on boundary separation, *t*(12) = 3.11, *p* = .009, c' = -0.62, and on non-decision time, *t*(12) = 2.66, *p* = .021, c' = 27.74, and a borderline significant direct effect on error proportion, *t*(22) = 2.31, *p* = .031, c' = 2.08. That is, with LF/HF ratio controlled, the three simple effects detailed above were not abolished. There were no significant indirect effects of cue congruity via LF/HF ratio on any of the five primary outcome variables. More specifically, bias-corrected bootstrap confidence intervals (2000 bootstrap samples) for the differences between the data collected during congruous versus incongruous conditions straddled zero. No additional simple effects of impulse stimulation on task performance variables were revealed by the mediation analyses. Overall, the results of these analyses indicate that impulse stimulation did not indirectly influence error proportion, boundary separation or non-decision time during SASS task blocks through its effect on autonomic balance as indexed by a measure of heart rate variability (LF/HF ratio).

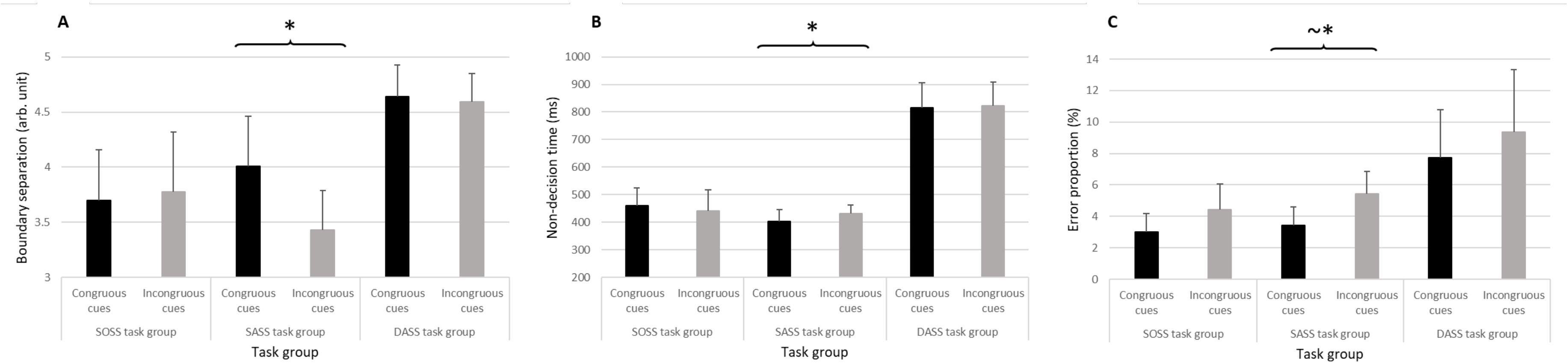


Figure 7.6: Bar charts showing mean boundary separation [A], non-decision time [B] and error proportion [C] segregated by task group (SASS task versus SOSS task versus DASS task) and by space-motion cue congruity (congruous [zero deceleration] versus incongruous [impulse deceleration] cues).

Error bars represent 95% confidence intervals. Asterisks denote significant differences as revealed by simple effects analyses. The asterisk preceded by a swung dash indicates a borderline significant difference (see section 3.14.3).

7.4.2.4 Supplementary analyses

To supplement the tests relating to null hypothesis 2, the secondary outcome variables were similarly subjected to paired samples t-tests, but mediation analyses were not undertaken. Regarding data from the SASS task group, there were significant effects of space-motion cue congruity on SSQ oculomotor score, $t(24) = 2.77$, $p = .016$, $r = .492$, SSQ disorientation score, $t(24) = 2.93$, $p = .007$, $r = .513$, and SSQ total score, $t(24) = 2.88$, $p = .017$, $r = .507$, indicating that reported simulator symptoms were better during the incongruous conditions following impulse stimulation than during the congruous conditions associated with zero deceleration. For the SOSS task group, there were borderline significant effects of space-motion cue congruity on SSQ nausea score, $t(23) = 2.23$, $p = .048$, $r = .422$, and SSQ total score, $t(23) = 2.32$, $p = .041$, $r = .436$, suggesting that reported simulator symptoms may have been worse during the incongruous conditions following impulse stimulation than during the congruous conditions associated with zero deceleration. There were no other simple effects of the cue congruity factor on any other secondary variables, the data from the DASS task group included. Specifically, there were non-significant effects of the within-subject factor on LF/HF ratios obtained from the three groups (SASS task group, $t(24) = 0.68$, $p = .526$, SOSS task group, $t(22) = 0.61$, $p = .560$, DASS task group, $t(23) = 0.21$, $p = .367$).

Between-task comparisons of the tertiary outcome variables, specifically the mental effort, perception of balance and strength of the post-rotatory illusion scores, also constituted supplementary analyses. These analyses, with the space-motion cue congruity factor collapsed, were carried out by way of Kruskal-Wallis tests (i.e. one-way ANOVAs on ranks). The results of all three tests were not statistically significant, indicating that there were no differences in the respective self-reports across the task groups. Median scores for mental effort and perception of balance can be found in Table 7.3, and for strength of the post-rotatory illusion in section 7.4.2.2.

Finally, Wilcoxon signed-rank tests were employed to analyse the within-subjects effects of space-motion cue congruity on ordinal data pertaining to reported mental effort and perception of balance. There was a borderline effect of cue congruity on the levels of mental effort reported by participants in the SASS task group, $z = 2.18$, $p = .029$, $r = .309$, and the DASS task group, $z = 1.97$, $p = .049$, $r = .284$. In both groups, impulse stimulation may have increased the level of mental effort participants felt they had to invest in their respective tasks. Only participants in the DASS task group reported having felt more off-balance during trial blocks which involved impulse stimulation, $z = 2.48$, $p = .013$, $r = .358$.

7.5 Discussion

7.5.1 Summary of the results

The present experiment investigated whether balance disorders, and the aberrant space-motion information they entail, can directly affect higher cognition by examining the effect of impulse stimulation on the performance of the three spatial tasks employed in the preceding studies. Impulse stimulation, involving abrupt deceleration, impaired mechanistic aspects of performance on the experimental task - the SASS task - relative to constant velocity rotation ('zero deceleration'). More specifically, simple effects analyses showed that the participants, who undertook the SASS task, were less cautious in making their laterality judgements after abrupt deceleration of the chair, as indicated by a reduction in boundary separation. They demonstrated longer non-explicit decision processing, as per an increase in non-decision time. In addition, impulse stimulation resulted in a borderline decrease in accuracy on the SASS task. Hence, there was a marginal difference in disruption between the two levels of space-motion cue congruity of a behavioural aspect of SASS task performance as well. Mediation analyses showed that the effects of impulse stimulation on SASS task boundary separation, non-decision time and error proportion were not caused by its effect on LF/HF ratio, a surrogate of anxiety. Even more importantly, the reduction in response caution was selective to the SASS task as implied by the significant task by space-motion cue congruity interaction effect on boundary separation.

Across the three independent task groups, both impulse and zero deceleration led to mean total SSQ scores which exceeded 20. Therefore, both levels of space-motion cue congruity were problematic in terms of the simulator or motion symptoms they provoked (see section 7.4.1.5.1 for further details). This was somewhat unexpected, since impulse and zero deceleration from constant angular velocity rotation are not as commonly linked with intrusive symptoms as other rotational stimuli are (see section 7.2). It is possible that, over the six experimental trial blocks, there was a steady accumulation of symptoms, just as there can be with repeated exposure to optokinetic stimulation. The ramping of symptoms secondary to OKS exposures is thought to be linked to the activity of the velocity storage mechanism (Nooij, Pretto, & Bülthoff, 2018) (see sections 1.4.2.2.1 and 1.4.3.1.2). Interestingly, participants in the SASS task group reported having less simulator symptoms during the incongruous conditions following impulse stimulation than during the congruous conditions associated with zero deceleration. Conversely, those in the SOSS task group reported a marginal increase in symptoms with impulse stimulation. Significant interactions between the task and space-motion cue congruity factors affected the SSQ nausea, disorientation and total scores. Taking all of the simple and factorial effects on the secondary outcome variables into account, it would appear that symptomatic improvement by impulse stimulation was selective to the SASS task group.

Regarding the tertiary outcome variables, participants in the SASS and DASS task groups reportedly exerted marginally more mental effort while performing the tasks during exposures to incongruous space-motion cues. Since reported mental effort may be a surrogate of motivation (see section 4.5.3), these groups of participants may have been more engrossed in their respective tasks during those exposures. Only participants in the DASS task group indicated that they had felt more unsteady following impulse stimulation. Given that related data were ordinal, it was not possible to confirm the group selectivity of any of these effects of stimulation on the tertiary variables.

Recruitment to, and randomisation within, the preset age and gender strata had been unproblematic and successfully led to independent task groups with equivalent distributions of these demographics. There were no differences between the groups in terms of the distributions of participants' psychological traits, handedness and levels of motion sickness susceptibility which might have confounded interpretation of the results.

7.5.2 Primary inferences about the direct effect of aberrant space-motion information on cognition

The selective reduction in response caution on the SASS task provides an initial indication that balance disorders, and the aberrant space-motion information they entail, can have a direct effect on higher cognition. However, there was also an improvement in motion symptoms recorded by way of the SSQ that was selective to the SASS task group. As far as the author is aware, there are no published reports of an improvement in motion symptoms having compromised markers of cognitive performance. Prior research has shown that the syndrome of motion sickness has either no discernible effect on cognitive resources (e.g. Bos, MacKinnon, & Patterson, 2005) or deleterious effects on those resources (e.g. Matsangas, Mccauley, & Becker, 2014; Valk, Munnoch, & Bos, 2008). Thus, it is implausible that improvement in motion symptoms could account for the preferential disruption by impulse stimulation of performance of the experimental task. Speculatively, it is possible that the improvement in symptoms was a corollary of an increase in cognitive difficulty participants in the SASS task group experienced following impulse stimulation, rather than the reduction in their response caution being due to symptomatic amelioration. This proposal is based on evidence which suggests that deep engagement in a mental task may decrease the severity of motion sickness (Bos, 2015; Matsangas et al., 2014). As inferred in section 7.5.1, mental effort ratings obtained from members of the SASS task group may indeed indicate that they were more motivated during the exposures to incongruous space-motion cues, perhaps in the attempt to overcome the compromise of their task performance. Further work could be carried out to assess this interpretation.

Before concluding that aberrant space-motion information can directly affect higher cognition, it is important to consider several possible limitations of the main investigation which might make that interpretation problematic. No real time recordings of eye movements were collected during the investigation which may mean that nystagmus, and its potential effects on cognitive performance, may not have been fully accounted for. The fact that participants in all task groups did not report worsened oculomotor symptoms following impulse stimulation, according to the relevant SSQ domain scores, supports the findings of the preliminary investigation. Most probably, nystagmus was sufficiently suppressible, and interpretations can be drawn in the absence of direct measures of it. The perception of balance scale that was employed was unvalidated. It may not have been sensitive to participants' subjective imbalance during exposure to incongruous space-motion cues, and the disruptive effects of their feeling of instability on cognition may have been overlooked. However, the study sample was relatively young. Berger and Bernard-Demanze (2011) suggested that, while older adults prioritise postural stability, younger adults may follow a 'cognition-first principle' when challenged by concurrent cognitive and balance tasks. Barra et al. (2006) also showed that younger participants were more willing to take balance risks in order to try to maintain their proficiency on a spatial task.

Therefore, even if the healthy participants who took part in the present study had had undetected subjective instability, it may not have compromised their engagement in the cognitive tasks. As discussed in section 7.4.1.5.5, the brevity of pulse recordings may have distorted the frequency domain analyses which yielded the LF/HF ratio data. Therefore, there may not have been an adequate measure of anxiety; another cardinal manifestation of balance disorders which may mediate cognitive disruption. However, self-reported anxiety was also recorded by way of the Y-6 item, and the scores on this did not differ between the congruous and incongruous space-motion conditions, just as there was no difference in LF/HF ratios between the two conditions. The lack of mediation by anxiety (as indexed by LF/HF ratio) of the decrease in boundary separation on the SASS task adds to the possibility that the aberrant space-motion information associated with impulse stimulation directly caused the decrement.

The final potential impediment to that interpretation relates to the contradictory data from the SSQ and the self-report space-motion misperception measure. Participants in the SASS task group had less dizziness with impulse deceleration than with zero deceleration, according to their SSQ scores. Contrary to this, they reported only every having experienced the post-rotatory illusion following impulse deceleration. 84% of participants in the SASS task group declared that they had contended with that illusion and, on average, they stated it had been moderately strong. These contradictory findings suggest that the SSQ did not fully capture the discrete misperception of self-rotation which occurred only after impulse stimulation. The disorientation score it yields may just be a vague marker of some difficulty in focusing or concentrating during or after any mode of relatively prolonged passive whole-body rotation. Participants in the two control groups (SOSS and DASS task groups) also reportedly experienced the post-rotatory illusion. Analysis by way of the Kruskal-Wallis test indicated that there were no differences, between the groups, in terms of the strength of the post-rotatory illusion. This implies that the discrete perceptual effects of the impulse stimulation probably did not account for the selective disruption of performance on the SASS task, lending support to the interpretation that this was a direct, unmediated effect of aberrant space-motion information.

The selective reduction in response caution on the SASS task, in the absence of concurrent preferential disruptions by impulse stimulation of the physiological or subjective states of the participants in the SASS task group, matches the pattern of results described in section

2.3 (also see section 3.12) as being the critical determinant of the direct effect of aberrant space-motion information. There was no reduction in drift rate on the SASS task so the aberrant space-motion information did not merely moderate the amount of attention devoted to task performance (see sections 2.3, 3.11.2.1.2 and 4.5.3 for further details). Drift rate was lower, and non-decision time was longer, on the DASS than SASS task, yet it was the latter task that was disrupted by impulse stimulation. This is further evidence that the vulnerability of higher cognitive functions to balance disorders is not simply related to their cognitive load; that is, to the difficulty of the non-decision and decision processing inherent in those functions (also see section 4.5.2). The results of this study provide support for the greater dependence of MS-TL on space-motion information as theorised throughout this thesis.

7.5.3 Additional inferences about the mechanism of impact of aberrant space-motion information

So far, the reduction in boundary separation on the SASS task has been interpreted as a decrease in response caution or conservativeness. This is in line with the standard view that changes in boundary separation reflect trade-offs between the speed and accuracy of responses on two-choice response-time tasks (Wagenmakers, van der Maas, & Grasman, 2007). A decision-maker can respond faster at the expense of accuracy, and this will manifest a decrement in boundary separation (Dutilh, Wagenmakers, Visser, & van der Maas, 2011). On the SASS task, the control tasks, and many more besides, participants are instructed to respond "as fast and as accurately as possible". These instructions are open to interpretation; participants are able to assess the relative importance of speed versus accuracy (Dutilh et al., 2011).

According to this standard account of the neural mechanisms of decision-making, the participants who undertook the SASS task appear to have placed more importance on speed after impulse stimulation; that is, they became less cautious and, hence, less accurate, in order to optimise the speed of their responses when exposed to incongruous space-motion cues. This account raises several interesting questions. It is unclear why participants in the SASS task group traded off response accuracy for speed when the participants in the control groups did not. There was no change in externally imposed speed stress on any of the tasks after impulse stimulation. That is, all participants had the same 2100 ms response window for each task stimulus under both the congruous and incongruous space-motion conditions. Typically, decision makers only start to sacrifice their response accuracy with increasing pressure to respond quickly (Dutilh et al., 2011). It is possible that just the participants in the SASS task group covertly put themselves under more pressure to respond faster. After all, these participants demonstrated longer non-decision times following impulse stimulation, according to simple effects analyses only. They may have had some awareness of the resultant compromise of the response window, by their extended non-decision processing, and reacted quicker as a result. Such self-imposed speed stress is not obviously documented in the relevant literature. Moreover, an increase in non-decision time is typically associated with increased rather than decreased response caution (Dutilh et al., 2018; Rinkenauer, Osman, Ulrich, Müler-Gethmann, & Mattes, 2004; Voss, Rothermund, & Voss, 2004). Finally, a larger increase in error on the SASS task, commensurate with the size of the decrease in boundary separation on the task, would have been predicted by the standard account of decision-making.

The disruption by impulse stimulation of the two mechanistic aspects of performance, notably of boundary separation, on the experimental task will be discussed further in the General Discussion (see section 8.3).

7.5.4 Conclusions

Impulse stimulation, and the resultant experimentally-induced balance disorder, disrupted mechanistic aspects of performance only on the experimental task - the SASS task. More specifically, following impulse decelerations of the rotating chair, responses on the SASS task were characterised by smaller boundary separations, longer non-decision times and marginally greater error propensity. Of particular importance, factorial ANOVAs revealed that the decrement in boundary separation, due to the incongruous space-motion cues associated with impulse stimulation, was selective to the SASS task. Because of the disruption of their performance, participants in the SASS task group may have become more engaged in the task and, therefore, less aware of the motion symptoms caused by the aberrant stimulation. This may explain why there was a selective diminution of symptoms reported on the Simulator Sickness Questionnaire by that group.

The selective disruption of an aspect of SASS task performance by impulse stimulation, in the absence of concurrent preferential disruptions of the physiological or subjective states of the participants in the SASS task group, suggests that the performance disruption was the direct effect of the aberrant space-motion information associated with the stimulation. More specifically, the compelling but inaccurate velocity information following impulse stimulation appears to have been the direct cause. The results of this study provide support for the greater dependence of MS-TL on space-motion information as theorised throughout this thesis.

The decrease in boundary separation plus the increase in non-decision time do not follow the predictions of the standard account of decision-making, which implies that the former represents a reduction of response caution. The effect of aberrant space-motion stimulation on these markers of cognitive performance will be interpreted further in the General Discussion. The practical relevance of the results will also be considered in the next chapter.

Chapter 8. General Discussion

8.1 Summary of the main results

The overarching aim of this research programme was to advance the mechanistic explanations for the higher cognitive sequelae of balance disorders. The explicit objective was to determine if aberrant space-motion information can directly affect higher cognition together with, or even in isolation of, the cardinal manifestations and attentional diversion caused by such misinformation. In three main studies, these goals were pursued by examining the effects of experimentally-induced balance disorders on spatial tasks which may call upon space-motion information to different extents. In all studies, the spatial perspective-taking (SPT) task was intended to have the greatest dependence on information pertaining to the temporo-spatial activity of the whole body, owing to the mental self-translocation (MS-TL) such tasks entail.

In the first study, participants undertook either the ‘Own Body Transformation’ (OBT) task (a SPT task) or the ‘Transpose’ task (a comparison task) during alternating exposures to static and rotating visual surrounds. The optokinetic stimulation (OKS) produced by rotation of the backdrop resulted in longer response times on both tasks, plus higher error and lower drift rates only on the Transpose task. Importantly, there was no difference between performance on the OBT and Transpose tasks in terms of the degree of disruption by OKS of the primary, task-related outcome variables. The lack of a differential disruption meant that it was not possible to determine whether aberrant space-motion information can have a direct, unmediated effect on cognition. Of note, participants in the OBT task group reported a low uptake of MS-TL. Therefore, their performance of this task probably did not call upon space-motion information any more than their counterparts’ performance of the Transpose task.

Owing to the limitations of the OBT task, in the second study, new SPT (the Single Avatar Stimulus Set [SASS] task) and control (the Single Object Stimulus Set [SOSS] task and the Double Avatar Stimulus Set [DASS] task) tasks were developed and validated. The results of this study indicated that the three new tasks are underpinned by separable cognitive processes, which may call upon space-motion information to differing extents. In turn, performance on the tasks may be variably susceptible to aberrant information. Notably, this was the first study to empirically show that progressively large disparities between the avatar's and participant's orientations do not simply incur systematically greater non-transformational costs associated with changing spatial compatibility. As such, the results of the study cast doubt on May and Wendt's (2013) account of performance monotonicity.

The new tasks were incorporated in the third study, which re-employed the methods of the first, albeit with a smaller number of participants per independent task group. To the author's knowledge, this was the first study to examine the effect of aberrant stimulation on a SPT task comprising 3-D avatars. During OKS, boundary separation reduced and non-decision time increased on the SASS task, according to simple effects analyses. However, there were no selective effects of OKS on task-related outcome variables, as indicated by non-significant factorial interactions. Mediation analyses showed no direct or indirect effects of OKS on performance of the SASS task. An inadequate sample size, indicated by post-hoc power analysis, may have accounted for the lack of a differential disruption of task performance and the consequent inability to draw firm conclusions as to whether aberrant space-motion information can have a direct, unmediated effect on cognition.

Following a preliminary study, which showed low nystagmus intensities shortly after abrupt deceleration from constant velocity rotation, the final study examined the effect of such impulse stimulation on the SASS, SOSS and DASS tasks. A larger sample was recruited and the participants' seated postures reduced the balance imperative, and the idiosyncratic postural and subjective responses that unfamiliar balance challenges may yield. With impulse stimulation, responses on the SASS task were characterised by smaller boundary separations and longer non-decision times. Mediation analyses showed that these simple effects of impulse stimulation were not secondary to its effect on LF/HF ratio, a parameter of heart rate variability and marker of anxiety. The decrement in boundary separation due to the incongruous vestibular stimulation was selective to the SASS task according to a significant task by cue congruity interaction effect. This selective disruption, in the absence of concurrent preferential disturbances of the physiological or subjective states of the participants in the SASS task group, implied that aberrant space-motion information can have a direct, unmediated effect on higher cognition.

This was the first empirical study to indicate that a direct effect can occur. As such, the final study served both to fulfil the research programme's goals and to make a novel contribution to knowledge. It appears to have been advantageous to have conceptualised the relationship between balance disorders and cognitive function in terms of mediation models of analysis. This conceptualisation had developed from the view that balance disorders can be reduced to the execution of balance system functions based on irregular information pertaining to the temporo-spatial activity of the body. That is, common to all balance disorders is the processing of aberrant space-motion information by the multimodal balance system. By conceiving (aberrant) space-motion information as the predictor variable and higher cognitive function as the outcome variable, it was possible to treat the cardinal manifestations of balance disorders as potential mediator variables. In effect, this research was facilitated by a novel differentiation of possible causal agents. In the reviews by Smith et al. (2005) and Smith and Zheng (2013), causal agents are conflated (see section ii of the Preface), which means they do not present a clear case in favour of a direct effect of balance disorders on cognition.

8.2 Convergent support for a direct effect

Only the results of Study 4 met the strict criteria set-out in section 2.3 for a direct effect of aberrant space-motion information on higher cognition, since only those results comprise a significant interaction effect on a primary, task-related variable. However, it is notable that the simple effects found in Study 3 correspond with those effects revealed in Study 4. In both studies, aberrant stimulation caused a decrease in boundary separation and an increase in non-decision time on the SASS task. The correspondence of the simple effects implies that the results of Study 4, and the interpretations that have been drawn from them, are not unreliable.

The present findings are also in line with some non-empirical evidence for a direct effect of aberrant space-motion information on higher cognition. Type I spatial disorientation is the term given to the condition of a pilot who unknowingly misrepresents the position, attitude or motion, relative to the aircraft, of the Earth's surface (Gillingham & Wolfe, 1986). It can lead to erroneous control inputs by the pilot and, therefore, to flight mishaps. A survey of UK military air accidents from 1983 to 2002 found that disorientation remained unrecognised, beyond the point at which the mishaps were rectifiable, in 85% of accidents (Stott, 2013). Evidently, piloting aircraft is a highly cognitive endeavour, so erroneous use of flight controls by pilots with Type I spatial disorientation suggests they are cognitively impaired when afflicted by the condition. This is despite the fact that they have no overt dizziness (i.e. space-motion misperceptions; see section 1.5.3), imbalance, nausea, anxiety or gaze instability[20]. The implication is that merely the propagation of aberrant temporo-spatial information, possibly related to the velocity or attitude of the aircraft embodied within the self, directly interferes with cognitive functions called upon when flying.

The present findings are also consistent with the empirical results reported by Gresty et al. (2003). In their study, 20 participants performed sets of verbal and spatial memory tasks while seated in a flight simulator which oscillated in the pitch plane. The participants were enclosed in the simulator but were shown a video feed of the room outside. The footage was manipulated such that the visual feedback participants were provided with about the simulator's motion varied in terms of its faithfulness. The video depicted that the simulator was either stationary, oscillating veridically (e.g. when the simulator pitched nose down, participants saw the external environment flow by infero-superiorly on the screen until they could see the floor), oscillating inversely (e.g. when the simulator pitched nose down, participants saw the external environment flow by supero-inferiorly on the screen until they could see the ceiling), or oscillating orthogonally. When the video and simulator were in inverse phase, the participants demonstrated greater variance of errors on the spatial task. According to ratings on the Simulator Sickness Questionnaire (see section 7.4.1.5.1), the participants' cognitive impairment did not occur in parallel with increased nausea, disorientation or oculomotor problems. They did not report anxiety or imbalance and even failed to recognise the visuo-vestibular conflict so were seemingly not distracted by it. Re-interpreting these results, aberrant self-motion velocity information, due to incongruous angular motion cues, appears to have had an unmediated effect on the participants' higher cognition.

Similarly, the results of the present research programme are in line with those obtained in the study by Ehrenfried et al. (2003). Seated participants' performance on verbal and

---

[20] Some of these overt manifestations of incongruous flight conditions are associated with other types of spatial disorientation (see Gillingham & Wolfe, 1986).

spatial memory tasks deteriorated when exposed to large field laminar optic flow. There was no reported effect of the optokinetic stimulus on heart rate or visual fixation, both of which were recorded. The authors concluded that "mere passive viewing of a moving visual field may interfere with cognitive tasks possibly because the threat of disorientation by whole field motion diverts attentional resources" (Ehrenfried et al., 2003, p. 140). No measures of attention were included, so it is just as plausible that the cognitive dysfunction was caused more directly by the experimentally-induced balance disorder and the aberrant space-motion information it entailed.

Thus, the mediation model (section 8.1) accommodates several existing findings and observations, in addition to the data presented in this thesis. It allows novel interpretations of Type I spatial disorientation and the results of Gresty et al. (2003) and Ehrenfried et al. (2003); interpretations that are based on the premise that cognitive functions may utilise velocity and other 'raw' space-motion information. This premise is in-keeping with contemporary, embodied approaches to cognition (see section i of the Preface), which view cognitive functions as being contingent on brain-body-environment interactions (Pezzulo, Donnarumma, Iodice, Maisto, & Stoianov, 2017).

8.3 Mechanistic interpretations of the results

As discussed in section 7.5.3, the results of Study 4 are not immediately consistent with the predications of the standard account of the neural mechanisms of decision-making, which posit that a reduction in boundary separation represents a decrease in response caution. The main discrepancy relates to the fact that participants in the SASS task group demonstrated longer non-decision time (NDT), as well as reduced boundary separation, following impulse stimulation. The participants in the SASS task group in Study 3 were also found to have changed their response parameters in the same manner during optokinetic stimulation, albeit a preferential disruption of boundary separation was not confirmed by a significant task by cue congruity interaction effect. An increase in NDT typically tallies with greater rather than lesser response caution (Dutilh et al., 2018; Rinkenauer, Osman, Ulrich, Müler-Gethmann, & Mattes, 2004; Voss, Rothermund, & Voss, 2004). Teichert et al. (2014) argue that it may be too simplistic to interpret adjustments of boundary separation in isolation, and merely as proxies of a speed-accuracy trade-off; that is, as markers of the degree of response cautiousness. Instead of this "onedimensional view" (Teichert et al., 2014, p. 20), the authors imply that the latency to decision onset, a component of NDT (Teichert, Grinband, & Ferrera, 2016), and boundary separation should be treated as mutual parameters that serve a two-dimensional decision optimisation strategy.

Thus, one may speculate that the reduction in boundary separation on the SASS task, found in studies 3 and 4, was a marker of a latent but adaptive strategy by the participants who completed that task in both studies. They may have adopted this strategy in response to experimentally-induced perturbations of MS-TL - an important part of the implicit decision process which preceded the explicit laterality decision they had to make (see section 3.11.2.1.2). With reference to the internal model formulation of MS-TL (see section 1.6.2), and its preferential vulnerability to aberrant space-motion information (see section 1.6.3), visuo-vestibular cue incongruity during the studies may have resulted in an inaccurate starting point for temporal integration of the amodal predictions iteratively produced by the forward model to transform the imaginary position of the body into the on-screen position of the avatar. As such, the cue incongruity may have caused participants to proceed with MS-TL based on a less precise but more accurate representation[21] of the body's temporo-spatial activity. A similar phenomenon occurs with angular path integration following impoverished visual referents (see Arthur, Philbeck, & Chichka, 2007, 2009; Israël, Bronstein, Kanayama, Faldon, & Gresty, 1996). This would have resulted in greater inter-trial variability (i.e. reduced precision) of the final imaginary body position yielded by MS-TL. In turn, the participants would have begun accumulating evidence for the explicit laterality decision based on a wider distribution of possible imaginary body positions. Essentially, explicit decision processing would have been noisier during incongruous than congruous space-motion cues. According to Teichert and colleagues' (2014) adaptive account of decision-making, by reducing their decision thresholds (i.e. boundary separation), the participants may have strategically limited the accumulation of noise occurrent with the laterality signal. The fact that there were only borderline significant increases in error proportion on the SASS task in studies 3 and 4 appears to be consistent with this account. Had the participants simply adopted a less cautious approach or "guess mode" (Dutilh, Wagenmakers, Visser, & van der Maas, 2011, p. 211), as asserted by the standard account, much higher, chance-level error rates would have been expected (Ratcliff

---

[21] This representation may be one that is stored in memory. Even though it may have been subject to drift, it may still be more accurate than the 'online' (as opposed to stored) representation provided by occurrent afferent information during exposure to incongruous visuo-vestibular cues.

& Tuerlinckx, 2002). The decrease in boundary separation is depicted in Figure 8.1, and the standard and adaptive accounts of this effect are re-visited in the caption.

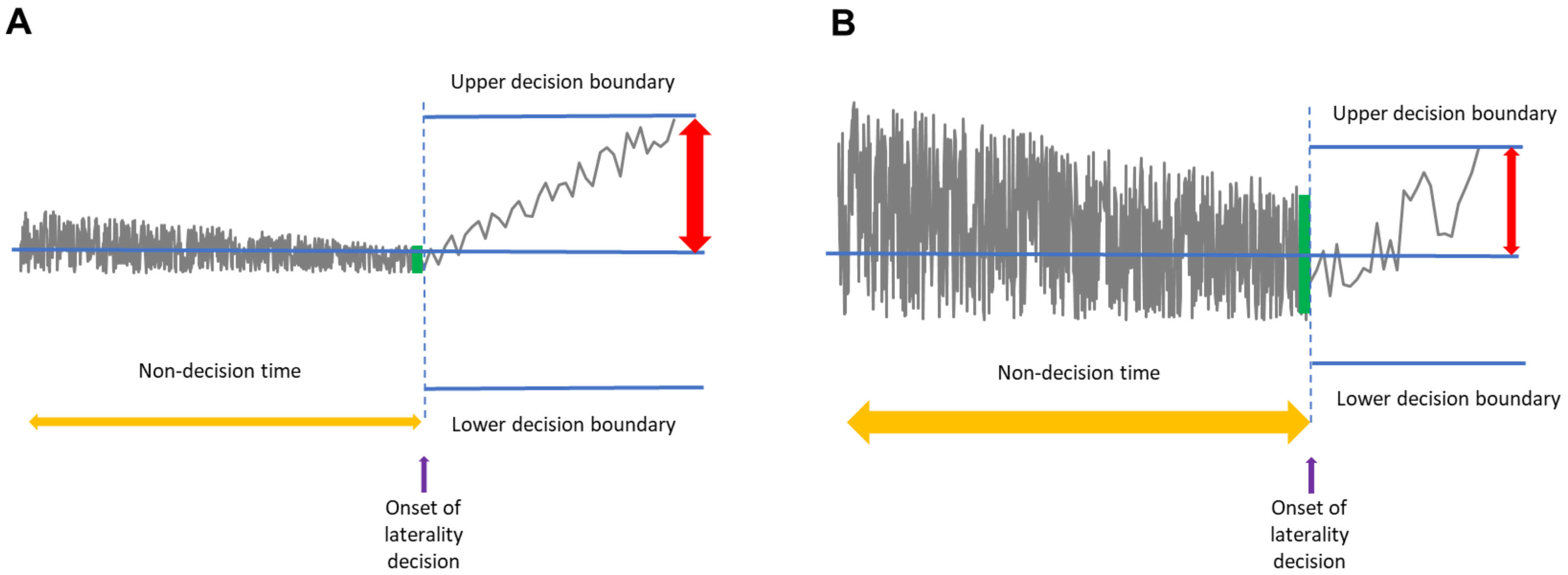


Figure 8.1: Drift diffusion models depicting performance on a spatial perspective-taking (SPT) task during exposure to congruous [A] and incongruous [B] space-motion cues.

Non-decision time is increased in [B] (compare orange arrows), as was found in studies 3 and 4, presumably because mental self-translocation (MS-TL) is less efficient during aberrant stimulation. MS-TL may also be more imprecise because the incongruous cues mean there is no accurate space-motion information to serve as a starting point and, therefore, to reset the temporal integration of imaginary changes in body position. The greater inter-trial variability of the final imaginary body position yielded by MS-TL is depicted by the longer vertical green bar in [B]. Decision processing for the explicit laterality judgement is noisier as a result; that is, more noise is accumulated as information is gathered in favour of one or other laterality response option. The response thresholds or boundary separations are narrower in [B] (compare red arrows), reflecting the results of studies 3 and 4. This implies that the participant has switched to a guess mode (i.e. become less cautious about his or her responses) due to processing difficulties imposed by the noise. Alternatively, the reduction in boundary separation is a latent, adaptive strategy to limit the accumulation of noise. Further details about the drift diffusion model are given in the caption for Figure 3.2, which is adapted from Teichert et al. (2016).

Both the standard and adaptive accounts of the reduction in boundary separation rest on the hypothesis that there was noisier MS-TL during exposures to incongruous space-motion cues. This hypothesis might be questioned on the basis that there was no preferential disruption of NDT in neither study 3 nor study 4. Given that NDT has been interpreted to be the parameter which most likely reflects MS-TL (see section 3.11.2.1.2), participants in the SASS task groups might have been expected to demonstrate longer NDTs than participants in the other groups during aberrant stimulation. However, it is plausible that a noisier process of MS-TL may not have led to it slowing down. It is also important to note that NDT derived from SPT tasks encompasses not only MS-TL but also afferent and efferent delays and other non-decision processes (see section 1.6.3). Therefore, even if MS-TL were prolonged by noise associated with incongruous cues, NDT might only increase by a smaller proportion of its typical duration, as recorded during congruous cues. That is, the increase in NDT might mask the degree to which MS-TL were prolonged by aberrant stimulation. This masking effect may have led to the non-significant task by cue congruity interaction effects found in studies 3 and 4.

Evidently, more research is needed to understand how the mechanistic variables assess performance on SPT tasks during exposures to both congruous and incongruous space-motion cues. This programme of research into the cognitive effects of balance disorders was one of the first to apply a diffusion model. It was only because of this novel modelling that alterations of the cognitive substrate of SASS task performance were demonstrated. It is possible that previous related research failed to uncover mechanistic consequences of aberrant space-motion information having only measured and analysed behavioural outcomes.

8.4 Temporo-spatial parameters important to mental self-translocation

A disturbance of the starting point, which is postulated to benefit the temporal integration inherent in MS-TL, is a plausible explanation for the disruption by aberrant stimulation of SASS task performance. According to Grush (2004) and Mast and Ellis (2015), MS-TL may be relatively impervious to aberrant space-motion information once the starting point has been referenced and the process is underway. This is because concurrent afference or prediction errors are actively attenuated during the transformation process so that it can successfully go to completion (see section 1.6.2). The results of study 4 imply that self-motion velocity is the key temporo-spatial parameter that is referenced at the outset of MS-TL. Impulse stimulation leads to incongruous semicircular canal signalling. Since the canals transmit velocity data (see section 1.3.2.2.1), impulse stimulation presumably leads to reliable but inaccurate signals about the body's velocity (see section 1.5.2). Despite the reliability or precision of the signals, top-down mechanisms may prevent them from forming the starting point for the temporal integration of covert body movements due to their inaccuracy (see section 1.5.3).

It follows that accurate velocity information may constitute the starting point for MS-TL since velocity is integrated to find body position. However, previous research by Furman et al. (2012) showed that stimulation of the semicircular canals by passive, sinusoidal, whole-body rotation did not affect performance on spatial and non-spatial choice reaction time tasks with auditory stimuli. While this might indicate that velocity information may not be an important resource for cognition, it is debatable whether sinusoidal stimulation compromises that information to the same extent as impulse stimulation. More specifically, the former stimulation probably does not generate such a stark contrast between visual- and vestibular-specific prediction errors, so occurrent velocity information may still form a relatively accurate basis for cognitive functions that call upon it. In fact, van Elk and Blanke (2014) found that performance on a 3-D SPT task improved when the direction of gentle angular whole-body acceleration was congruent with the occurrent imaginary rotation of body position. Shorter RTs were recorded on the SPT task when such congruency occurred. This finding may imply that highly reliable and yet accurate canal-related prediction errors regarding the body's velocity may enhance the starting point for MS-TL, leading to a more precise transformation of body position and, in turn, to a less noisy and more efficient laterality decision.

As self-motion velocity information is provided by optic flow (Raudies & Neumann, 2013 see section 1.3.3.2.3), it is not unreasonable that SASS task performance was affected in study 3, which involved exposures to aberrant optokinetic stimulation, as well as in study 4, wherein the semicircular canals were stimulated. The results of study 3 indicate that any situation that disrupts self-motion velocity information, and not just those that mediate the disruption via the vestibular system, could have a direct effect on MS-TL and possibly other higher cognitions. Judging by the studies reviewed in Chapter 2, aberrant stimulation of the vestibular system has featured more often in research into the processing of MS-TL. It is almost as if the individual space-motion systems have been considered to be discrete information modules. Perhaps, in the future, research should focus more on investigating the type of temporo-spatial information that influences MS-TL, and less on specific sensory system impairments and their influence.

Although the focus has so far been on the importance of self-motion velocity information, body position itself may also be a relevant temporo-spatial parameter at the outset of MS-TL. Kessler and Thomson (2010) showed that RTs on a SPT task were shorter when participants' bodies faced the direction in which they had to rotate their body image. The authors concur that space-motion information is recruited at the very beginning of MS-TL "when the emulation process [i.e. forward modelling; see section 1.6.2] of the mental body rotation is initiated" (Kessler & Thomson, 2010, p. 86).

8.5 Theoretical relevance of the results

A disrupting effect on MS-TL of an inaccurate starting point, due to aberrant space-motion information, is predicted by the internal model formulation of this covert cognitive function, which is presented in full in section 1.6.2. As such, the results of studies 3 and 4 lend support to this novel formulation, which combines the theories of Grush (2004) and Mast and Ellis (2015). The internal model formulation of MS-TL is also original in its incorporation of three important computations (predictive coding, optimal cue integration and temporal integration) which utilise ascending space-motion information (see section 1.4). The formulation is based on the idea that covert transformations of whole-body position capitalise on, or are enabled by, the sensorimotor circuitry for moving the body overtly. It is probable that many higher cognitive functions do not utilise this circuitry and, therefore, do not call upon space-motion information to the same extent. Therefore, MS-TL may be one of the only higher cognitions that can be directly affected by aberrant space-motion information. That might make it one of the most vulnerable cognitions; balance disorders may exert a disruptive effect on MS-TL directly as well as indirectly via mediator variables including dizziness, imbalance and/or attentional diversion. In contrast, most other cognitive functions may only be susceptible to the indirect, mediated effects of aberrant space-motion information.

The particular sensitivity of MS-TL is highlighted by studies 3 and 4, which did not show simple, disruptive effects of incongruous space-motion cues on the performance of the DASS task, a mental object rotation (MOR) task. As presented in section 1.8.2, MOR may also utilise sensorimotor circuitry but that which controls limb as opposed to whole-body movement. This circuitry may not be so dependent on space-motion information. Instead, it may call largely upon body segment information as a starting point for temporal integration.

However, the empirical and non-empirical evidence for a direct effect of aberrant space-motion information on higher cognition, presented in section 8.2, would suggest that such an effect is not restricted to MS-TL. It is important to note that the criteria for a direct effect of aberrant space-motion information on higher cognition, which are laid out in section 2.3 (see Figure 2.1 in particular), are rather strict. According to these criteria, a direct effect could only be interpreted from the results of each of the studies if there was a preferential disruption of at least one primary outcome variable yielded by the SPT task, in the absence of any preferential disturbances of secondary outcome variables relating to the physiological and subjective states of the participants in the SPT task group. These criteria imply that any non-selective, general disruptions of task performance are solely the result of the indirect, mediated effects of aberrant space-motion information. However, it is plausible that part of the general disruption by aberrant space-motion information of higher cognition may be accounted for by a direct effect. This would explain why cognitive performance suffered in the studies by Gresty et al. (2003) and Ehrenfried et al. (2003) even though: (i) the participants displayed no cardinal manifestations of the experimentally-induced balance disorders, and (ii) the tasks they performed do not appear to have evoked MS-TL. In summary, a range of higher cognitive functions may be susceptible to direct, as well as indirect, disruptive effects of aberrant space-motion information. According to the present findings, MS-TL is particularly susceptible to direct effects implying that tasks which call upon this cognitive process may be some of the most affected in persons contending with balance disorders.

Also of relevance, this research project has indicated that the vulnerability of higher cognitive functions to balance disorders is not simply related to their cognitive load; that is, to the difficulty of the non-decision and decision processing inherent in those functions. Furman et al. (2012) also found that a spatial task was more disrupted by aberrant space-motion information than a more challenging non-spatial task. The interpretations of cognitive vulnerability to aberrant information, presented in this section, constitute an original contribution to knowledge.

8.6 Practical relevance of the results

The results of this research programme could benefit the care of patients with pathological balance disorders or at least broaden the understanding of their functional limitations. The finding that MS-TL is susceptible to aberrant space-motion information indicates that consideration should be given to the potential issues patients may face secondary to its disruption. MS-TL does not only enable laterality judgements from somebody else's perspective (i.e. spatial perspective taking - SPT). The ability to mentally transform one's perspective also allows for action planning and covert rehearsal in one's current environment or even in an abstract setting. In turn, these facilitate problem solving and afford predictions of the consequences of future actions (Creem-Regehr, 2010; Grabherr et al., 2007; Mast, Preuss, Hartmann, & Grabherr, 2014). The more complex the action planning, the more MS-TL may be engaged, so the more vulnerable the planning may be to balance disorders. This may partly explain why sportspersons afflicted by balance disorders associated with traumatic brain injury have a three- to six-fold increased risk of sustaining a second concussion on return to play (D'hemecourt, 2011). They may be less able to foresee the results of potential on-field manoeuvres, leaving themselves more vulnerable to harm.

According to Creem-Regehr et al. (2013), MS-TL enables humans to understand what purposeful actions another person can take given his or her current posture and environment. That is, humans are able to perceive others' action affordances, as well as their own, by way of MS-TL. If patients with balance disorders are less able to predict other people's movements, it may help explain why they often dislike being in crowds (Bronstein, 1995; Guerraz et al., 2001). More specifically, the aversion some patients with peripheral vestibular disorders have to crowds may be because of difficulties they have anticipating people's gait trajectories together with abnormalities of their visual motion perception and/or affect (Guerraz et al., 2001).

Visual motion sensitivity is a feature of persistent postural-perceptual dizziness (PPPD), a newly defined functional balance disorder (see Staab et al., 2017). PPPD develops due to maladaptation to neuro-otological, medical or psychological pathologies that disturb balance system function (Popkirov, Staab, & Stone, 2017; Staab et al., 2017). Based on the present findings, tasks which evoke MS-TL may offer an opportunity to investigate further patients' motion sensitivities and their central maladaptation. It is plausible that impaired judgements of others' action affordances, due to alterations in the sensorimotor circuitry for whole-body movement, may account for part of their sensitivities.

Converging evidence indicates that MS-TL enables visual perspective taking as well as SPT (see Surtees, Apperly, & Samson, 2013). Visual perspective taking involves judging the appearance of objects, or identifying them, from another person's perspective. The ability to do this has not been shown in infants younger than 4 years of age, or in any other species (Kessler & Thomson, 2010; Surtees et al., 2013), so visual perspective taking is sophisticated in terms of computational complexity. Moreover, it may form the basis for cognitive or conceptual perspective taking (Surtees et al., 2013), which constitutes one of the main dimensions of empathy (Mooradian, Davis, & Matzler, 2011). Often cognitive perspective taking is referred to as 'Theory of Mind' (Lamm & Majdandžić, 2015), which encompasses "the ability to represent, understand or act sensitively based on the mental states of others" (Surtees et al., 2013, p. 427). It is possible that MS-TL is the commonality between visual and cognitive perspective taking. Expressions in several languages, such as "I understand your point of view" and "put yourself in my position", hint at the potential dependence of cognitive perspective taking on MS-TL (Kessler & Thomson 2010; van Elk & Blanke, 2014). The vulnerability of MS-TL to balance disorders implies that patients may be rendered less able to empathise and cooperate with others. In effect, the perturbation by aberrant space-motion information of MS-TL may culminate in problematic social cognition. The potential for disruption of social cognition to arise, secondary to vestibular disorders in particular, has been proposed by Deroualle and Lopez (2014) and Pfeiffer (2015). These authors imply that perturbed MS-TL may indeed be one of the mediators of the disruption. However, there is little if any empirical evidence to support such claims.

In summary, the results of this research programme have afforded novel interpretations of the functional limitations which patients with balance disorders may contend with. In particular, the vulnerability of MS-TL to aberrant space-motion information implies that pathological balance disorders may affect action planning and social cognition. Disruptions of these important aspects of human function in patients may have been under-recognised to date.

8.7 Limitations

As discussed in the respective chapters and in section 8.1, studies 1 to 3 had at least one notable methodological limitation each. The OBT task employed in Study 1 does not appear to have been a valid SPT task based on the low uptake of MS-TL reported by participants. Therefore, performance of this task probably did not call upon space-motion information any more than performance of the Transpose task. This may have led to the lack of a preferential disruption by OKS of the OBT task, and the resultant inability to discern whether aberrant space-motion information can directly affect higher cognition. In Study 2, the direction in which the measuring scale was rotated had a variable effect on response times on the SOSS task, albeit this effect was limited to trials wherein the scale was orientated side-on to the viewer (see section 5.4.3.1). This particular stimulus had to be dropped from the SOSS task, meaning that, for parity, the stimuli depicting avatars rotated by 90º in the SASS and DASS tasks were also dropped. This issue would not have arisen had the new tasks comprised stimuli with angular disparities, relative to the viewer, of 0º (rear-facing), 60º to the left and right, 120º to the left and right, and 180º (front-facing). However, if the SASS task were to be employed in isolation in future research, for example in an attempt to determine the electrophysiological correlates of MS-TL (see section 8.8), re-inclusion of the avatar rotated by 90º would add further useful variety to the stimulus set.

Similar to Study 1, and despite simple disruptive effects, there was no preferential impact of OKS on the SASS task in Study 3 according to non-significant factorial ANOVAs on primary, task-related variables. Consequently, it was not possible to determine whether balance disorders, and the aberrant space-motion information they entail, can directly affect higher cognition. However, the size of the sample recruited in Study 3 was inadequate, as suggested by a post hoc power analysis. This may explain why the mixed design analyses yielded non-significant results. The samples of studies 1 and 3 had not been stratified by gender; a demographic factor which may influence performance on spatial tasks (see section 6.5.4 for further details). Although the effect of the unbalanced gender proportions between the task groups, particularly in Study 3, appears to have been inconsequential in comparison to the effects of the task validity and sample size issues noted above, it was controlled by way of stratified randomisation in Study 4 for the sake of prudence. This method of recruiting and allocating participants to the three independent task groups also meant it was possible to raise the mean age of the sample in Study 4. In the preceding studies, convenience samples largely comprising younger, undergraduate psychology students had been recruited. Therefore, potential problems with the external validity of studies 1 to 3 do not apply as much to Study 4 (see section 6.5.4).

Despite the methodological improvements implemented in Study 4, there were some limitations that were not fully addressed and, therefore, recurred throughout the programme of research. All of the studies employed ordinal, sometimes unvalidated measures of one or more cardinal manifestation of the experimentally-induced balance disorders. These measures did not allow for inferential, mixed design analyses, which may have meant it was not possible to exclude the potential mediating effects of the respective manifestations on cognitive function. In studies 1 and 3, a custom, ordinal measure of malaise was used to try to capture all manner of disturbances caused by OKS, but mainly motion sickness and undifferentiated space-motion misperceptions (see section 1.5.3). These are important manifestations of balance disorders, but their potential to mediate a disruptive effect on cognitive functions, specifically in studies 1 and 3, was probably less than that of postural instability. The latter was adequately measured both objectively, by way of stabilometry, and subjectively, by way of modified visual analogue scales. In Study 4, subjective imbalance was measured using an unvalidated, ordinal measure, which may have meant the disruptive effects of participants' perceived unsteadiness on cognition may not have been fully accounted for. However, the younger participants, who made up the largest age stratum in Study 4, may not have been distracted, even if they had had a strong perception of unsteadiness while seated. This is because younger participants have been shown to be more willing to take balance risks in order to maintain their proficiency on spatial tasks (see section 7.5.2 for further details).

For consistency, the perceived stability and fear-of-falling scales used in studies 1 and 3 should have been employed in Study 4 instead of the ordinal measure of subjective imbalance referred to in the paragraph above. In addition, the SSQ should have been used in studies 1 and 3, not just in Study 4, so that interval level data about nausea, gaze instability and dizziness were consistently captured throughout the research. Had there been more uniform outcome measurement, it may have been possible to pool the data from the studies during which participants were exposed to aberrant space-motion stimulation. A meta-analysis of data from studies 3 and 4 could have been conducted, and this may have helped to resolve the sample size issue which affected Study 3. However, as discussed in section 7.5.2, the SSQ was not sufficiently responsive to the post-rotatory illusion participants in Study 4 contended with. Therefore, it may not have captured the vection illusion and tilted verticality perceptions participants may have experienced in studies 1 and 3. Further related research would need to supplement the SSQ with a visual analogue scale measuring the misperception of self-motion associated with the aberrant form of stimulation employed, be that vection with OKS or the post-rotatory or similar illusions caused by incongruous vestibular stimulation. The rod and disc test (Guerraz et al., 2001) may also be a useful addition to measure participants' perceptions of self-orientation in future studies employing exposures to roll-plane OKS.

The path-analytic mediation models tested in studies 1, 2 and 4 were simplistic given that they incorporated only one of several potential mediator variables. This analytical limitation was offset by the factorial ANOVAs, which provided insight, albeit less directly, into the mediating effects of cardinal manifestations left out of the path analyses. Therefore, the two analytical strategies were complementary and, together, probably covered the most pertinent pathways by which balance disorders may affect higher cognition.

Potential theoretical limitations of the present research also need to be considered. In this and previous chapters, the results of the studies have been discussed and interpreted with reference to the internal model formulation of MS-TL. However, internal model theories of control are not universally accepted. Criticism is largely directed at the way these theories propose that movement or action is specified by an inverse model. This model, located centrally in the brain, computes the optimum control policy for achieving a desired (goal) state with reference to the current state (see section 1.4.4 for further details). Accordingly, the inverse model may have to establish joint torques, muscle activation patterns and/or other biomechanical parameters necessary to produce desired movements. Several scholars argue that such a detailed central specification by the inverse model is unfeasible (e.g. Balasubramaniam, 2004; Friston, Daunizeau, Kilner, & Kiebel, 2010). The specification would be vulnerable to noise and/or temporal delays. It would probably be incomplete as well, owing to the innumerable degrees of freedom of the body (Friston et al., 2010). Balasubramaniam (2004) states that the inverse model may even add further degrees of freedom to the control process, thereby exacerbating the so-called 'redundancy problem' rather than resolving it. Friston et al. (2010) propose an alternative to the internal model of control which they refer to as 'active inference'. This theory is based on descending as well as ascending prediction errors. In effect, the descending errors are transformed by the periphery (spinal cord and effectors) into a control policy, implying that the inverse model is downstream rather than upstream of the forward model (Friston et al., 2010). Active inference proposes that movement is generated to minimise prediction errors. Although it and other 'radically embodied' theories appear to make the computations necessary for overt movement more tractable, they are less appealing when it comes to the covert movements MS-TL and other forms of imagery entail. According to Pezzulo et al. (2017, p. 2), "[internal] model-based solutions [still] seem more suited to address the problem of detached cognition - or how living organisms can temporarily detach from the here-and-now, to implement (for example) future-oriented forms of cognition".

8.8 Future research

This project has highlighted the need for further research to clarify the diffusion model correlates of performance on SPT tasks. As per sections 2.3 and 3.11.2.1.2, NDT has been assumed to be the mechanistic marker of MS-TL. This could be clarified by studying performance on the SASS task, with the full stimulus set (i.e. with reincorporation of stimuli depicting avatars orientated by 90º to the viewer), by a large sample under congruous space-motion conditions. With a greater yield of mechanistic data, bivariate correlations between each of the diffusion model parameters and the angular disparity of the SASS task's avatar would be possible. A monotonic function for a particular parameter would indicate that it has an association with MS-TL.

It would also be useful to determine the effects of aberrant space-motion stimulation on the electrophysiological correlates of MS-TL, as this is also yet to be explicated. As noted in section 1.7.3.1, MS-TL was associated with temporo-parietal activation 330 to 400 ms after the onset of the SPT task's avatar in the study by Tadi et al. (2009). The duration of this period of activation increased with larger angular disparities between participants' and the on-screen avatars' orientations. If this activation were further prolonged by experimentally-mediated cue incongruity, it would confirm that aberrant space-motion information disrupts MS-TL, but may not provide further insight into the directness of that effect. OKS may be the more suitable form of aberrant stimulation for this electrophysiology study, because the chair rotation required for impulse stimulation may introduce too much noise in the EEG signal. This study might also afford the opportunity to correlate diffusion model parameters with electrophysiological markers of MS-TL.

Empirically testing whether the selective disruption by aberrant space-motion stimulation of SASS task performance is due to obscuration of the starting point for temporal integration (see section 8.3) would be novel and informative. This could be done by having participants repeat the SASS task while galvanic stimulation (see section 2.4.2) was applied at different time points relative to the onset of the task's avatar. If performance on the task were disrupted by stimulation applied just before but not just after the avatar appeared, it would suggest that a stable starting point is indeed important for the integrity of MS-TL, and that the cognitive function is impervious to cue incongruity once it is underway (see section 8.3).

These mechanistic research ideas aside, further pre-clinical research is warranted in order to test the conjecture in section 8.5. Most importantly, there is a need to examine whether the selective disruption of SASS task performance by experimentally-induced balance disorders translates into action planning and social cognition problems. Tasks that evoke empathetic responses, for example, could be undertaken by healthy participants exposed to OKS or impulse stimulation. A selective disruption of the tasks by the visuo-vestibular incongruity associated with the experimental stimulations would further imply that social cognition is vulnerable to aberrant space-motion information. Clinical research could follow-on from such a finding. Patients, such as those with PPPD, and control participants could be surveyed using a tool that provides insight into social functioning. Further research involving patients with PPPD was outlined in section 8.6. Such research would have potential to provide new insights into the functional burden which balance-disordered patients contend with and possibly even into new treatment targets.

8.9 Conclusions

The explicit objective of this programme of research was to determine if aberrant space-motion information can directly affect higher cognition together with, or even in isolation of, the cardinal manifestations and attentional diversion caused by such misinformation. To fulfil this objective, the effects of experimentally-induced balance disorders on spatial tasks, which may call upon space-motion information to different extents, were examined. The results of the first study were not informative because the spatial perspective-taking (SPT) task did not recursively evoke mental self-translocation (MS-TL). Therefore, it did not call upon space-motion information any more than the control task. This led to the creation and validation of new experimental and control tasks in the second study. There was a monotonic response time function on the new SPT task, the SASS task, but not on the new choice-reaction time task. This was the first study to show empirically that performance monotonicity on a SPT task is not accounted for by graded spatial compatibility effects. A subsequent study (Study 4) indicated that the monotonic function yielded by the SASS task is also not explained by the process of mental object rotation. Therefore, this novel task is a new measure of MS-TL.

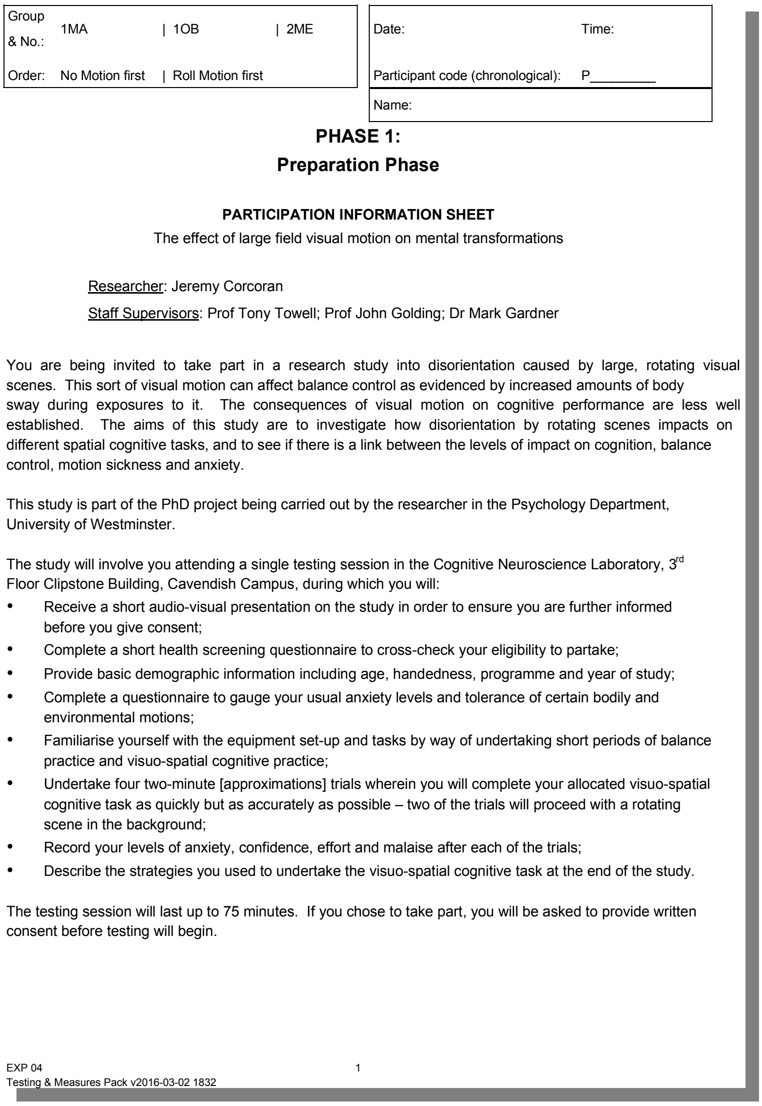
In studies 3 and 4, participants completed the new tasks while exposed to optokinetic and impulse stimulations, respectively. Study 4 had the strongest internal and external validity. Following impulse stimulation, responses on the SASS task were characterised by smaller boundary separations and longer non-decision times. Mediation analyses showed that these simple effects of impulse stimulation were not secondary to its effect on an aspect of heart rate variability that measures anxiety. The decrement in boundary separation due to incongruous vestibular stimulation was selective to the SASS task, as indicated by a significant task by cue congruity interaction effect. This selective disruption, in the absence of concurrent preferential disturbances of the physiological or subjective states of the participants in the SASS task group, implied that aberrant space-motion information can have a direct effect on higher cognition.

This was the first empirical study to indicate that a direct effect can occur. As such, the final study served both to fulfil the research programme's goals and to make an original contribution to knowledge. This contribution was underpinned by novel mediation modelling of the relationship between balance disorders and higher cognition, and the analysis of diffusion model parameters yielded by the spatial tasks. The direct effect was interpreted as having occurred because the erroneous self-motion velocity information caused by the experimental stimulation disrupted the starting point for the temporal integration of covert body movements during MS-TL. According to this account, participants engaged in the imaginary transformation process based on a less precise representation of the body's temporo-spatial activity. This would have resulted in greater inter-trial variability (i.e. reduced precision) of the final imaginary body position yielded by MS-TL and, in turn, to increased accumulation of noise during the laterality decision-making. This explanation lends support to a contemporary, internal model-based theory of MS-TL.

The direct effect of aberrant space-motion information, specifically on MS-TL, has clinical implications. This cognitive process and its dependent cognitive functions, including theory of mind, may be particularly vulnerable. Moreover, the findings of this research imply that patients with pathological balance disorders may have under-recognised impairments of action planning and social cognition. According to the results of this project, further research is warranted to explore social functioning in the context of aberrant visuo-vestibular information.

Appendices

Appendix A: Testing and Measures Pack (Study 3)



Group & No.: 1MA | 1OB | 2ME

Order: No Motion first | Roll Motion first

Date: Time:

Participant code (chronological): P_________

Name:

PHASE 1:
Preparation Phase

PARTICIPATION INFORMATION SHEET

The effect of large field visual motion on mental transformations

Researcher: Jeremy Corcoran

Staff Supervisors: Prof Tony Towell; Prof John Golding; Dr Mark Gardner

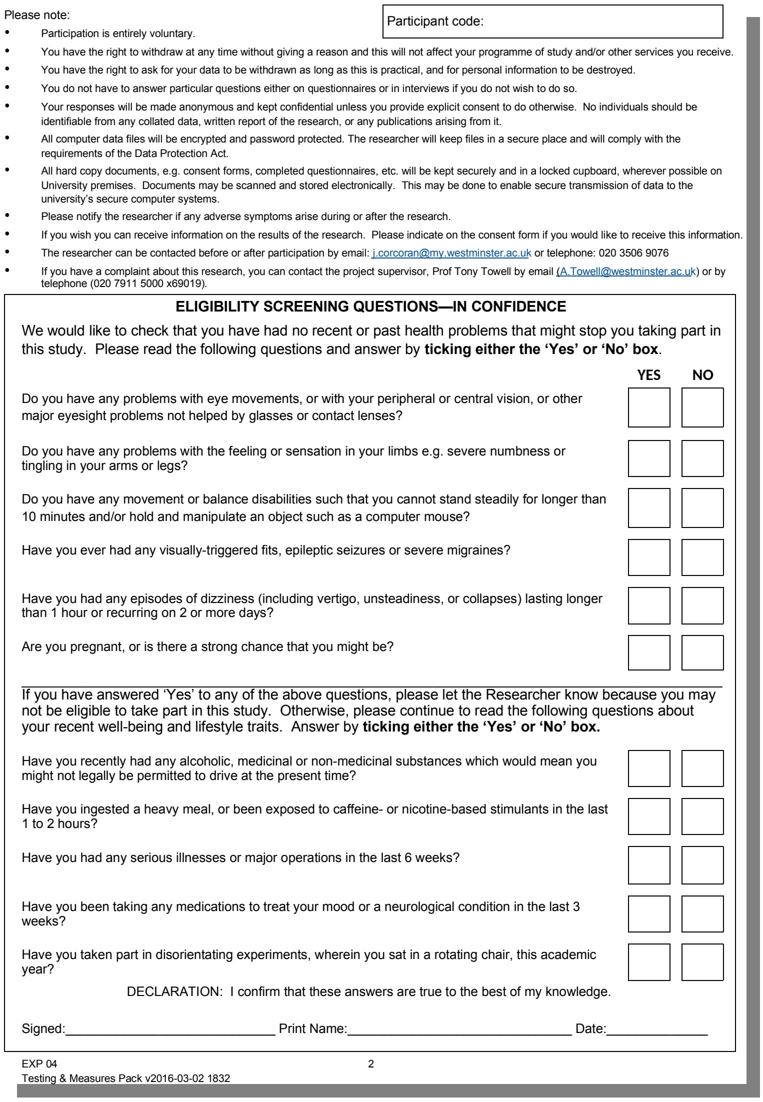
You are being invited to take part in a research study into disorientation caused by large, rotating visual scenes. This sort of visual motion can affect balance control as evidenced by increased amounts of body sway during exposures to it. The consequences of visual motion on cognitive performance are less well established. The aims of this study are to investigate how disorientation by rotating scenes impacts on different spatial cognitive tasks, and to see if there is a link between the levels of impact on cognition, balance control, motion sickness and anxiety.

This study is part of the PhD project being carried out by the researcher in the Psychology Department, University of Westminster.

The study will involve you attending a single testing session in the Cognitive Neuroscience Laboratory, 3^{rd} Floor Clipstone Building, Cavendish Campus, during which you will:

- Receive a short audio-visual presentation on the study in order to ensure you are further informed before you give consent;
- Complete a short health screening questionnaire to cross-check your eligibility to partake;
- Provide basic demographic information including age, handedness, programme and year of study;
- Complete a questionnaire to gauge your usual anxiety levels and tolerance of certain bodily and environmental motions;
- Familiarise yourself with the equipment set-up and tasks by way of undertaking short periods of balance practice and visuo-spatial cognitive practice;
- Undertake four two-minute [approximations] trials wherein you will complete your allocated visuo-spatial cognitive task as quickly but as accurately as possible – two of the trials will proceed with a rotating scene in the background;
- Record your levels of anxiety, confidence, effort and malaise after each of the trials;
- Describe the strategies you used to undertake the visuo-spatial cognitive task at the end of the study.

The testing session will last up to 75 minutes. If you chose to take part, you will be asked to provide written consent before testing will begin.



Please note:

Participant code:

- Participation is entirely voluntary.
- You have the right to withdraw at any time without giving a reason and this will not affect your programme of study and/or other services you receive.
- You have the right to ask for your data to be withdrawn as long as this is practical, and for personal information to be destroyed.
- You do not have to answer particular questions either on questionnaires or in interviews if you do not wish to do so.
- Your responses will be made anonymous and kept confidential unless you provide explicit consent to do otherwise. No individuals should be identifiable from any collated data, written report of the research, or any publications arising from it.
- All computer data files will be encrypted and password protected. The researcher will keep files in a secure place and will comply with the requirements of the Data Protection Act.
- All hard copy documents, e.g. consent forms, completed questionnaires, etc. will be kept securely and in a locked cupboard, wherever possible on University premises. Documents may be scanned and stored electronically. This may be done to enable secure transmission of data to the university's secure computer systems.
- Please notify the researcher if any adverse symptoms arise during or after the research.
- If you wish you can receive information on the results of the research. Please indicate on the consent form if you would like to receive this information.
- The researcher can be contacted before or after participation by email: j.corcoran@my.westminster.ac.uk or telephone: 020 3506 9076
- If you have a complaint about this research, you can contact the project supervisor, Prof Tony Towell by email (A.Towell@westminster.ac.uk) or by telephone (020 7911 5000 x69019).

ELIGIBILITY SCREENING QUESTIONS—IN CONFIDENCE

We would like to check that you have had no recent or past health problems that might stop you taking part in this study. Please read the following questions and answer by **ticking either the 'Yes' or 'No' box**.

	YES	NO
Do you have any problems with eye movements, or with your peripheral or central vision, or other major eyesight problems not helped by glasses or contact lenses?	☐	☐
Do you have any problems with the feeling or sensation in your limbs e.g. severe numbness or tingling in your arms or legs?	☐	☐
Do you have any movement or balance disabilities such that you cannot stand steadily for longer than 10 minutes and/or hold and manipulate an object such as a computer mouse?	☐	☐
Have you ever had any visually-triggered fits, epileptic seizures or severe migraines?	☐	☐
Have you had any episodes of dizziness (including vertigo, unsteadiness, or collapses) lasting longer than 1 hour or recurring on 2 or more days?	☐	☐
Are you pregnant, or is there a strong chance that you might be?	☐	☐

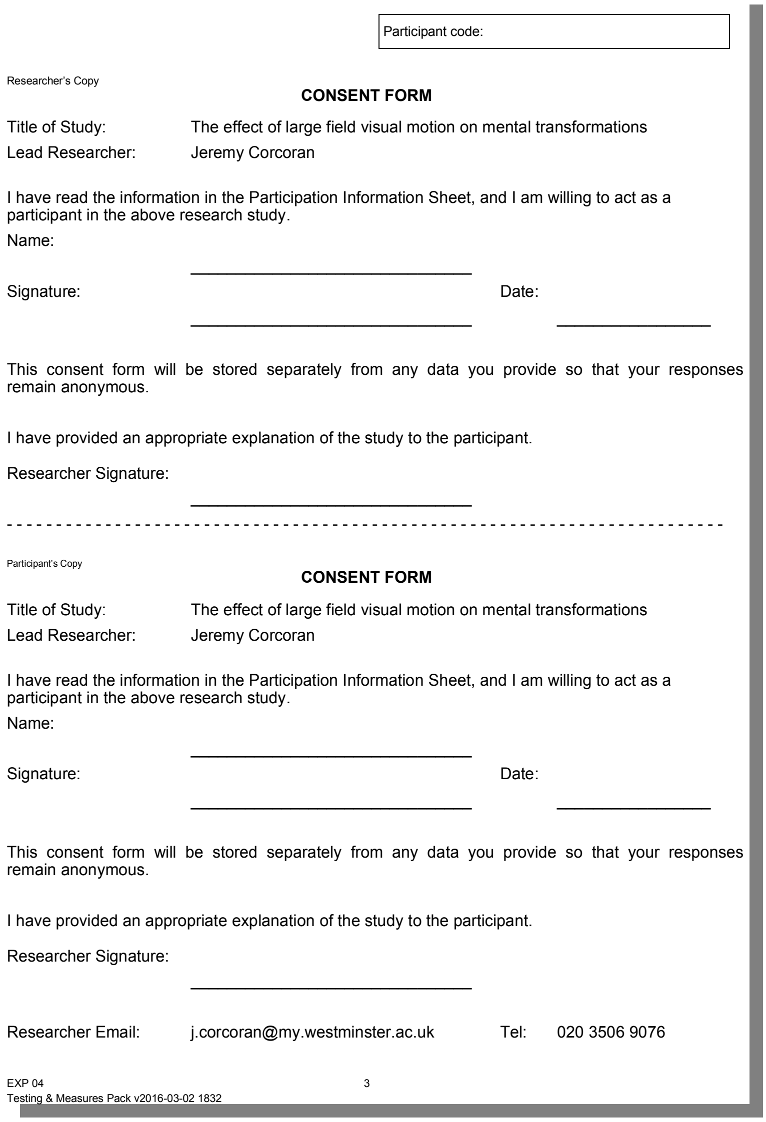
If you have answered 'Yes' to any of the above questions, please let the Researcher know because you may not be eligible to take part in this study. Otherwise, please continue to read the following questions about your recent well-being and lifestyle traits. Answer by **ticking either the 'Yes' or 'No' box.**

Have you recently had any alcoholic, medicinal or non-medicinal substances which would mean you might not legally be permitted to drive at the present time?	☐	☐
Have you ingested a heavy meal, or been exposed to caffeine- or nicotine-based stimulants in the last 1 to 2 hours?	☐	☐
Have you had any serious illnesses or major operations in the last 6 weeks?	☐	☐
Have you been taking any medications to treat your mood or a neurological condition in the last 3 weeks?	☐	☐
Have you taken part in disorientating experiments, wherein you sat in a rotating chair, this academic year?	☐	☐

DECLARATION: I confirm that these answers are true to the best of my knowledge.

Signed:____________________________ Print Name:______________________________ Date:_____________

EXP 04 2
Testing & Measures Pack v2016-03-02 1832



Participant code:

Researcher's Copy

CONSENT FORM

Title of Study: The effect of large field visual motion on mental transformations

Lead Researcher: Jeremy Corcoran

I have read the information in the Participation Information Sheet, and I am willing to act as a participant in the above research study.

Name: ______________________________

Signature: ______________________________ Date: ________________

This consent form will be stored separately from any data you provide so that your responses remain anonymous.

I have provided an appropriate explanation of the study to the participant.

Researcher Signature: ______________________________

- -

Participant's Copy

CONSENT FORM

Title of Study: The effect of large field visual motion on mental transformations

Lead Researcher: Jeremy Corcoran

I have read the information in the Participation Information Sheet, and I am willing to act as a participant in the above research study.

Name: ______________________________

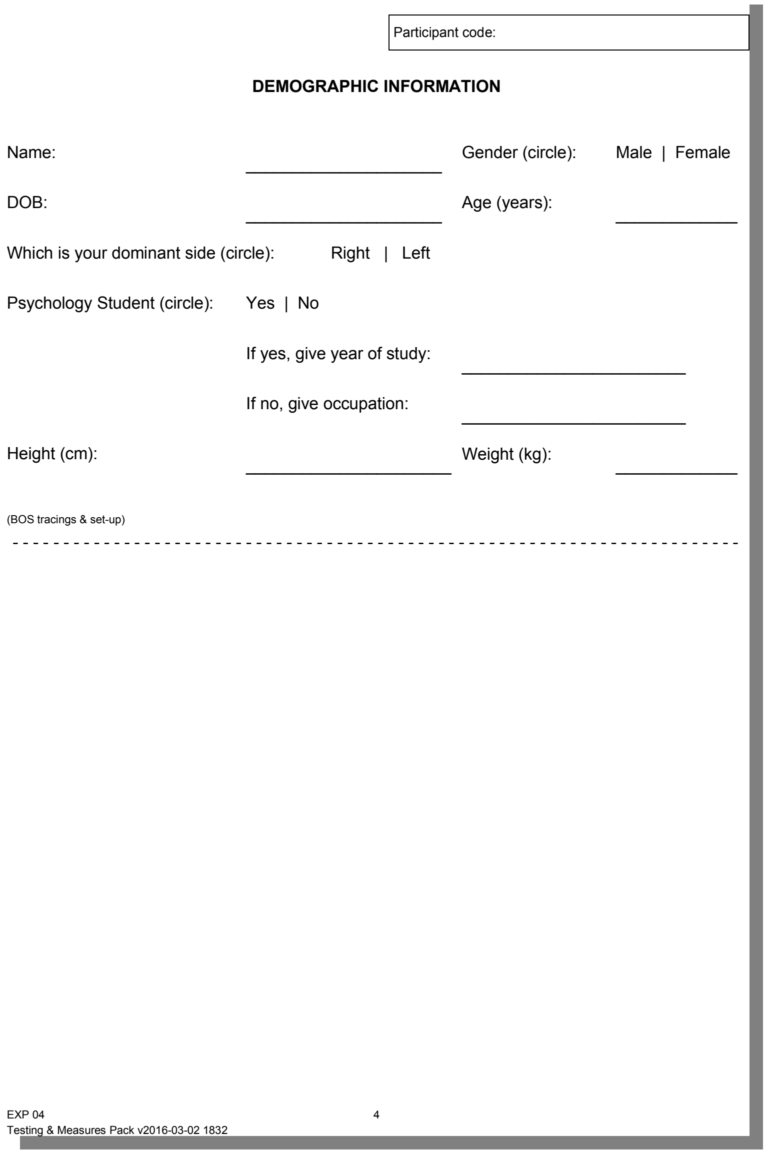
Signature: ______________________________ Date: ________________

This consent form will be stored separately from any data you provide so that your responses remain anonymous.

I have provided an appropriate explanation of the study to the participant.

Researcher Signature: ______________________________

Researcher Email: j.corcoran@my.westminster.ac.uk Tel: 020 3506 9076



Participant code:

DEMOGRAPHIC INFORMATION

Name: ____________________ Gender (circle): Male | Female

DOB: ____________________ Age (years): ____________

Which is your dominant side (circle): Right | Left

Psychology Student (circle): Yes | No

If yes, give year of study: ____________________

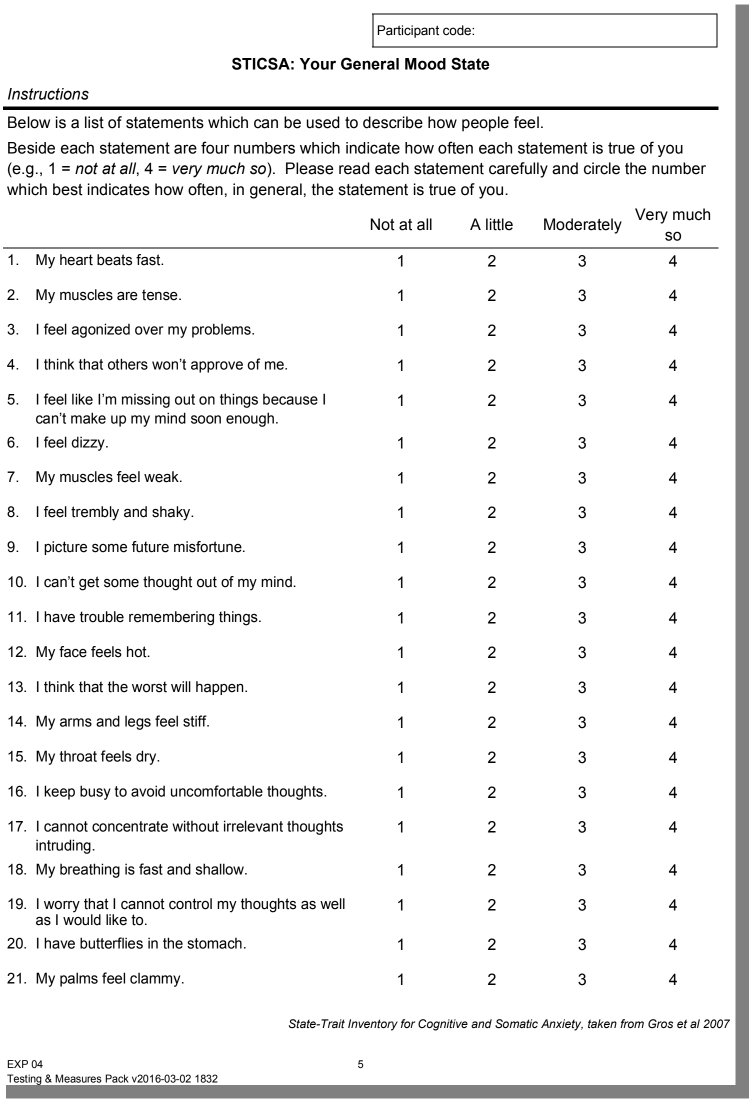
If no, give occupation: ____________________

Height (cm): ____________________ Weight (kg): ____________

(BOS tracings & set-up)

- -

EXP 04 4
Testing & Measures Pack v2016-03-02 1832



Participant code:

STICSA: Your General Mood State

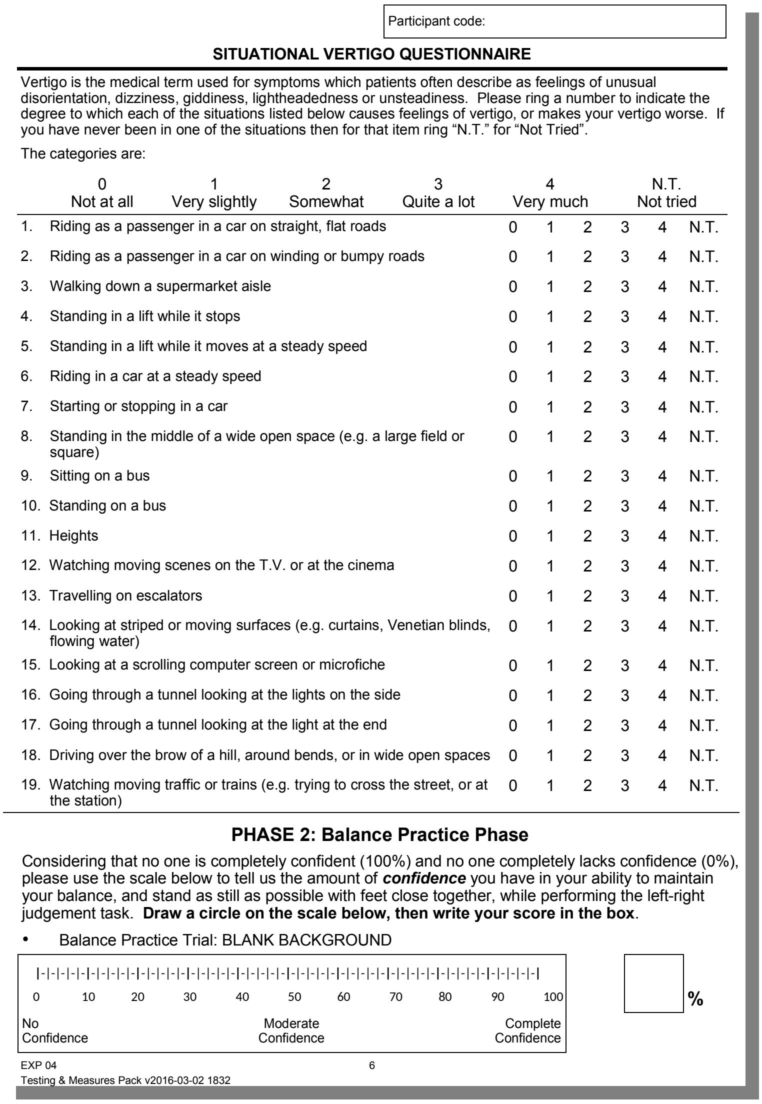
Instructions

Below is a list of statements which can be used to describe how people feel.

Beside each statement are four numbers which indicate how often each statement is true of you (e.g., 1 = *not at all*, 4 = *very much so*). Please read each statement carefully and circle the number which best indicates how often, in general, the statement is true of you.

	Not at all	A little	Moderately	Very much so
1. My heart beats fast.	1	2	3	4
2. My muscles are tense.	1	2	3	4
3. I feel agonized over my problems.	1	2	3	4
4. I think that others won't approve of me.	1	2	3	4
5. I feel like I'm missing out on things because I can't make up my mind soon enough.	1	2	3	4
6. I feel dizzy.	1	2	3	4
7. My muscles feel weak.	1	2	3	4
8. I feel trembly and shaky.	1	2	3	4
9. I picture some future misfortune.	1	2	3	4
10. I can't get some thought out of my mind.	1	2	3	4
11. I have trouble remembering things.	1	2	3	4
12. My face feels hot.	1	2	3	4
13. I think that the worst will happen.	1	2	3	4
14. My arms and legs feel stiff.	1	2	3	4
15. My throat feels dry.	1	2	3	4
16. I keep busy to avoid uncomfortable thoughts.	1	2	3	4
17. I cannot concentrate without irrelevant thoughts intruding.	1	2	3	4
18. My breathing is fast and shallow.	1	2	3	4
19. I worry that I cannot control my thoughts as well as I would like to.	1	2	3	4
20. I have butterflies in the stomach.	1	2	3	4
21. My palms feel clammy.	1	2	3	4

State-Trait Inventory for Cognitive and Somatic Anxiety, taken from Gros et al 2007



Participant code:

SITUATIONAL VERTIGO QUESTIONNAIRE

Vertigo is the medical term used for symptoms which patients often describe as feelings of unusual disorientation, dizziness, giddiness, lightheadedness or unsteadiness. Please ring a number to indicate the degree to which each of the situations listed below causes feelings of vertigo, or makes your vertigo worse. If you have never been in one of the situations then for that item ring "N.T." for "Not Tried".

The categories are:

0	1	2	3	4	N.T.
Not at all	Very slightly	Somewhat	Quite a lot	Very much	Not tried

1.	Riding as a passenger in a car on straight, flat roads	0	1	2	3	4	N.T.
2.	Riding as a passenger in a car on winding or bumpy roads	0	1	2	3	4	N.T.
3.	Walking down a supermarket aisle	0	1	2	3	4	N.T.
4.	Standing in a lift while it stops	0	1	2	3	4	N.T.
5.	Standing in a lift while it moves at a steady speed	0	1	2	3	4	N.T.
6.	Riding in a car at a steady speed	0	1	2	3	4	N.T.
7.	Starting or stopping in a car	0	1	2	3	4	N.T.
8.	Standing in the middle of a wide open space (e.g. a large field or square)	0	1	2	3	4	N.T.
9.	Sitting on a bus	0	1	2	3	4	N.T.
10.	Standing on a bus	0	1	2	3	4	N.T.
11.	Heights	0	1	2	3	4	N.T.
12.	Watching moving scenes on the T.V. or at the cinema	0	1	2	3	4	N.T.
13.	Travelling on escalators	0	1	2	3	4	N.T.
14.	Looking at striped or moving surfaces (e.g. curtains, Venetian blinds, flowing water)	0	1	2	3	4	N.T.
15.	Looking at a scrolling computer screen or microfiche	0	1	2	3	4	N.T.
16.	Going through a tunnel looking at the lights on the side	0	1	2	3	4	N.T.
17.	Going through a tunnel looking at the light at the end	0	1	2	3	4	N.T.
18.	Driving over the brow of a hill, around bends, or in wide open spaces	0	1	2	3	4	N.T.
19.	Watching moving traffic or trains (e.g. trying to cross the street, or at the station)	0	1	2	3	4	N.T.

PHASE 2: Balance Practice Phase

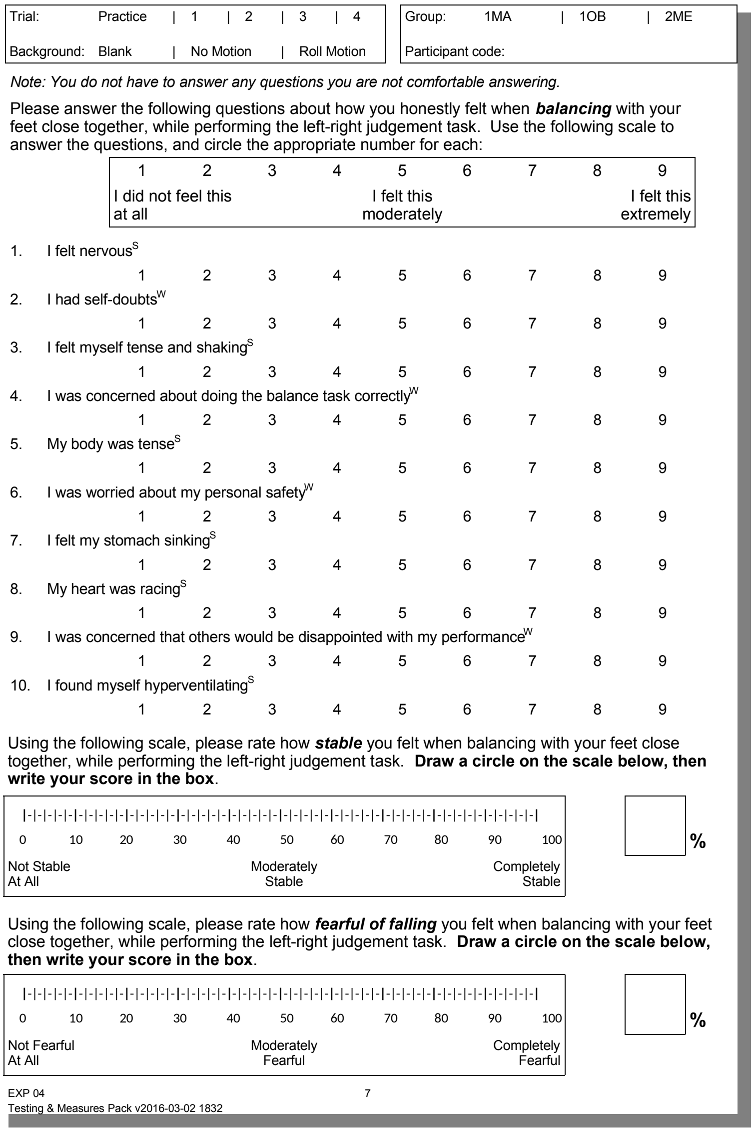
Considering that no one is completely confident (100%) and no one completely lacks confidence (0%), please use the scale below to tell us the amount of ***confidence*** you have in your ability to maintain your balance, and stand as still as possible with feet close together, while performing the left-right judgement task. **Draw a circle on the scale below, then write your score in the box**.

- Balance Practice Trial: BLANK BACKGROUND

0 10 20 30 40 50 60 70 80 90 100

No Confidence — Moderate Confidence — Complete Confidence

☐ %



Trial:	Practice	| 1	| 2	| 3	| 4		
Background:	Blank	| No Motion	| Roll Motion				

Group:	1MA	| 1OB	| 2ME
Participant code:			

Note: You do not have to answer any questions you are not comfortable answering.

Please answer the following questions about how you honestly felt when ***balancing*** with your feet close together, while performing the left-right judgement task. Use the following scale to answer the questions, and circle the appropriate number for each:

1	2	3	4	5	6	7	8	9
I did not feel this at all				I felt this moderately				I felt this extremely

1. I felt nervous^{S}
   1 2 3 4 5 6 7 8 9
2. I had self-doubts^{W}
   1 2 3 4 5 6 7 8 9
3. I felt myself tense and shaking^{S}
   1 2 3 4 5 6 7 8 9
4. I was concerned about doing the balance task correctly^{W}
   1 2 3 4 5 6 7 8 9
5. My body was tense^{S}
   1 2 3 4 5 6 7 8 9
6. I was worried about my personal safety^{W}
   1 2 3 4 5 6 7 8 9
7. I felt my stomach sinking^{S}
   1 2 3 4 5 6 7 8 9
8. My heart was racing^{S}
   1 2 3 4 5 6 7 8 9
9. I was concerned that others would be disappointed with my performance^{W}
   1 2 3 4 5 6 7 8 9
10. I found myself hyperventilating^{S}
    1 2 3 4 5 6 7 8 9

Using the following scale, please rate how ***stable*** you felt when balancing with your feet close together, while performing the left-right judgement task. **Draw a circle on the scale below, then write your score in the box**.

|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|

0 10 20 30 40 50 60 70 80 90 100

Not Stable At All	Moderately Stable	Completely Stable

☐ %

Using the following scale, please rate how ***fearful of falling*** you felt when balancing with your feet close together, while performing the left-right judgement task. **Draw a circle on the scale below, then write your score in the box**.

|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|

0 10 20 30 40 50 60 70 80 90 100

Not Fearful At All	Moderately Fearful	Completely Fearful

☐ %

EXP 04 7
Testing & Measures Pack v2016-03-02 1832

Participant code:

Rating Scale for Malaise

Please rate what level of ***malaise*** you felt when balancing with your feet close together, while performing the left-right judgement task against the visual backdrop. Malaise includes any feelings of: vertigo, fullness of head, or other dizziness feelings; stomach awareness, nausea, or other general discomfort; eyestrain, headache, fatigue, or other difficulties focusing or concentrating.

	No Malaise	Mild Malaise	Moderate Malaise	Severe Malaise
(tick one box)	☐	☐	☐	☐

To be repeated for all experimental trials (as per Gresty et al 2008)

PHASE 3: Cognitive Task Practice Phase

Rating Scale for Mental Effort

Please rate how much ***mental effort*** you exerted while performing the left-right judgement task in a sitting position **(tick one box)**:

Mentally At Rest	Minimal Mental Effort	Moderate Mental Effort	Maximal Mental Effort
☐	☐	☐	☐

To be the baseline marker for all subsequent ratings (as per Gardner et al in press)

PHASE 4: Experimentation Phase

Considering that no one is completely confident (100%) and no one completely lacks confidence (0%), please use the scale below to tell us the amount of ***confidence*** you have in your ability to maintain your balance, and stand as still as possible with feet close together, while performing the left-right judgement task. **Draw a circle on the scales below, then write your scores in the boxes**.

- Experimental Trial 1: No Motion | Roll Motion

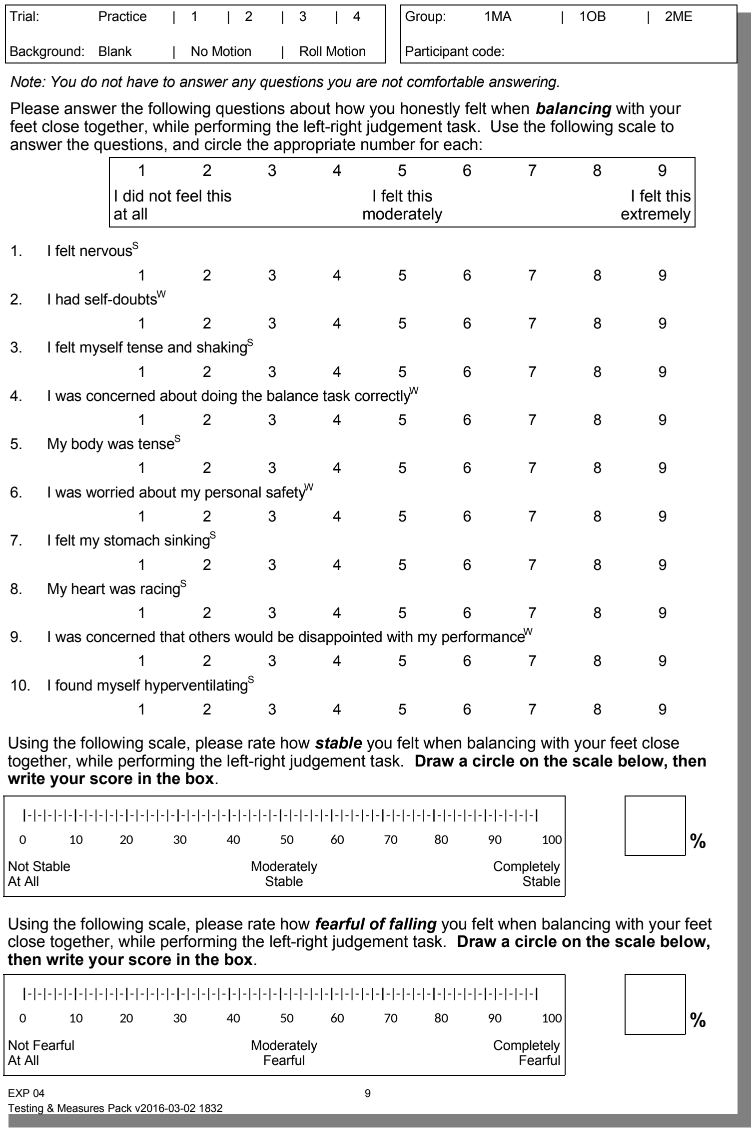
0	10	20	30	40	50	60	70	80	90	100
No Confidence					Moderate Confidence					Complete Confidence

☐ %

- Experimental Trial 2: No Motion | Roll Motion

0	10	20	30	40	50	60	70	80	90	100
No Confidence					Moderate Confidence					Complete Confidence

☐ %



Trial: Practice | 1 | 2 | 3 | 4
Background: Blank | No Motion | Roll Motion

Group: 1MA | 1OB | 2ME
Participant code:

Note: You do not have to answer any questions you are not comfortable answering.

Please answer the following questions about how you honestly felt when ***balancing*** with your feet close together, while performing the left-right judgement task. Use the following scale to answer the questions, and circle the appropriate number for each:

1	2	3	4	5	6	7	8	9
I did not feel this at all				I felt this moderately				I felt this extremely

1. I felt nervous^{S}
   1 2 3 4 5 6 7 8 9
2. I had self-doubts^{W}
   1 2 3 4 5 6 7 8 9
3. I felt myself tense and shaking^{S}
   1 2 3 4 5 6 7 8 9
4. I was concerned about doing the balance task correctly^{W}
   1 2 3 4 5 6 7 8 9
5. My body was tense^{S}
   1 2 3 4 5 6 7 8 9
6. I was worried about my personal safety^{W}
   1 2 3 4 5 6 7 8 9
7. I felt my stomach sinking^{S}
   1 2 3 4 5 6 7 8 9
8. My heart was racing^{S}
   1 2 3 4 5 6 7 8 9
9. I was concerned that others would be disappointed with my performance^{W}
   1 2 3 4 5 6 7 8 9
10. I found myself hyperventilating^{S}
   1 2 3 4 5 6 7 8 9

Using the following scale, please rate how ***stable*** you felt when balancing with your feet close together, while performing the left-right judgement task. **Draw a circle on the scale below, then write your score in the box**.

0	10	20	30	40	50	60	70	80	90	100
Not Stable At All					Moderately Stable					Completely Stable

☐ %

Using the following scale, please rate how ***fearful of falling*** you felt when balancing with your feet close together, while performing the left-right judgement task. **Draw a circle on the scale below, then write your score in the box**.

0	10	20	30	40	50	60	70	80	90	100
Not Fearful At All					Moderately Fearful					Completely Fearful

☐ %

EXP 04 9
Testing & Measures Pack v2016-03-02 1832

Participant code:

Rating Scale for Malaise

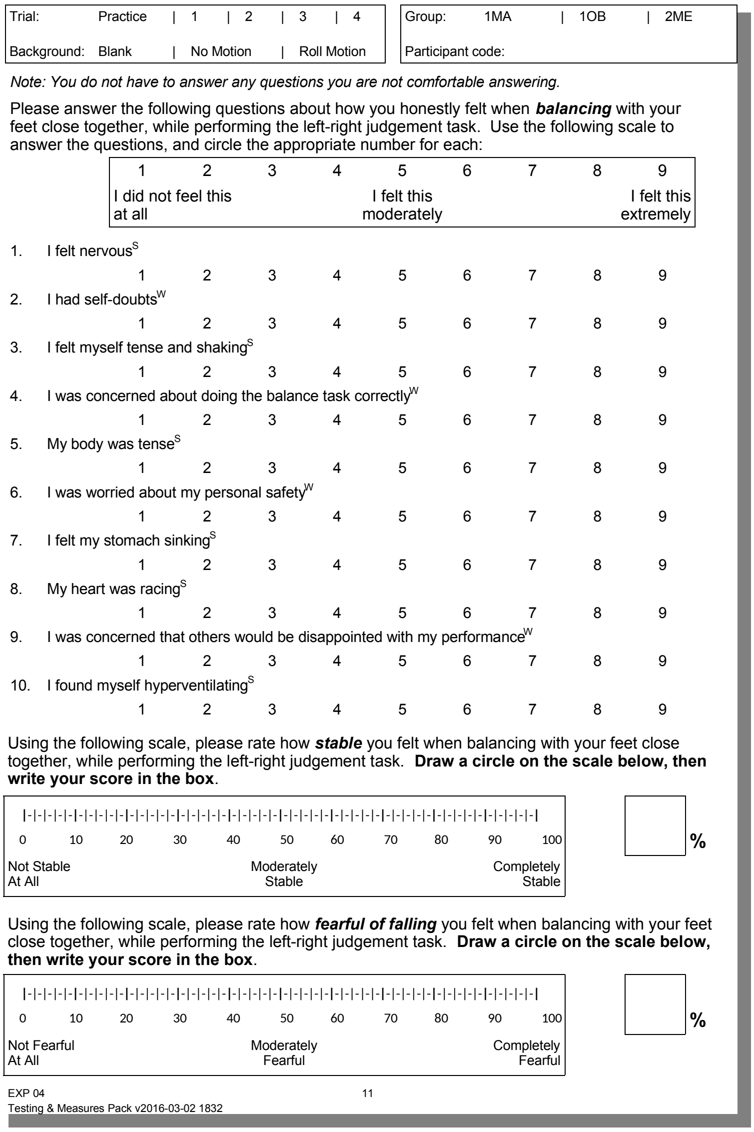
Please rate what level of ***malaise*** you felt when balancing with your feet close together, while performing the left-right judgement task against the visual backdrop. Malaise includes any feelings of: vertigo, fullness of head, or other dizziness feelings; stomach awareness, nausea, or other general discomfort; eyestrain, headache, fatigue, or other difficulties focusing or concentrating.

	No Malaise	Mild Malaise	Moderate Malaise	Severe Malaise
(tick one box)	☐	☐	☐	☐

Rating Scale for Mental Effort

Please rate how much ***mental effort*** you exerted while performing the left-right judgement task. Compared to the practice trial WHEN YOU WERE SITTING DOWN, was the amount of mental effort you just put in to the last trial **(tick one box)**:

A Lot Less	Moderately Less	Mildly Less	No Different	Mildly More	Moderately More	A Lot More
☐	☐	☐	☐	☐	☐	☐



Trial:	Practice	1	2	3	4
Background:	Blank	No Motion	Roll Motion		

Group:	1MA	1OB	2ME
Participant code:			

Note: You do not have to answer any questions you are not comfortable answering.

Please answer the following questions about how you honestly felt when ***balancing*** with your feet close together, while performing the left-right judgement task. Use the following scale to answer the questions, and circle the appropriate number for each:

1	2	3	4	5	6	7	8	9
I did not feel this at all				I felt this moderately				I felt this extremely

1. I felt nervous^{S}
   1 2 3 4 5 6 7 8 9
2. I had self-doubts^{W}
   1 2 3 4 5 6 7 8 9
3. I felt myself tense and shaking^{S}
   1 2 3 4 5 6 7 8 9
4. I was concerned about doing the balance task correctly^{W}
   1 2 3 4 5 6 7 8 9
5. My body was tense^{S}
   1 2 3 4 5 6 7 8 9
6. I was worried about my personal safety^{W}
   1 2 3 4 5 6 7 8 9
7. I felt my stomach sinking^{S}
   1 2 3 4 5 6 7 8 9
8. My heart was racing^{S}
   1 2 3 4 5 6 7 8 9
9. I was concerned that others would be disappointed with my performance^{W}
   1 2 3 4 5 6 7 8 9
10. I found myself hyperventilating^{S}
    1 2 3 4 5 6 7 8 9

Using the following scale, please rate how ***stable*** you felt when balancing with your feet close together, while performing the left-right judgement task. **Draw a circle on the scale below, then write your score in the box**.

0	10	20	30	40	50	60	70	80	90	100
Not Stable At All					Moderately Stable					Completely Stable

☐ %

Using the following scale, please rate how ***fearful of falling*** you felt when balancing with your feet close together, while performing the left-right judgement task. **Draw a circle on the scale below, then write your score in the box**.

0	10	20	30	40	50	60	70	80	90	100
Not Fearful At All					Moderately Fearful					Completely Fearful

☐ %

EXP 04 11
Testing & Measures Pack v2016-03-02 1832

Participant code:

Rating Scale for Malaise

Please rate what level of ***malaise*** you felt when balancing with your feet close together, while performing the left-right judgement task against the visual backdrop. Malaise includes any feelings of: vertigo, fullness of head, or other dizziness feelings; stomach awareness, nausea, or other general discomfort; eyestrain, headache, fatigue, or other difficulties focusing or concentrating.

	No Malaise	Mild Malaise	Moderate Malaise	Severe Malaise
(tick one box)	☐	☐	☐	☐

Rating Scale for Mental Effort

Please rate how much ***mental effort*** you exerted while performing the left-right judgement task. Compared to the practice trial WHEN YOU WERE SITTING DOWN, was the amount of mental effort you just put in to the last trial **(tick one box)**:

A Lot Less	Moderately Less	Mildly Less	No Different	Mildly More	Moderately More	A Lot More
☐	☐	☐	☐	☐	☐	☐

Considering that no one is completely confident (100%) and no one completely lacks confidence (0%), please use the scale below to tell us the amount of ***confidence*** you have in your ability to maintain your balance, and stand as still as possible with feet close together, while performing the left-right judgement task. **Draw a circle on the scales below, then write your scores in the boxes**.

- Experimental Trial 3: No Motion | Roll Motion

|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|

0 10 20 30 40 50 60 70 80 90 100

No Confidence | Moderate Confidence | Complete Confidence

☐ %

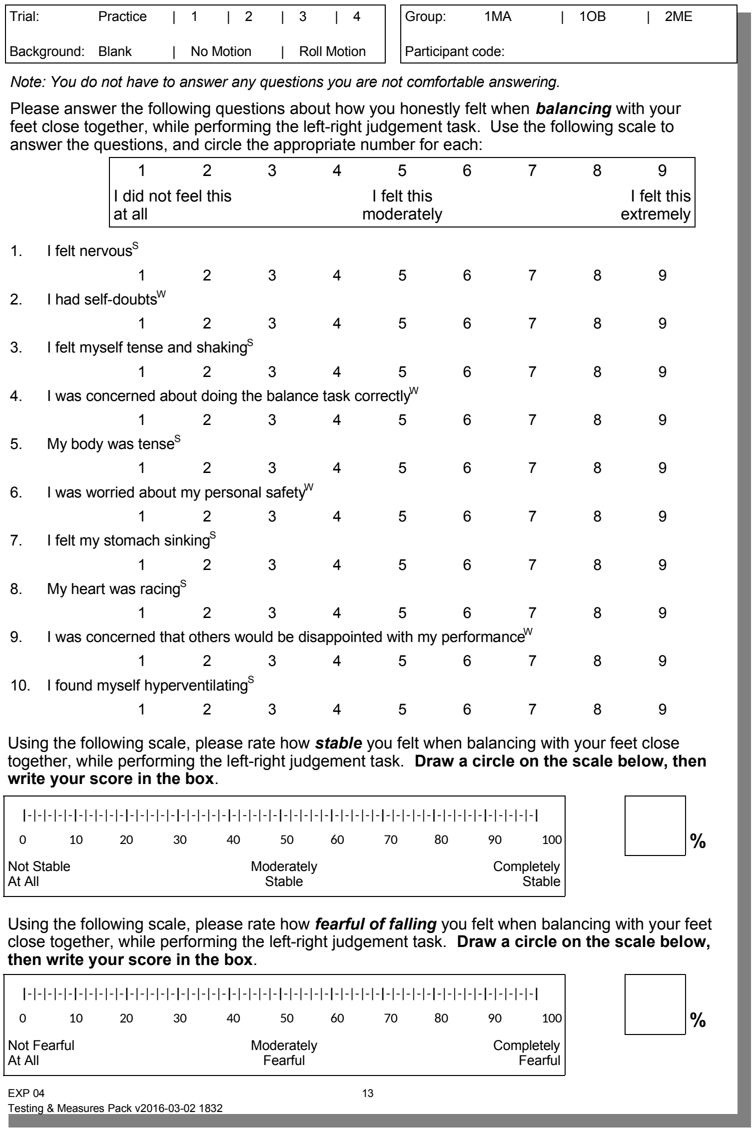
- Experimental Trial 4: No Motion | Roll Motion

|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|

0 10 20 30 40 50 60 70 80 90 100

No Confidence | Moderate Confidence | Complete Confidence

☐ %



Trial:	Practice	| 1	| 2	| 3	| 4	Group: 1MA	| 1OB	| 2ME
Background:	Blank	| No Motion	| Roll Motion			Participant code:		

Note: You do not have to answer any questions you are not comfortable answering.

Please answer the following questions about how you honestly felt when ***balancing*** with your feet close together, while performing the left-right judgement task. Use the following scale to answer the questions, and circle the appropriate number for each:

1	2	3	4	5	6	7	8	9
I did not feel this at all				I felt this moderately				I felt this extremely

1. I felt nervous^{S}
   1 2 3 4 5 6 7 8 9
2. I had self-doubts^{W}
   1 2 3 4 5 6 7 8 9
3. I felt myself tense and shaking^{S}
   1 2 3 4 5 6 7 8 9
4. I was concerned about doing the balance task correctly^{W}
   1 2 3 4 5 6 7 8 9
5. My body was tense^{S}
   1 2 3 4 5 6 7 8 9
6. I was worried about my personal safety^{W}
   1 2 3 4 5 6 7 8 9
7. I felt my stomach sinking^{S}
   1 2 3 4 5 6 7 8 9
8. My heart was racing^{S}
   1 2 3 4 5 6 7 8 9
9. I was concerned that others would be disappointed with my performance^{W}
   1 2 3 4 5 6 7 8 9
10. I found myself hyperventilating^{S}
    1 2 3 4 5 6 7 8 9

Using the following scale, please rate how ***stable*** you felt when balancing with your feet close together, while performing the left-right judgement task. **Draw a circle on the scale below, then write your score in the box.**

|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|

0 10 20 30 40 50 60 70 80 90 100

Not Stable At All | Moderately Stable | Completely Stable

☐ %

Using the following scale, please rate how ***fearful of falling*** you felt when balancing with your feet close together, while performing the left-right judgement task. **Draw a circle on the scale below, then write your score in the box.**

|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|

0 10 20 30 40 50 60 70 80 90 100

Not Fearful At All | Moderately Fearful | Completely Fearful

☐ %

EXP 04 13
Testing & Measures Pack v2016-03-02 1832

Participant code:

Rating Scale for Malaise

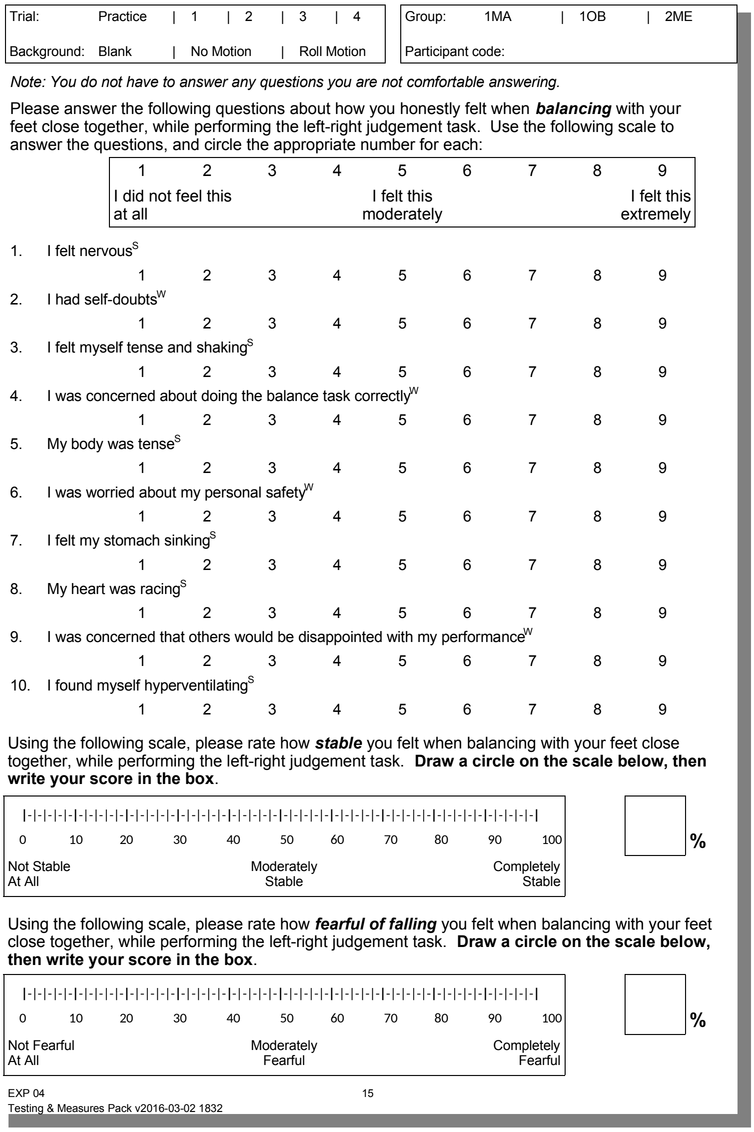
Please rate what level of ***malaise*** you felt when balancing with your feet close together, while performing the left-right judgement task against the visual backdrop. Malaise includes any feelings of: vertigo, fullness of head, or other dizziness feelings; stomach awareness, nausea, or other general discomfort; eyestrain, headache, fatigue, or other difficulties focusing or concentrating.

	No Malaise	Mild Malaise	Moderate Malaise	Severe Malaise
(tick one box)	☐	☐	☐	☐

Rating Scale for Mental Effort

Please rate how much ***mental effort*** you exerted while performing the left-right judgement task. Compared to the practice trial WHEN YOU WERE SITTING DOWN, was the amount of mental effort you just put in to the last trial **(tick one box)**:

A Lot Less	Moderately Less	Mildly Less	No Different	Mildly More	Moderately More	A Lot More
☐	☐	☐	☐	☐	☐	☐



Trial: Practice | 1 | 2 | 3 | 4
Background: Blank | No Motion | Roll Motion

Group: 1MA | 1OB | 2ME
Participant code:

Note: You do not have to answer any questions you are not comfortable answering.

Please answer the following questions about how you honestly felt when ***balancing*** with your feet close together, while performing the left-right judgement task. Use the following scale to answer the questions, and circle the appropriate number for each:

1	2	3	4	5	6	7	8	9
I did not feel this at all				I felt this moderately				I felt this extremely

1. I felt nervous^{S}
   1 2 3 4 5 6 7 8 9
2. I had self-doubts^{W}
   1 2 3 4 5 6 7 8 9
3. I felt myself tense and shaking^{S}
   1 2 3 4 5 6 7 8 9
4. I was concerned about doing the balance task correctly^{W}
   1 2 3 4 5 6 7 8 9
5. My body was tense^{S}
   1 2 3 4 5 6 7 8 9
6. I was worried about my personal safety^{W}
   1 2 3 4 5 6 7 8 9
7. I felt my stomach sinking^{S}
   1 2 3 4 5 6 7 8 9
8. My heart was racing^{S}
   1 2 3 4 5 6 7 8 9
9. I was concerned that others would be disappointed with my performance^{W}
   1 2 3 4 5 6 7 8 9
10. I found myself hyperventilating^{S}
    1 2 3 4 5 6 7 8 9

Using the following scale, please rate how ***stable*** you felt when balancing with your feet close together, while performing the left-right judgement task. **Draw a circle on the scale below, then write your score in the box**.

0	10	20	30	40	50	60	70	80	90	100
Not Stable At All					Moderately Stable					Completely Stable

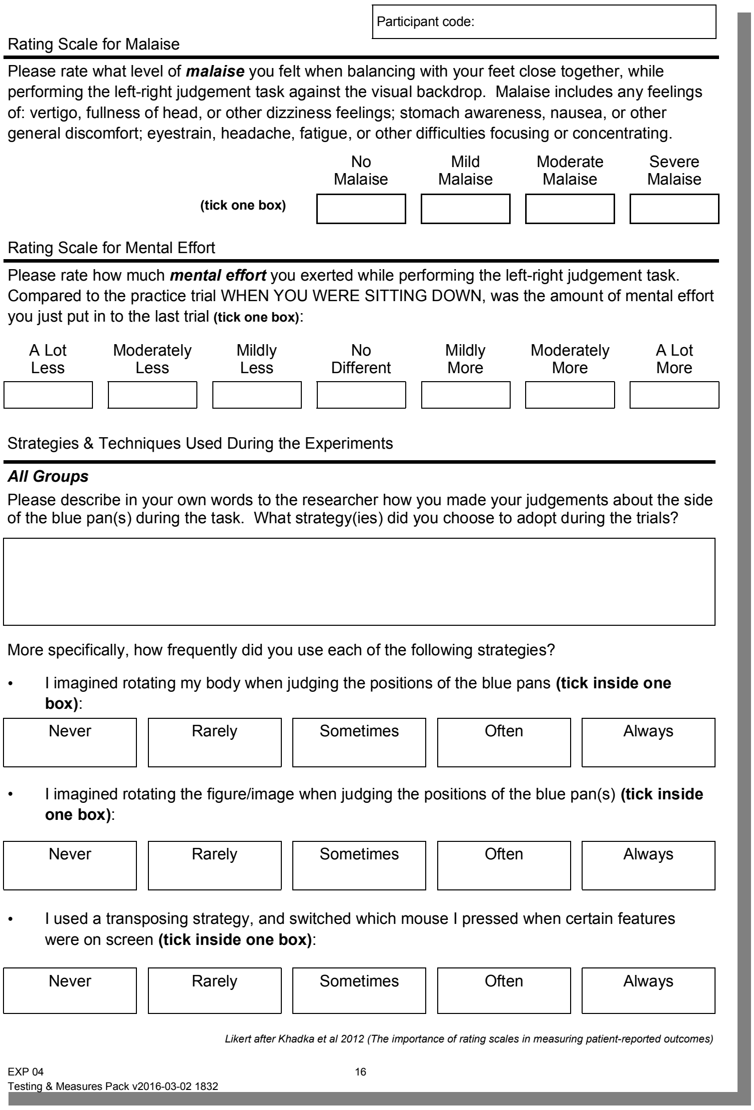
☐ %

Using the following scale, please rate how ***fearful of falling*** you felt when balancing with your feet close together, while performing the left-right judgement task. **Draw a circle on the scale below, then write your score in the box**.

0	10	20	30	40	50	60	70	80	90	100
Not Fearful At All					Moderately Fearful					Completely Fearful

☐ %

EXP 04 15
Testing & Measures Pack v2016-03-02 1832



Participant code:

Rating Scale for Malaise

Please rate what level of ***malaise*** you felt when balancing with your feet close together, while performing the left-right judgement task against the visual backdrop. Malaise includes any feelings of: vertigo, fullness of head, or other dizziness feelings; stomach awareness, nausea, or other general discomfort; eyestrain, headache, fatigue, or other difficulties focusing or concentrating.

	No Malaise	Mild Malaise	Moderate Malaise	Severe Malaise
(tick one box)	☐	☐	☐	☐

Rating Scale for Mental Effort

Please rate how much ***mental effort*** you exerted while performing the left-right judgement task. Compared to the practice trial WHEN YOU WERE SITTING DOWN, was the amount of mental effort you just put in to the last trial **(tick one box)**:

A Lot Less	Moderately Less	Mildly Less	No Different	Mildly More	Moderately More	A Lot More
☐	☐	☐	☐	☐	☐	☐

Strategies & Techniques Used During the Experiments

All Groups

Please describe in your own words to the researcher how you made your judgements about the side of the blue pan(s) during the task. What strategy(ies) did you choose to adopt during the trials?

☐

More specifically, how frequently did you use each of the following strategies?

- I imagined rotating my body when judging the positions of the blue pans **(tick inside one box)**:

☐ Never	☐ Rarely	☐ Sometimes	☐ Often	☐ Always

- I imagined rotating the figure/image when judging the positions of the blue pan(s) **(tick inside one box)**:

☐ Never	☐ Rarely	☐ Sometimes	☐ Often	☐ Always

- I used a transposing strategy, and switched which mouse I pressed when certain features were on screen **(tick inside one box)**:

☐ Never	☐ Rarely	☐ Sometimes	☐ Often	☐ Always

Likert after Khadka et al 2012 (The importance of rating scales in measuring patient-reported outcomes)

EXP 04 16
Testing & Measures Pack v2016-03-02 1832

Participant code:

Illusion of motion *(Gresty et al 2008 Experiment 2)*

All Groups

Roll motion can cause the illusion of self motion—that is, you can feel like you are spinning, instead of, or as well as, the background spinning. This illusion is called ‘vection’, or the ‘train illusion’.

Read the questions below, and answer by circling a response option:

During the experimental trials, was vection: Present? | Absent?

If present, did vection occur in: Brief Episodes? | Sustained Episodes?

If present, was the illusion: Weak? | Moderate? | Strong?

PHASE 5: Recovery Phase

Rating Scale for Malaise (Optional)

To check you have recovered from the experimental conditions, please rate what level of ***malaise*** you have at the following time points after the last trial:

	No Malaise	Mild Malaise	Moderate Malaise	Severe Malaise
5 minutes after final trial (tick)				
10 minutes after final trial (tick)				

Appendix B: The design of new spatial perspective-taking and comparator tasks

The avatar incorporated in the new spatial perspective-taking (SPT) task was a three-dimensional (3-D) wireframe with masculine features. Using Autocad 2015 (Autodesk, San Rafael, CA, USA), and based on the studies by Tadi et al. (2009) and van Elk and Blanke (2014), the male figure was rendered in eight yawing increments from 0º (rear-facing) to 180º (front-facing), through 45, 90 and 135º turns to the right and left. The finer detail of the avatar's pose and the demarcation, about which participants would be required to make laterality judgements, were refined once the stimulus for the spatial control task had been chosen and built using Autocad (see section 5.2.3). To differentiate the new 3-D SPT task from pre-existing versions, it was called the 'Single Avatar Stimulus Set' (SASS) task.

Choosing a stimulus for the spatial control task (i.e. the 3-D version of the Transpose task - see sections 4.2 and 4.3.3) required careful consideration. It had to satisfy several criteria, which were conceived by the doctoral researcher and supervisory team. Specifically, the stimulus had to:

- Have a clearly distinguishable front and back and, hence, left and right sides like humans do,
- Have an elongated vertical axis as per the human form,
- Be inanimate - shapes of other animals, which fit the two previous criteria, might otherwise be interpretable as humanoid,
- Have no clear and specific spatial relationship with a human operator or onlooker. Therefore, the inanimate object was not to be something that is drivable, or otherwise operable from inside or out, or something that is wearable (ornamental objects rather than interactive devices were preferable on this basis),
- Allow for laterality demarcations at the same spatial separation and relative horizontal position as per the demarcations on the avatar in the SASS task. Furthermore, the stimulus for the spatial control task needed to display the lateralising feature with similar levels of conspicuousness as the SASS task's avatar.

In part, the above criteria were delineated on the basis that the spatial control task's stimulus material needed to have similar visual complexity to the avatar in the SASS task, so that the same degree of contour integration was required by both (Gilbert & Li., 2013). Only if the tasks' stimuli demanded the same level of cognitive activity to assemble their contour elements into global forms were the tasks likely to be of matching difficulty. Therefore, the dimensions of the control task's stimulus needed to be the same as those of the male figure that had been rendered for the SASS task. Standardising the dimensions of the stimuli would also help ensure both tasks had the same spatial mappings or compatibilities. The criteria above were also intended to ensure the control task's stimulus discouraged participants from engaging in MS-TL to solve the task. That is, the stimulus had to prevent imaginary changes in self-location from being an intuitive strategy for participants to adopt.

A custom-designed, 3-D measuring scale satisfied all of the above criteria the best. It was rendered in the same eight yawing increments as the avatar in the SASS task was. The measuring scale is shown in its eight orientations in Figure B.1 [B]. Each orientation is positioned next to the respective orientation of the avatar incorporated in the SASS task (Figure B.1 [A]). To differentiate the new 3-D control task from the SASS task, it was named the 'Single Object Stimulus Set' (SOSS) task.

As can be seen in Figure B.1, the SASS task's avatar was rendered in an erect pose with its feet and legs together, so that the dimensions of its body and legs were not too dissimilar from the dimensions of the measuring scale's vertical supporting strut. The avatar's red tie but otherwise grey form matched the measuring scale's red pointer against its brushed chrome finish. The scale pans held by the avatar in its outstretched arms also resembled the measuring scale's cross beam and scale pans. Every stimulus shown during both the SASS and SOSS tasks depicted one grey and one blue scale pan. The significance of this, plus the different strategies participants were instructed to adopt during the tasks, are explained in the Methods section of Chapter 5 (see section 5.3.2). The colour schemes of both tasks were based on those applied by Creem-Regehr et al. (2007) to their custom mental spatial transformation tasks.

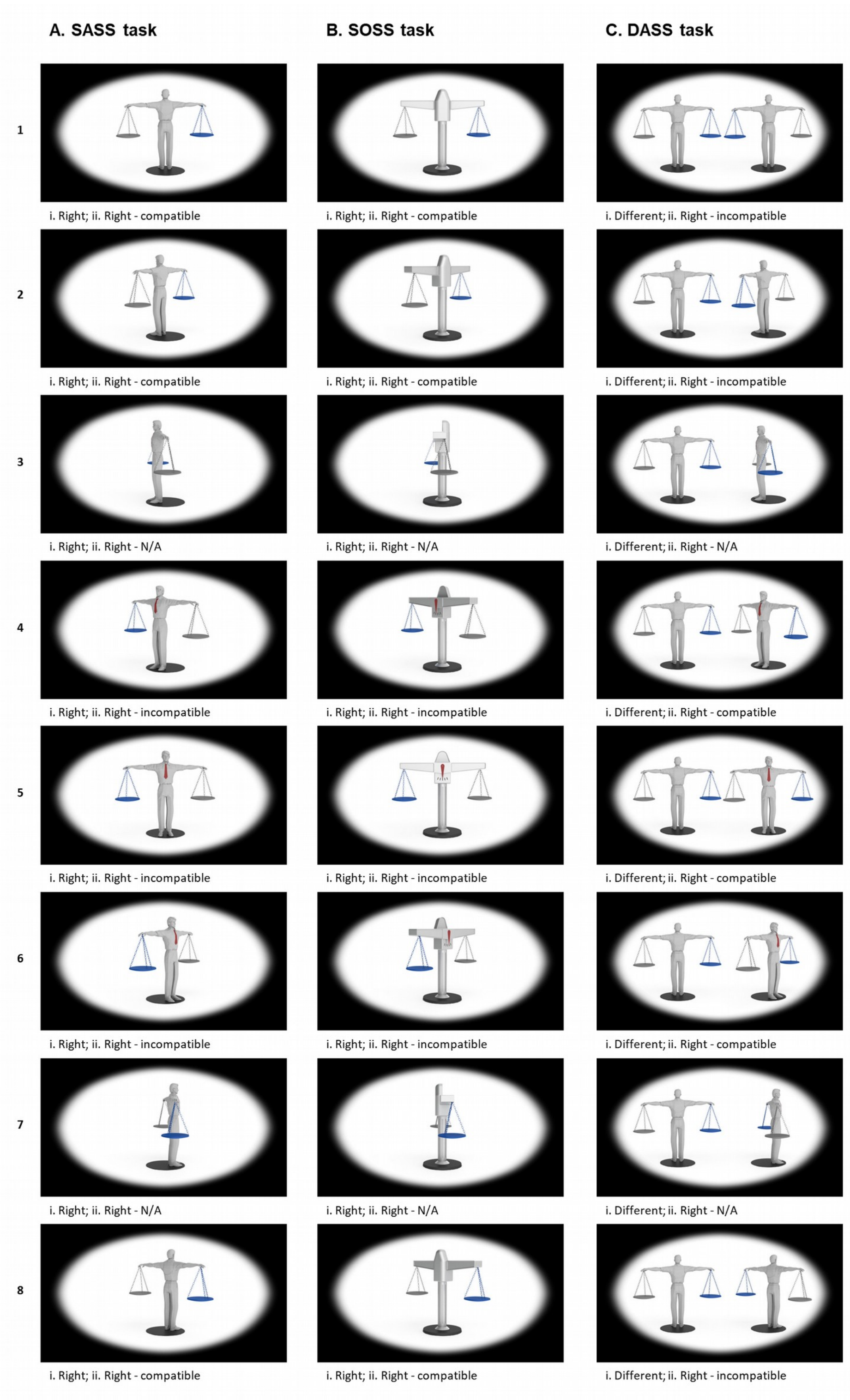
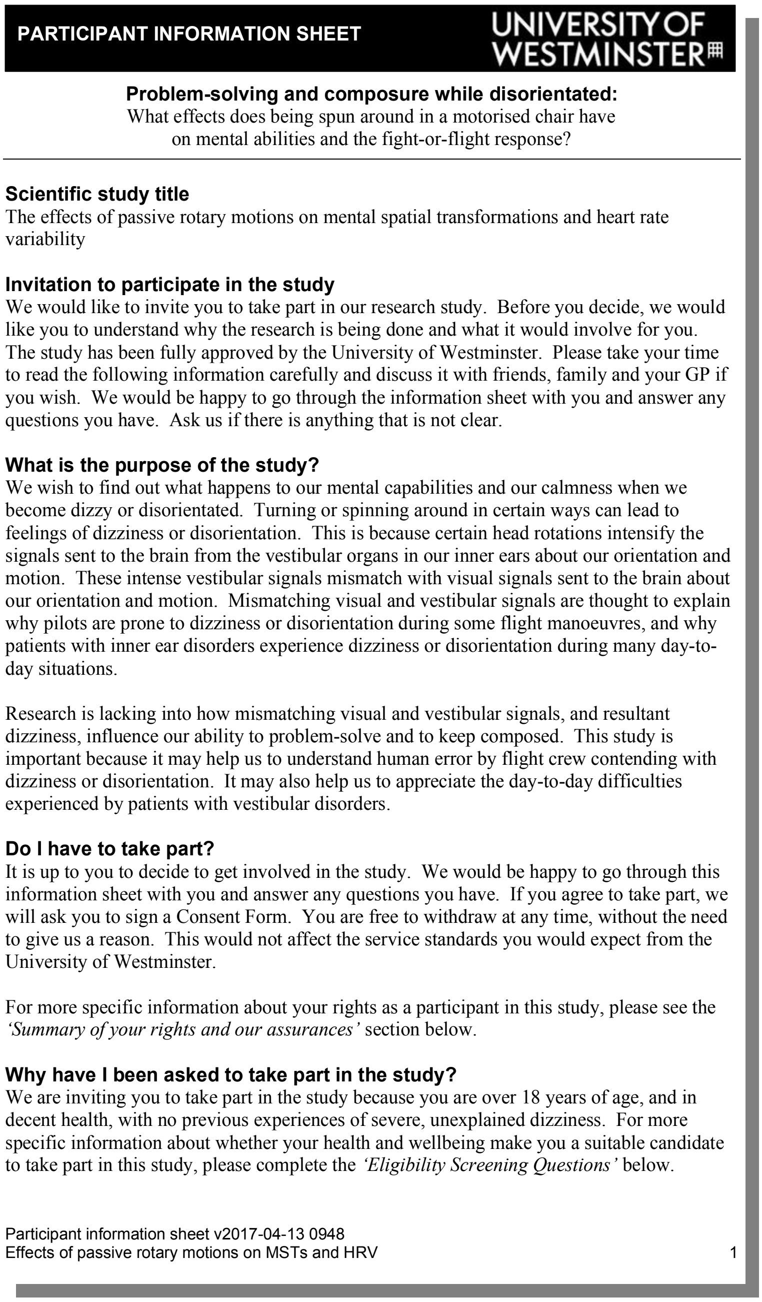


Figure B.1: Sample stimuli presented as part of the Single Avatar Stimulus Set (SASS) task [A1-8], the Single Object Stimulus Set (SOSS) task [B1-8] and the Double Avatar Stimulus Set (DASS) task [C1-8].

In the text boxes below each stimulus: i. Refers to the laterality of the blue pan with respect to the avatar (SASS task) or measuring scale (SOSS task), or to the commonality of the hands in which the two avatars are holding in the blue pan (DASS task), ii. Refers to the laterality of the response required for each stimulus, and the stimulus-response compatibility of the response.

The new mental object rotation (MOR) task was also built in Autocad. In line with the studies of Candidi et al. (2013) and Kaltner et al. (2014), avatars were used as the stimulus material. More specifically, the male figure incorporated in the SASS task was rendered in duplicate. The two avatars were positioned side-by-side. The avatar on the left was orientated so that it was always facing away from the observer, and the blue scale pan was always suspended from its right hand. The avatar on the right was rendered in eight yawing increments from 0º (rear-facing) to 180º (front-facing), through 45, 90 and 135º turns to the right and left, just as the avatar in the SASS task and the measuring scale in the SOSS task had been. The blue scale pan was held either in its left or right hand. More details about how these new stimuli were displayed and implemented as a MOR task are given in the Methods section of Chapter 5 (see section 5.3.2). The task was labelled the ‘Double Avatar Stimulus Set’ (DASS) task, and eight permutations of the two avatars are depicted in Figure B.1 [C].

Appendix C: Participant Information Sheet (Study 4)



PARTICIPANT INFORMATION SHEET UNIVERSITY OF WESTMINSTER

Problem-solving and composure while disorientated:
What effects does being spun around in a motorised chair have
on mental abilities and the fight-or-flight response?

Scientific study title

The effects of passive rotary motions on mental spatial transformations and heart rate variability

Invitation to participate in the study

We would like to invite you to take part in our research study. Before you decide, we would like you to understand why the research is being done and what it would involve for you. The study has been fully approved by the University of Westminster. Please take your time to read the following information carefully and discuss it with friends, family and your GP if you wish. We would be happy to go through the information sheet with you and answer any questions you have. Ask us if there is anything that is not clear.

What is the purpose of the study?

We wish to find out what happens to our mental capabilities and our calmness when we become dizzy or disorientated. Turning or spinning around in certain ways can lead to feelings of dizziness or disorientation. This is because certain head rotations intensify the signals sent to the brain from the vestibular organs in our inner ears about our orientation and motion. These intense vestibular signals mismatch with visual signals sent to the brain about our orientation and motion. Mismatching visual and vestibular signals are thought to explain why pilots are prone to dizziness or disorientation during some flight manoeuvres, and why patients with inner ear disorders experience dizziness or disorientation during many day-to-day situations.

Research is lacking into how mismatching visual and vestibular signals, and resultant dizziness, influence our ability to problem-solve and to keep composed. This study is important because it may help us to understand human error by flight crew contending with dizziness or disorientation. It may also help us to appreciate the day-to-day difficulties experienced by patients with vestibular disorders.

Do I have to take part?

It is up to you to decide to get involved in the study. We would be happy to go through this information sheet with you and answer any questions you have. If you agree to take part, we will ask you to sign a Consent Form. You are free to withdraw at any time, without the need to give us a reason. This would not affect the service standards you would expect from the University of Westminster.

For more specific information about your rights as a participant in this study, please see the *'Summary of your rights and our assurances'* section below.

Why have I been asked to take part in the study?

We are inviting you to take part in the study because you are over 18 years of age, and in decent health, with no previous experiences of severe, unexplained dizziness. For more specific information about whether your health and wellbeing make you a suitable candidate to take part in this study, please complete the *'Eligibility Screening Questions'* below.

By studying 80 people's problem-solving abilities and composure while being spun around, we should gain enough information to identify gaps in the safety and wellbeing of professionals and patients with dizziness or disorientation.

Will I have to prepare anything before taking part?
If you volunteer to take part, the Lead Researcher will offer you a choice of days and times to attend an appointment with him at the University of Westminster. The study appointment will be held in the Health Psychology Laboratory, a quiet and secure room in the main University buildings (see full *'Laboratory Address'* below). Before you attend your appointment, you should:

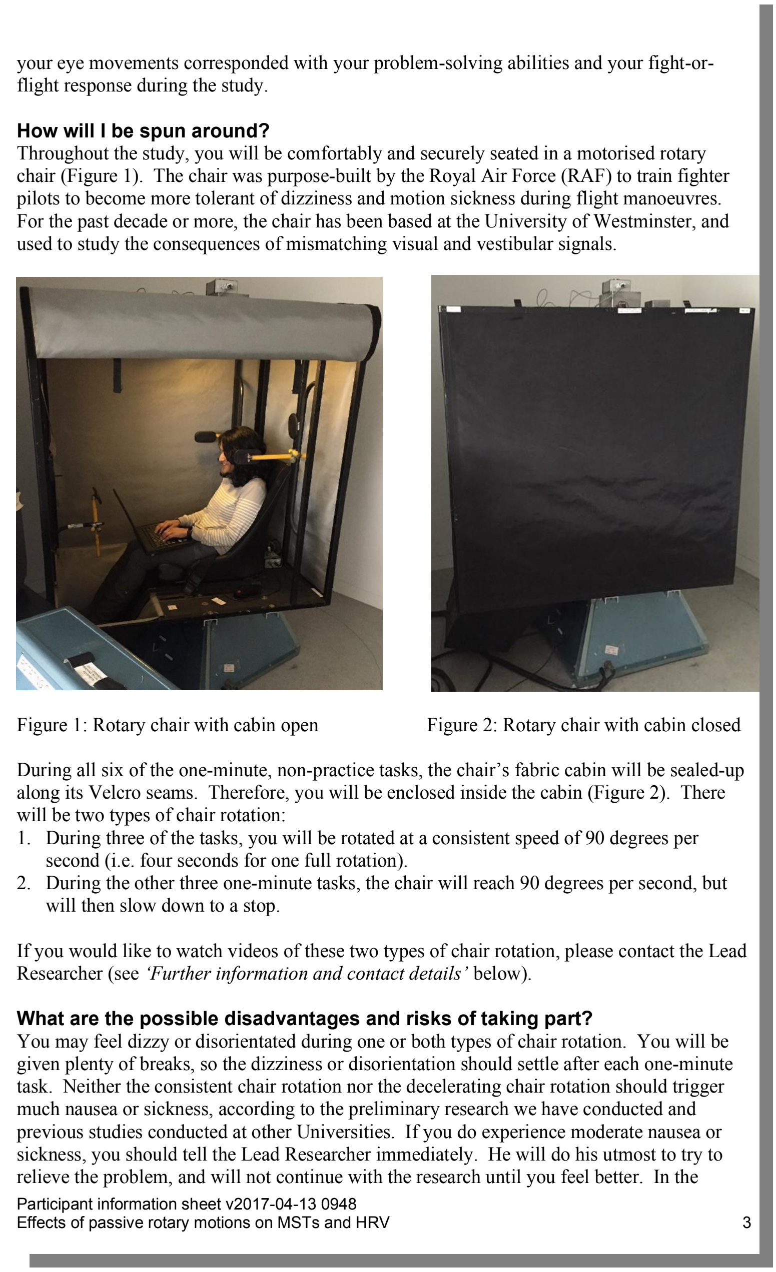
- Complete the Eligibility Screening Questions – see below;
- Avoid consuming any alcoholic substances for 24 hours prior to the appointment;
- Avoid taking any types of medicinal or non-medicinal substances, which specifically affect your ability to drive or operate heavy machinery, for 24 hours prior to the appointment. PLEASE NOTE, do not stop any medications without consulting your GP first;
- Aim to have a good night's sleep just before the appointment;
- Avoid having a heavy meal at least two hours prior to the appointment;
- Notify the Lead Researcher before attending your appointment if you are unwell or recovering from illness or surgery on the day of the appointment.

What will I have to do during the study, and how long will it last?
When you arrive for your study appointment, you will be greeted by the Lead Researcher, who will give you a short presentation on the research to aid your understanding of it. He will double-check you have had no recent or past health problems preventing you from taking part in the study, and ask you to fill-in a consent form. You will then be requested to complete three questionnaires to gauge your tendencies for motion sickness and anxiety, and whether you are left- or right-handed.

You will be shown how to put on a wireless heart rate monitor, which will record your heart rate throughout the study so we can tell how composed you were during it. More specifically, the recordings will tell us how much of a fight-or-flight response your nervous system reacted with during the study. The fight-or-flight response tends to occur to varying extents when we encounter new or surprising situations. You will have the privacy of nearby toilet facilities in which to fit the light-weight monitor around your chest.

You will be seated throughout the remainder of the study, with a laptop computer resting on your lap. You will be given a problem-solving task to do on the laptop, which will involve judging whether certain features of on-screen images are left- or right-sided. The task will only last one minute, but you will be asked to do it twice for practice, then six times in a row for real. During those six times, you will be spun around (see *'How will I be spun around?'* below). In-between each task, you will be asked to rate your motion sickness, anxiety, stability and mental effort. You will also be given a break between each task, which is why the appointment in the Laboratory might last an hour even though you will only be doing the task for eight minutes in total.

We may also record your eye movements while you are doing the task. A small eye tracking device positioned just under the screen of the laptop will enable us to do this. You will not be aware that the device is turned on. It will only capture the movement of your pupils and not your other facial features or expressions. The recordings will allow us to analyse whether



your eye movements corresponded with your problem-solving abilities and your fight-or-flight response during the study.

How will I be spun around?

Throughout the study, you will be comfortably and securely seated in a motorised rotary chair (Figure 1). The chair was purpose-built by the Royal Air Force (RAF) to train fighter pilots to become more tolerant of dizziness and motion sickness during flight manoeuvres. For the past decade or more, the chair has been based at the University of Westminster, and used to study the consequences of mismatching visual and vestibular signals.

Figure 1: Rotary chair with cabin open

Figure 2: Rotary chair with cabin closed

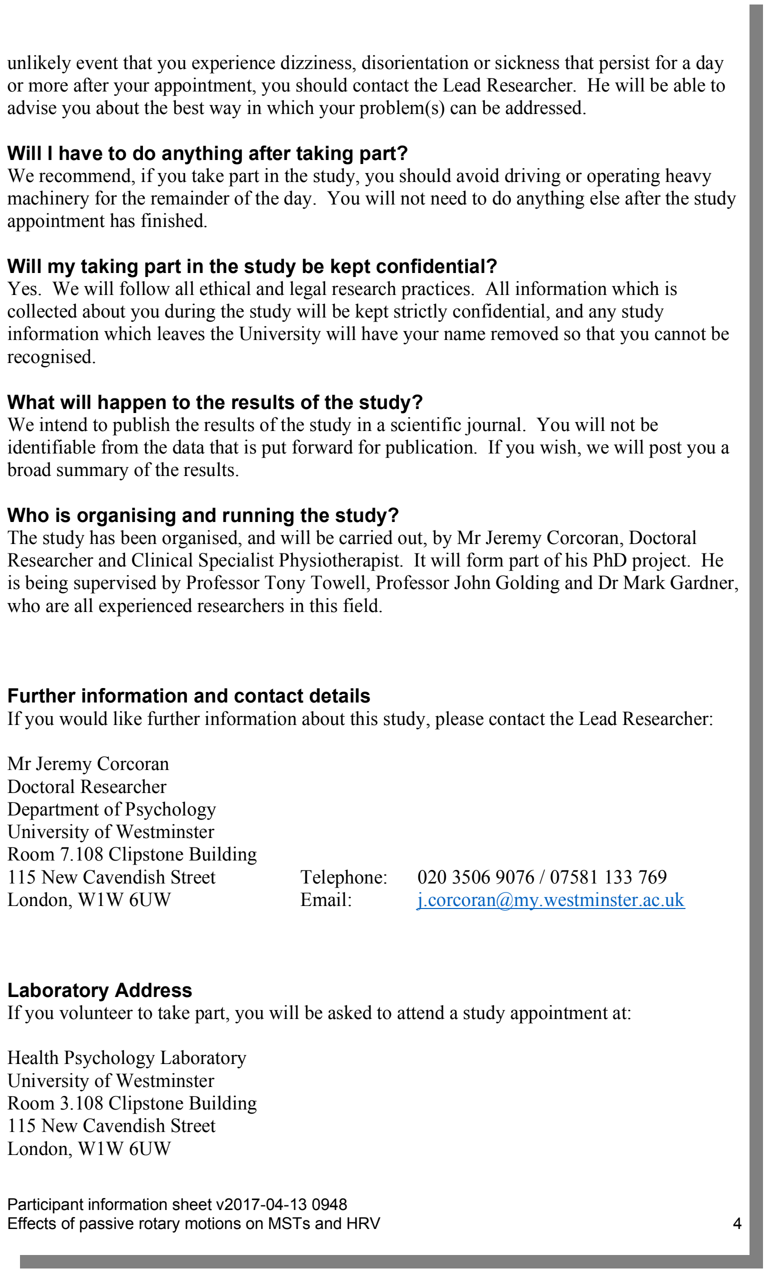
During all six of the one-minute, non-practice tasks, the chair's fabric cabin will be sealed-up along its Velcro seams. Therefore, you will be enclosed inside the cabin (Figure 2). There will be two types of chair rotation:

1. During three of the tasks, you will be rotated at a consistent speed of 90 degrees per second (i.e. four seconds for one full rotation).
2. During the other three one-minute tasks, the chair will reach 90 degrees per second, but will then slow down to a stop.

If you would like to watch videos of these two types of chair rotation, please contact the Lead Researcher (see *'Further information and contact details'* below).

What are the possible disadvantages and risks of taking part?

You may feel dizzy or disorientated during one or both types of chair rotation. You will be given plenty of breaks, so the dizziness or disorientation should settle after each one-minute task. Neither the consistent chair rotation nor the decelerating chair rotation should trigger much nausea or sickness, according to the preliminary research we have conducted and previous studies conducted at other Universities. If you do experience moderate nausea or sickness, you should tell the Lead Researcher immediately. He will do his utmost to try to relieve the problem, and will not continue with the research until you feel better. In the



unlikely event that you experience dizziness, disorientation or sickness that persist for a day or more after your appointment, you should contact the Lead Researcher. He will be able to advise you about the best way in which your problem(s) can be addressed.

Will I have to do anything after taking part?

We recommend, if you take part in the study, you should avoid driving or operating heavy machinery for the remainder of the day. You will not need to do anything else after the study appointment has finished.

Will my taking part in the study be kept confidential?

Yes. We will follow all ethical and legal research practices. All information which is collected about you during the study will be kept strictly confidential, and any study information which leaves the University will have your name removed so that you cannot be recognised.

What will happen to the results of the study?

We intend to publish the results of the study in a scientific journal. You will not be identifiable from the data that is put forward for publication. If you wish, we will post you a broad summary of the results.

Who is organising and running the study?

The study has been organised, and will be carried out, by Mr Jeremy Corcoran, Doctoral Researcher and Clinical Specialist Physiotherapist. It will form part of his PhD project. He is being supervised by Professor Tony Towell, Professor John Golding and Dr Mark Gardner, who are all experienced researchers in this field.

Further information and contact details

If you would like further information about this study, please contact the Lead Researcher:

Mr Jeremy Corcoran
Doctoral Researcher
Department of Psychology
University of Westminster
Room 7.108 Clipstone Building
115 New Cavendish Street
London, W1W 6UW

Telephone: 020 3506 9076 / 07581 133 769
Email: j.corcoran@my.westminster.ac.uk

Laboratory Address

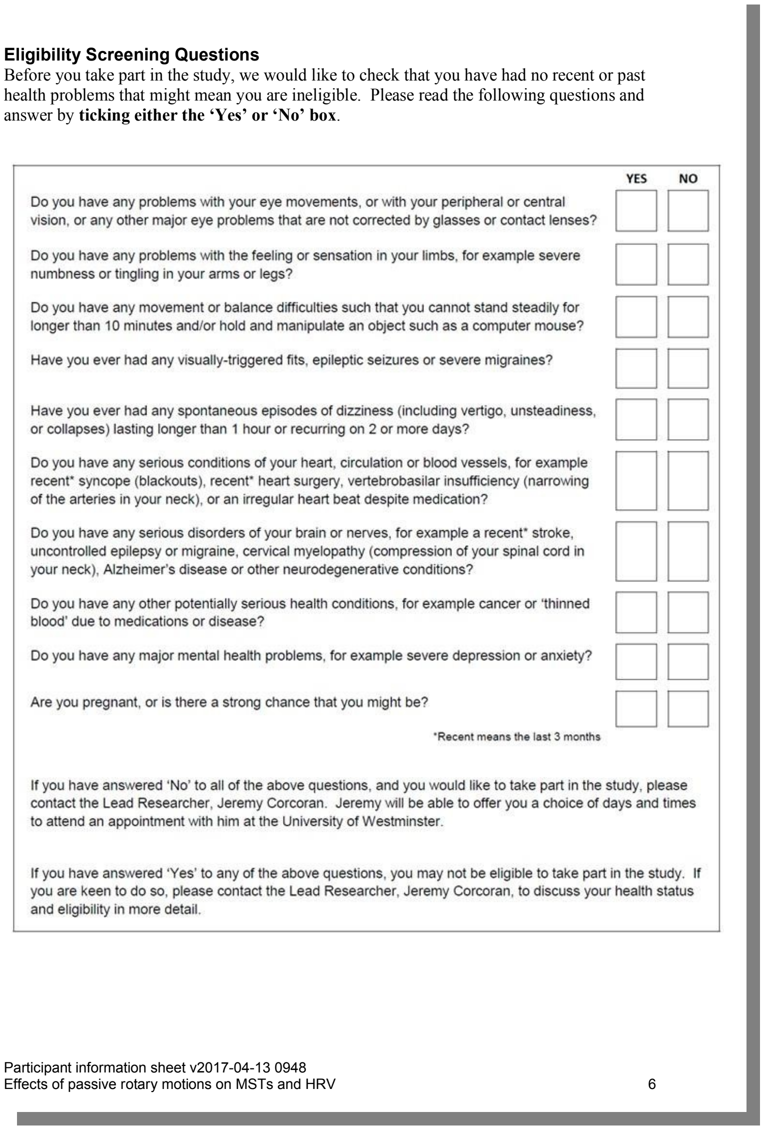
If you volunteer to take part, you will be asked to attend a study appointment at:

Health Psychology Laboratory
University of Westminster
Room 3.108 Clipstone Building
115 New Cavendish Street
London, W1W 6UW

Summary of your rights and our assurances

Please note:

- Your participation in this research is entirely voluntary.
- You have the right to withdraw at any time without giving a reason.
- Withdrawal from the research will not affect any treatment and/or services that you receive at the University of Westminster.
- You have the right to ask for your data to be withdrawn, as long as this is practical, and for personal information to be destroyed.
- You do not have to answer particular questions, either on questionnaires or in interviews, if you do not wish to do so.
- Your responses will be made anonymous, and will be kept confidential.
- No individuals should be identifiable from any collated data, written report, or any publications arising from the research.
- All computer data files will be encrypted and password protected. The researcher will keep files in a secure place and will comply with the requirements of the Data Protection Act.
- All hard copy documents, e.g. consent forms, completed questionnaires, etc. will be kept securely and in a locked cupboard on University premises. Documents may be scanned and stored electronically on the University's secure computer systems.
- If you wish, you can receive information on the results of the research. Please indicate on the consent form if you would like to receive this information.
- If you have a complaint about this study you can contact the project supervisor, Professor Tony Towell, by e-mail (A.Towell@westminster.ac.uk) or by telephone (0207 911 5000 x69019).



Eligibility Screening Questions

Before you take part in the study, we would like to check that you have had no recent or past health problems that might mean you are ineligible. Please read the following questions and answer by **ticking either the 'Yes' or 'No' box**.

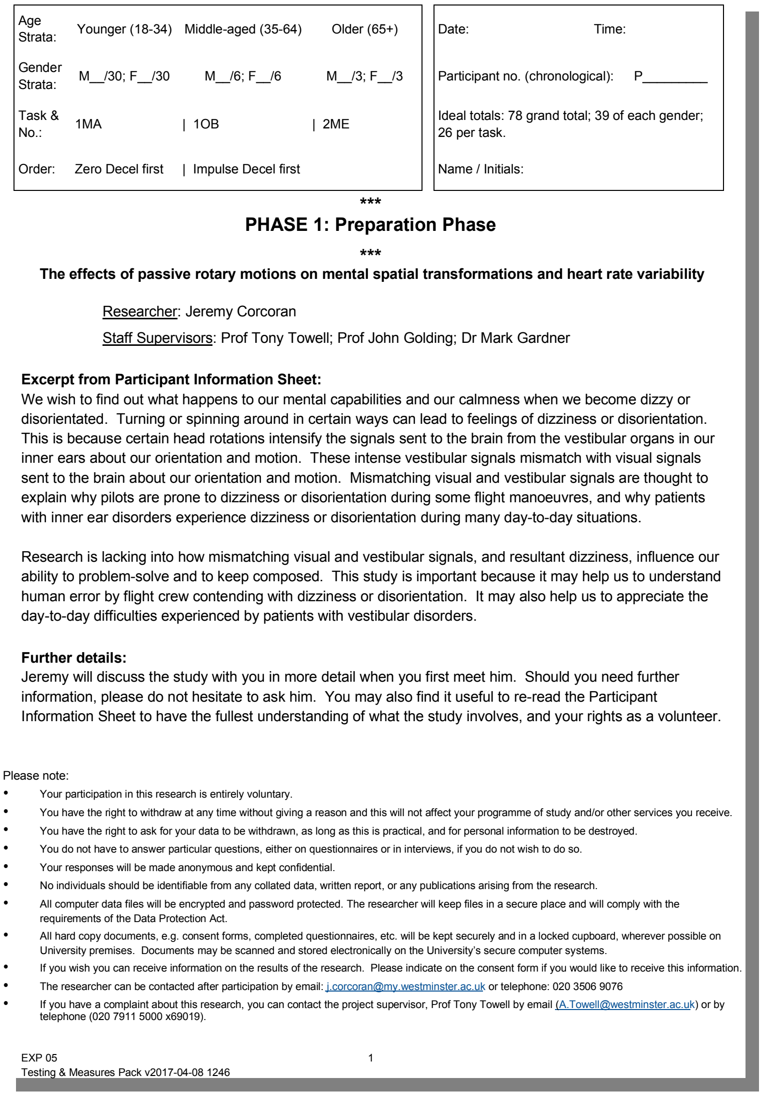
	YES	NO
Do you have any problems with your eye movements, or with your peripheral or central vision, or any other major eye problems that are not corrected by glasses or contact lenses?	☐	☐
Do you have any problems with the feeling or sensation in your limbs, for example severe numbness or tingling in your arms or legs?	☐	☐
Do you have any movement or balance difficulties such that you cannot stand steadily for longer than 10 minutes and/or hold and manipulate an object such as a computer mouse?	☐	☐
Have you ever had any visually-triggered fits, epileptic seizures or severe migraines?	☐	☐
Have you ever had any spontaneous episodes of dizziness (including vertigo, unsteadiness, or collapses) lasting longer than 1 hour or recurring on 2 or more days?	☐	☐
Do you have any serious conditions of your heart, circulation or blood vessels, for example recent* syncope (blackouts), recent* heart surgery, vertebrobasilar insufficiency (narrowing of the arteries in your neck), or an irregular heart beat despite medication?	☐	☐
Do you have any serious disorders of your brain or nerves, for example a recent* stroke, uncontrolled epilepsy or migraine, cervical myelopathy (compression of your spinal cord in your neck), Alzheimer's disease or other neurodegenerative conditions?	☐	☐
Do you have any other potentially serious health conditions, for example cancer or 'thinned blood' due to medications or disease?	☐	☐
Do you have any major mental health problems, for example severe depression or anxiety?	☐	☐
Are you pregnant, or is there a strong chance that you might be?	☐	☐

*Recent means the last 3 months

If you have answered 'No' to all of the above questions, and you would like to take part in the study, please contact the Lead Researcher, Jeremy Corcoran. Jeremy will be able to offer you a choice of days and times to attend an appointment with him at the University of Westminster.

If you have answered 'Yes' to any of the above questions, you may not be eligible to take part in the study. If you are keen to do so, please contact the Lead Researcher, Jeremy Corcoran, to discuss your health status and eligibility in more detail.

Appendix D: Testing and Measures Pack (Study 4)



Age Strata:	Younger (18-34)	Middle-aged (35-64)	Older (65+)
Gender Strata:	M__/30; F__/30	M__/6; F__/6	M__/3; F__/3
Task & No.:	1MA	1OB	2ME
Order:	Zero Decel first	Impulse Decel first	

Date:	Time:
Participant no. (chronological):	P_________
Ideal totals: 78 grand total; 39 of each gender; 26 per task.	
Name / Initials:	

***

PHASE 1: Preparation Phase

***

The effects of passive rotary motions on mental spatial transformations and heart rate variability

Researcher: Jeremy Corcoran

Staff Supervisors: Prof Tony Towell; Prof John Golding; Dr Mark Gardner

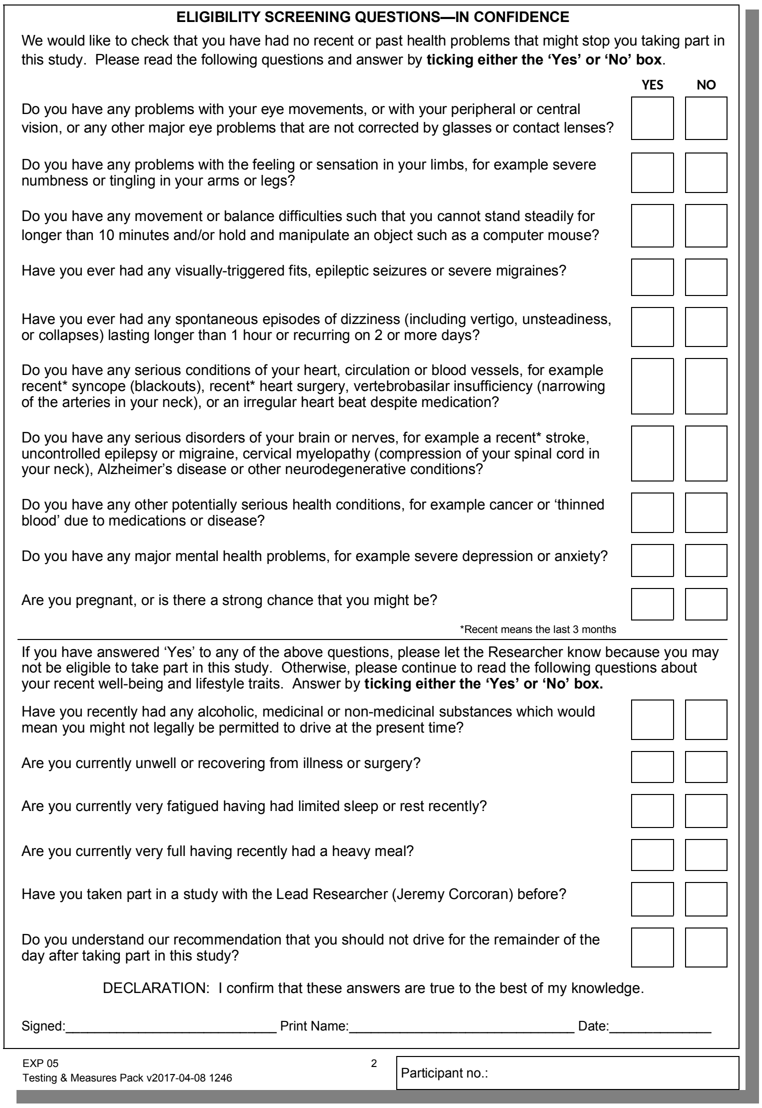
Excerpt from Participant Information Sheet:
We wish to find out what happens to our mental capabilities and our calmness when we become dizzy or disorientated. Turning or spinning around in certain ways can lead to feelings of dizziness or disorientation. This is because certain head rotations intensify the signals sent to the brain from the vestibular organs in our inner ears about our orientation and motion. These intense vestibular signals mismatch with visual signals sent to the brain about our orientation and motion. Mismatching visual and vestibular signals are thought to explain why pilots are prone to dizziness or disorientation during some flight manoeuvres, and why patients with inner ear disorders experience dizziness or disorientation during many day-to-day situations.

Research is lacking into how mismatching visual and vestibular signals, and resultant dizziness, influence our ability to problem-solve and to keep composed. This study is important because it may help us to understand human error by flight crew contending with dizziness or disorientation. It may also help us to appreciate the day-to-day difficulties experienced by patients with vestibular disorders.

Further details:
Jeremy will discuss the study with you in more detail when you first meet him. Should you need further information, please do not hesitate to ask him. You may also find it useful to re-read the Participant Information Sheet to have the fullest understanding of what the study involves, and your rights as a volunteer.

Please note:
- Your participation in this research is entirely voluntary.
- You have the right to withdraw at any time without giving a reason and this will not affect your programme of study and/or other services you receive.
- You have the right to ask for your data to be withdrawn, as long as this is practical, and for personal information to be destroyed.
- You do not have to answer particular questions, either on questionnaires or in interviews, if you do not wish to do so.
- Your responses will be made anonymous and kept confidential.
- No individuals should be identifiable from any collated data, written report, or any publications arising from the research.
- All computer data files will be encrypted and password protected. The researcher will keep files in a secure place and will comply with the requirements of the Data Protection Act.
- All hard copy documents, e.g. consent forms, completed questionnaires, etc. will be kept securely and in a locked cupboard, wherever possible on University premises. Documents may be scanned and stored electronically on the University's secure computer systems.
- If you wish you can receive information on the results of the research. Please indicate on the consent form if you would like to receive this information.
- The researcher can be contacted after participation by email: j.corcoran@my.westminster.ac.uk or telephone: 020 3506 9076
- If you have a complaint about this research, you can contact the project supervisor, Prof Tony Towell by email (A.Towell@westminster.ac.uk) or by telephone (020 7911 5000 x69019).

EXP 05 1
Testing & Measures Pack v2017-04-08 1246



ELIGIBILITY SCREENING QUESTIONS—IN CONFIDENCE

We would like to check that you have had no recent or past health problems that might stop you taking part in this study. Please read the following questions and answer by **ticking either the 'Yes' or 'No' box**.

	YES	NO
Do you have any problems with your eye movements, or with your peripheral or central vision, or any other major eye problems that are not corrected by glasses or contact lenses?	☐	☐
Do you have any problems with the feeling or sensation in your limbs, for example severe numbness or tingling in your arms or legs?	☐	☐
Do you have any movement or balance difficulties such that you cannot stand steadily for longer than 10 minutes and/or hold and manipulate an object such as a computer mouse?	☐	☐
Have you ever had any visually-triggered fits, epileptic seizures or severe migraines?	☐	☐
Have you ever had any spontaneous episodes of dizziness (including vertigo, unsteadiness, or collapses) lasting longer than 1 hour or recurring on 2 or more days?	☐	☐
Do you have any serious conditions of your heart, circulation or blood vessels, for example recent* syncope (blackouts), recent* heart surgery, vertebrobasilar insufficiency (narrowing of the arteries in your neck), or an irregular heart beat despite medication?	☐	☐
Do you have any serious disorders of your brain or nerves, for example a recent* stroke, uncontrolled epilepsy or migraine, cervical myelopathy (compression of your spinal cord in your neck), Alzheimer's disease or other neurodegenerative conditions?	☐	☐
Do you have any other potentially serious health conditions, for example cancer or 'thinned blood' due to medications or disease?	☐	☐
Do you have any major mental health problems, for example severe depression or anxiety?	☐	☐
Are you pregnant, or is there a strong chance that you might be?	☐	☐

*Recent means the last 3 months

If you have answered 'Yes' to any of the above questions, please let the Researcher know because you may not be eligible to take part in this study. Otherwise, please continue to read the following questions about your recent well-being and lifestyle traits. Answer by **ticking either the 'Yes' or 'No' box.**

Have you recently had any alcoholic, medicinal or non-medicinal substances which would mean you might not legally be permitted to drive at the present time?	☐	☐
Are you currently unwell or recovering from illness or surgery?	☐	☐
Are you currently very fatigued having had limited sleep or rest recently?	☐	☐
Are you currently very full having recently had a heavy meal?	☐	☐
Have you taken part in a study with the Lead Researcher (Jeremy Corcoran) before?	☐	☐
Do you understand our recommendation that you should not drive for the remainder of the day after taking part in this study?	☐	☐

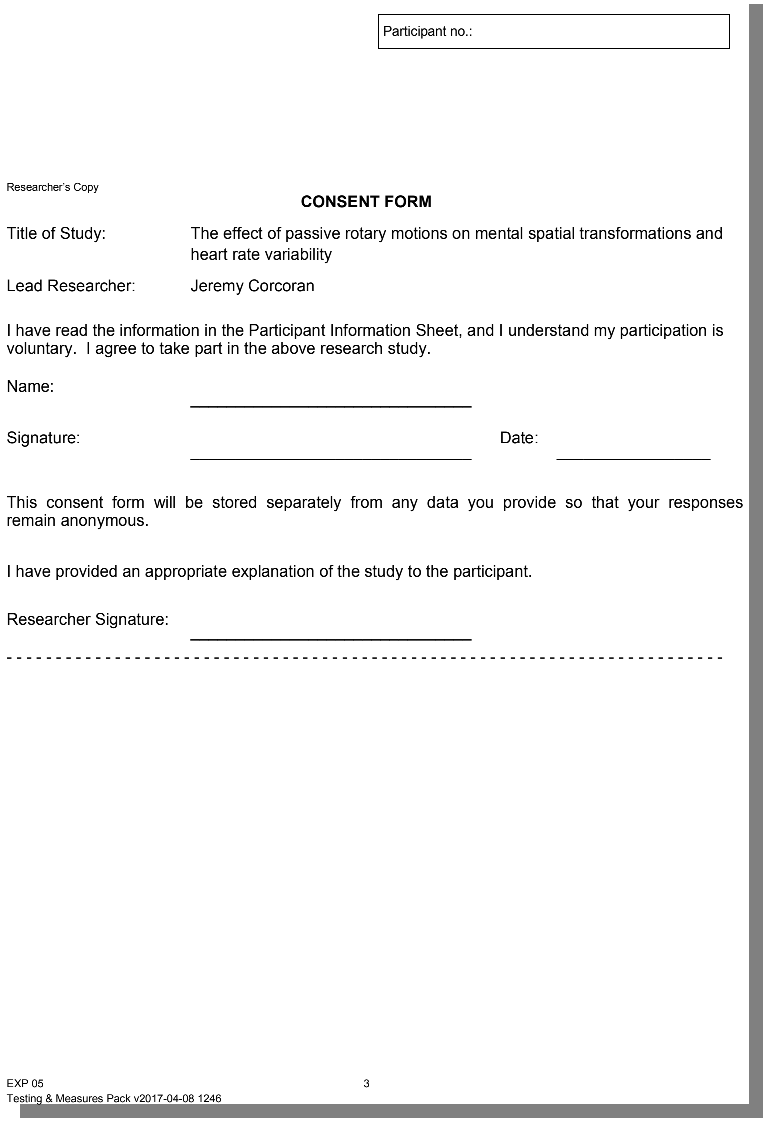
DECLARATION: I confirm that these answers are true to the best of my knowledge.

Signed:___________________________ Print Name:_____________________________ Date:_____________

EXP 05
Testing & Measures Pack v2017-04-08 1246

2

Participant no.:



Participant no.:

Researcher's Copy

CONSENT FORM

Title of Study: The effect of passive rotary motions on mental spatial transformations and heart rate variability

Lead Researcher: Jeremy Corcoran

I have read the information in the Participant Information Sheet, and I understand my participation is voluntary. I agree to take part in the above research study.

Name: ______________________________

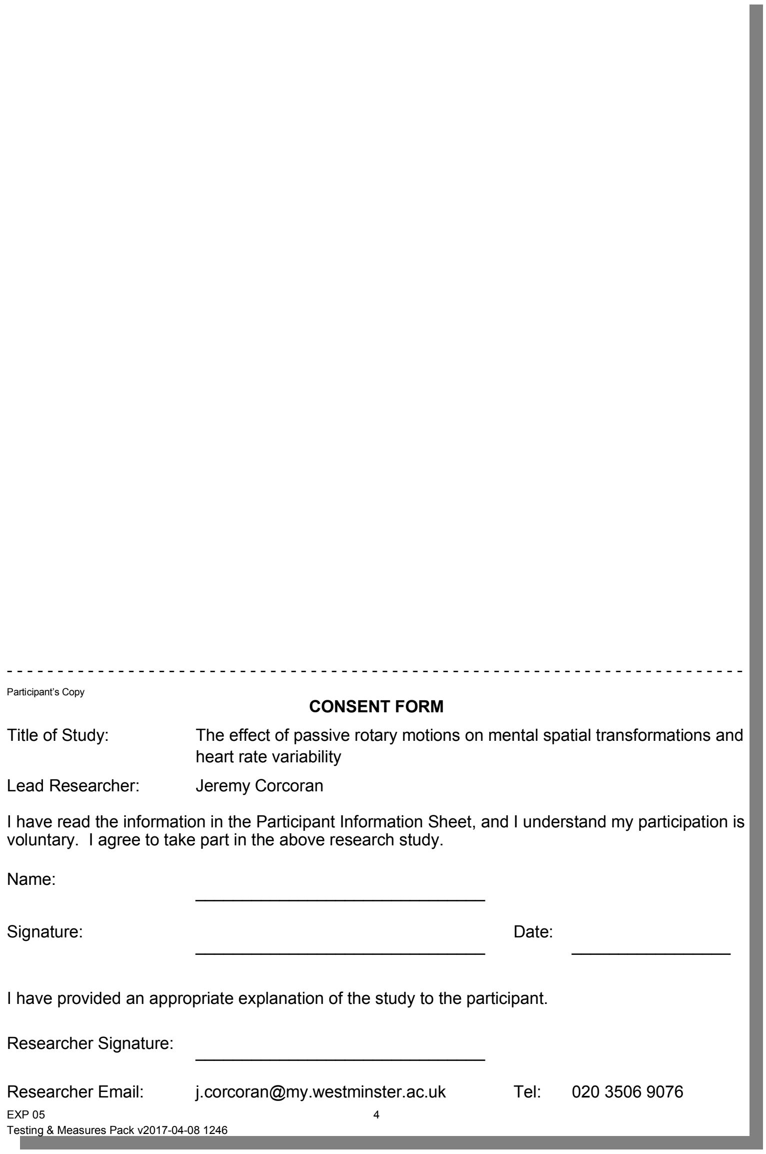
Signature: ______________________________ Date: ________________

This consent form will be stored separately from any data you provide so that your responses remain anonymous.

I have provided an appropriate explanation of the study to the participant.

Researcher Signature: ______________________________

- -



Participant's Copy

CONSENT FORM

Title of Study: The effect of passive rotary motions on mental spatial transformations and heart rate variability

Lead Researcher: Jeremy Corcoran

I have read the information in the Participant Information Sheet, and I understand my participation is voluntary. I agree to take part in the above research study.

Name: ______________________________

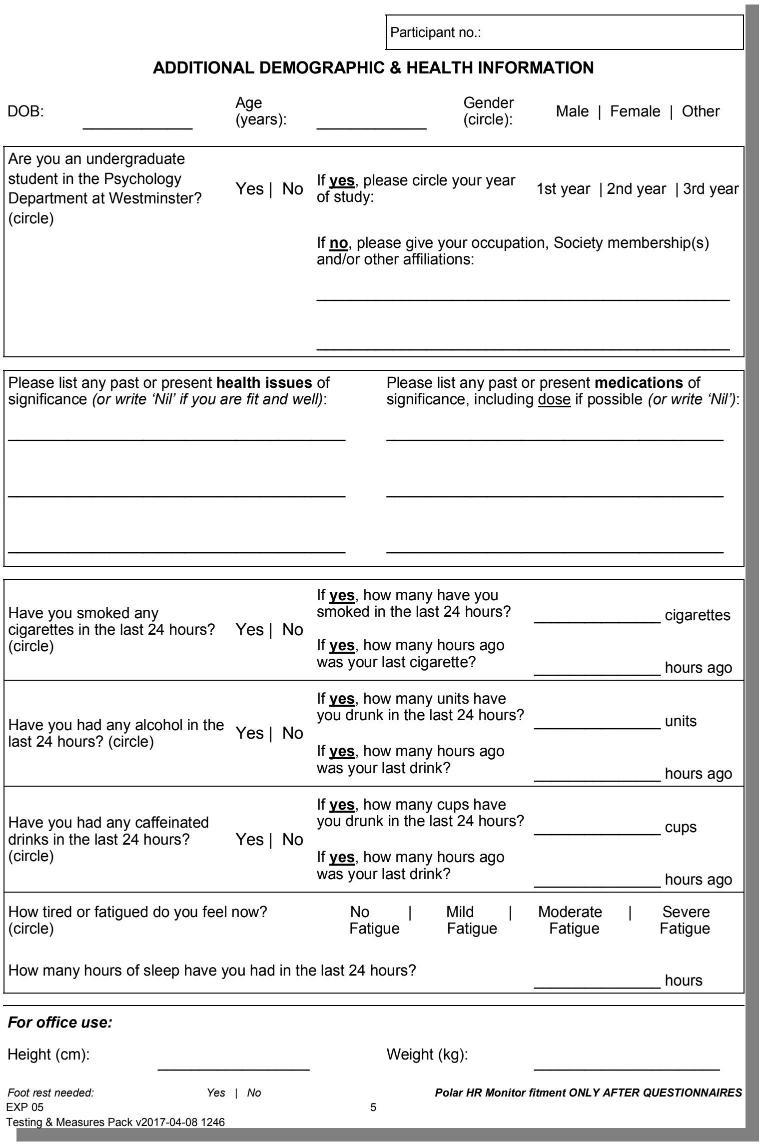
Signature: ______________________________ Date: ________________

I have provided an appropriate explanation of the study to the participant.

Researcher Signature: ______________________________

Researcher Email: j.corcoran@my.westminster.ac.uk Tel: 020 3506 9076

EXP 05 4
Testing & Measures Pack v2017-04-08 1246



Participant no.:

ADDITIONAL DEMOGRAPHIC & HEALTH INFORMATION

DOB: ____________ Age (years): ____________ Gender (circle): Male | Female | Other

Are you an undergraduate student in the Psychology Department at Westminster? (circle)	Yes | No	If **yes**, please circle your year of study:	1st year | 2nd year | 3rd year
		If **no**, please give your occupation, Society membership(s) and/or other affiliations: ______________________________ ______________________________	

Please list any past or present **health issues** of significance *(or write 'Nil' if you are fit and well)*: ______________________________ ______________________________ ______________________________	Please list any past or present **medications** of significance, including dose if possible *(or write 'Nil')*: ______________________________ ______________________________ ______________________________

Have you smoked any cigarettes in the last 24 hours? (circle)	Yes | No	If **yes**, how many have you smoked in the last 24 hours?	____________ cigarettes
		If **yes**, how many hours ago was your last cigarette?	____________ hours ago
Have you had any alcohol in the last 24 hours? (circle)	Yes | No	If **yes**, how many units have you drunk in the last 24 hours?	____________ units
		If **yes**, how many hours ago was your last drink?	____________ hours ago
Have you had any caffeinated drinks in the last 24 hours? (circle)	Yes | No	If **yes**, how many cups have you drunk in the last 24 hours?	____________ cups
		If **yes**, how many hours ago was your last drink?	____________ hours ago

How tired or fatigued do you feel now? (circle) No Fatigue | Mild Fatigue | Moderate Fatigue | Severe Fatigue

How many hours of sleep have you had in the last 24 hours? ____________ hours

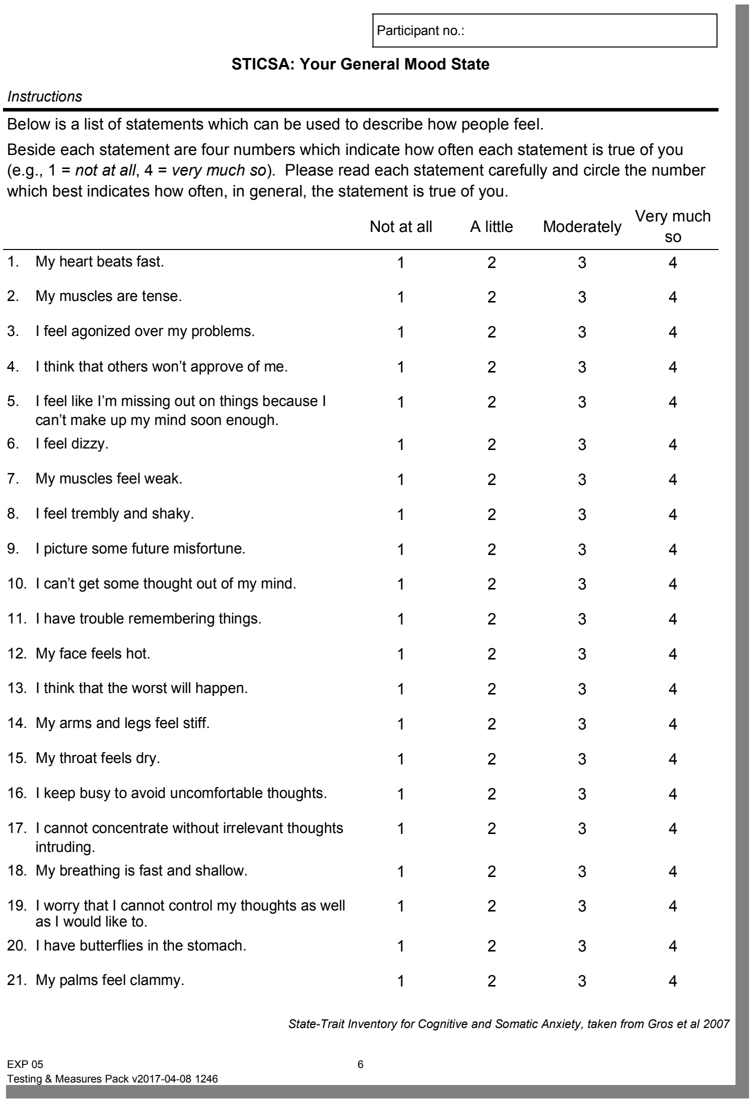
For office use:

Height (cm): ____________ Weight (kg): ____________

Foot rest needed: *Yes | No* ***Polar HR Monitor fitment ONLY AFTER QUESTIONNAIRES***

EXP 05 5

Testing & Measures Pack v2017-04-08 1246



Participant no.:

STICSA: Your General Mood State

Instructions

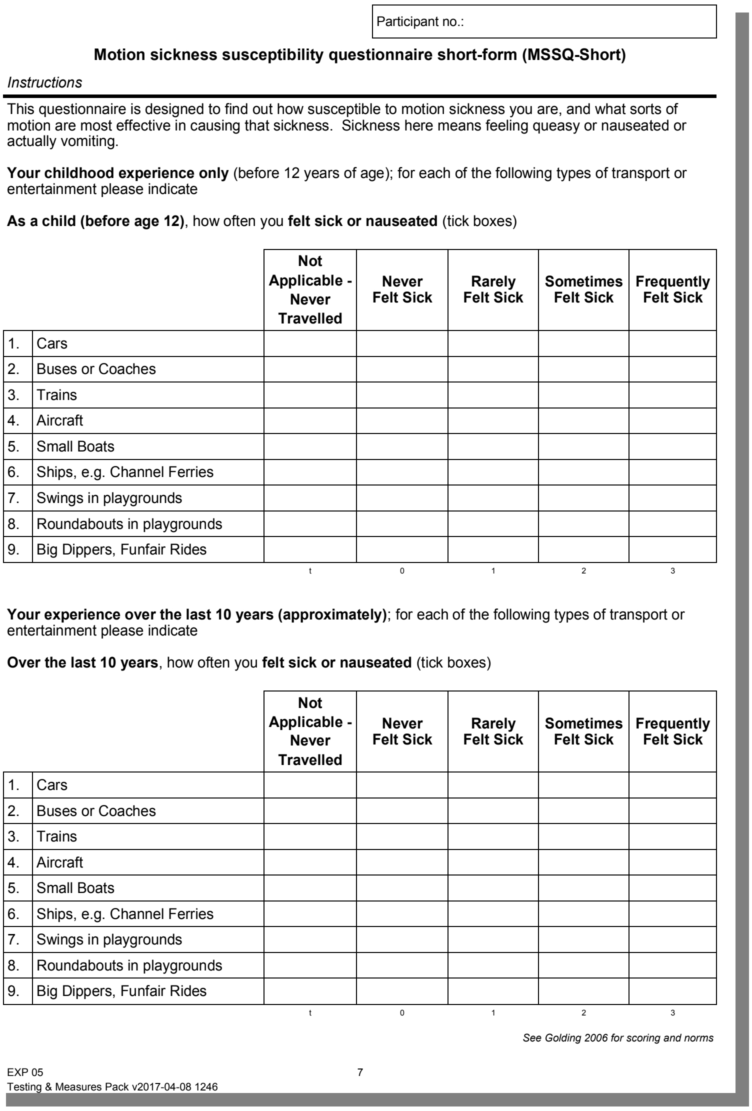
Below is a list of statements which can be used to describe how people feel.

Beside each statement are four numbers which indicate how often each statement is true of you (e.g., 1 = *not at all*, 4 = *very much so*). Please read each statement carefully and circle the number which best indicates how often, in general, the statement is true of you.

	Not at all	A little	Moderately	Very much so
1. My heart beats fast.	1	2	3	4
2. My muscles are tense.	1	2	3	4
3. I feel agonized over my problems.	1	2	3	4
4. I think that others won't approve of me.	1	2	3	4
5. I feel like I'm missing out on things because I can't make up my mind soon enough.	1	2	3	4
6. I feel dizzy.	1	2	3	4
7. My muscles feel weak.	1	2	3	4
8. I feel trembly and shaky.	1	2	3	4
9. I picture some future misfortune.	1	2	3	4
10. I can't get some thought out of my mind.	1	2	3	4
11. I have trouble remembering things.	1	2	3	4
12. My face feels hot.	1	2	3	4
13. I think that the worst will happen.	1	2	3	4
14. My arms and legs feel stiff.	1	2	3	4
15. My throat feels dry.	1	2	3	4
16. I keep busy to avoid uncomfortable thoughts.	1	2	3	4
17. I cannot concentrate without irrelevant thoughts intruding.	1	2	3	4
18. My breathing is fast and shallow.	1	2	3	4
19. I worry that I cannot control my thoughts as well as I would like to.	1	2	3	4
20. I have butterflies in the stomach.	1	2	3	4
21. My palms feel clammy.	1	2	3	4

State-Trait Inventory for Cognitive and Somatic Anxiety, taken from Gros et al 2007

EXP 05 6
Testing & Measures Pack v2017-04-08 1246



Participant no.:

Motion sickness susceptibility questionnaire short-form (MSSQ-Short)

Instructions

This questionnaire is designed to find out how susceptible to motion sickness you are, and what sorts of motion are most effective in causing that sickness. Sickness here means feeling queasy or nauseated or actually vomiting.

Your childhood experience only (before 12 years of age); for each of the following types of transport or entertainment please indicate

As a child (before age 12), how often you **felt sick or nauseated** (tick boxes)

		Not Applicable - Never Travelled	**Never Felt Sick**	**Rarely Felt Sick**	**Sometimes Felt Sick**	**Frequently Felt Sick**
1.	Cars					
2.	Buses or Coaches					
3.	Trains					
4.	Aircraft					
5.	Small Boats					
6.	Ships, e.g. Channel Ferries					
7.	Swings in playgrounds					
8.	Roundabouts in playgrounds					
9.	Big Dippers, Funfair Rides					
		t	0	1	2	3

Your experience over the last 10 years (approximately); for each of the following types of transport or entertainment please indicate

Over the last 10 years, how often you **felt sick or nauseated** (tick boxes)

		Not Applicable - Never Travelled	**Never Felt Sick**	**Rarely Felt Sick**	**Sometimes Felt Sick**	**Frequently Felt Sick**
1.	Cars					
2.	Buses or Coaches					
3.	Trains					
4.	Aircraft					
5.	Small Boats					
6.	Ships, e.g. Channel Ferries					
7.	Swings in playgrounds					
8.	Roundabouts in playgrounds					
9.	Big Dippers, Funfair Rides					
		t	0	1	2	3

See Golding 2006 for scoring and norms

EXP 05 7
Testing & Measures Pack v2017-04-08 1246

Participant no.:

Hand preference questionnaire

Instructions

Please indicate your preferences in the use of hands in the following activities by *putting a tick (√) in the appropriate column*.

Some of the activities require both hands. In these cases the part of the task, or object, for which hand preference is wanted is indicated in brackets.

Please try to answer all the questions, and only leave a blank if you have no experience at all of the object or task.

		Strongly left-handed (-2)	Left-handed (-1)	Indifferent (0)	Right-handed (1)	Strongly right-handed (2)
1.	Throwing					
2.	Scissors					
3.	Comb					
4.	Toothbrush					
5.	Knife (without fork)					
6.	Spoon					
7.	Hammer					
8.	Screwdriver					
9.	Striking match (match)					
10.	Threading needle (needle or thread according to which is moved)					

(Instruction on HR monitor fitment)

For office use:

Adapted Edinburgh Handedness Questionnaire, taken from Salmaso & Longoni 1985
Instructions adapted from Oldfield 1971

(see Hand preference questionnaire laterality quotient calc v2017-03-15 1646; W:\FOLDERS & DOCS\Study - PhD U of W\EXP 05 Experiment Set-up)

Laterality quotient = $(\Sigma / \Sigma(\sqrt{(n_i^2)}))*100$ = (+/-) ___________ If **+**, rotate participant to **RIGHT**

If **-**, rotate participant to **LEFT**

Rotate in **OPPOSITE** for practice trial block; based on the predominant stimulation of the ipsilateral cortex (de Waele et al 2001) combined with the fact that the predominant vestibular cortex is in the non-dominant hemisphere (Dieterich et al 2003).

Participant no.:

***

PHASE 2: Cognitive Task Practice Phase

***

Part 1: Practising the allotted task with cabin **OPEN** and chair **STATIONARY**

Part 2: Practising the allotted task with cabin **CLOSED** and chair **ROTATING (30°/s; opposite dir.)**

For office use:

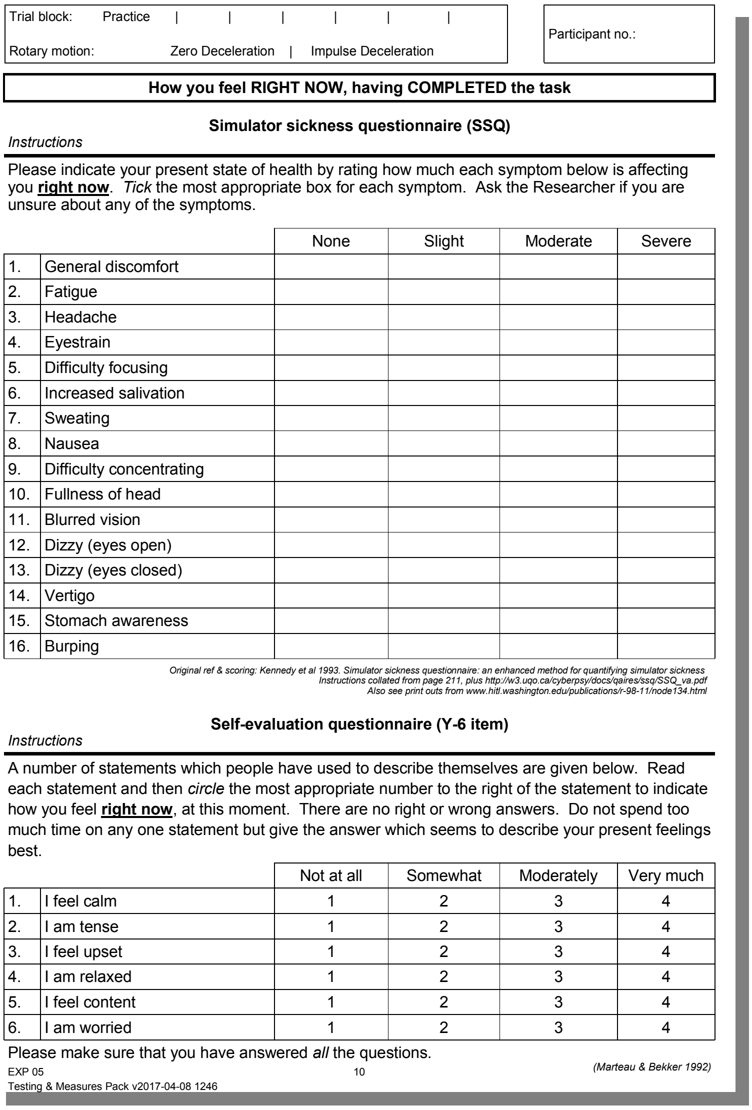
<u>Checks:</u>

- Familiarity with nausea scale ☐
- FaceTime feed ☐
- HR signal ☐
- Dizziness with head motion (Coriolis) ☐
- Emphasis on accuracy ☐
- Speed of task ramping up this time and next (5 seconds available during initial practice; 3 seconds to make a response during this next practice; 2 seconds [2.1 sec] to make a response during experimental trials. Also the cross and feedback will quicken, so there will be less time between stimuli) ☐
- Stop watch at the ready to standardise pauses of 30 seconds after reaching speed (before each trial block starts), and of 90 seconds after trial blocks finish (before administering questionnaires). ☐

(Timing for delivery of impulse will be based on LabChart feed.)

START 2ND PRACTICE

- Impulse stimulus after practice trial block ☐



Trial block: Practice | | | | | |

Rotary motion: Zero Deceleration | Impulse Deceleration

Participant no.:

How you feel RIGHT NOW, having COMPLETED the task

Simulator sickness questionnaire (SSQ)

Instructions

Please indicate your present state of health by rating how much each symptom below is affecting you **right now**. *Tick* the most appropriate box for each symptom. Ask the Researcher if you are unsure about any of the symptoms.

		None	Slight	Moderate	Severe
1.	General discomfort				
2.	Fatigue				
3.	Headache				
4.	Eyestrain				
5.	Difficulty focusing				
6.	Increased salivation				
7.	Sweating				
8.	Nausea				
9.	Difficulty concentrating				
10.	Fullness of head				
11.	Blurred vision				
12.	Dizzy (eyes open)				
13.	Dizzy (eyes closed)				
14.	Vertigo				
15.	Stomach awareness				
16.	Burping				

Original ref & scoring: Kennedy et al 1993. Simulator sickness questionnaire: an enhanced method for quantifying simulator sickness
Instructions collated from page 211, plus http://w3.uqo.ca/cyberpsy/docs/qaires/ssq/SSQ_va.pdf
Also see print outs from www.hitl.washington.edu/publications/r-98-11/node134.html

Self-evaluation questionnaire (Y-6 item)

Instructions

A number of statements which people have used to describe themselves are given below. Read each statement and then *circle* the most appropriate number to the right of the statement to indicate how you feel **right now**, at this moment. There are no right or wrong answers. Do not spend too much time on any one statement but give the answer which seems to describe your present feelings best.

		Not at all	Somewhat	Moderately	Very much
1.	I feel calm	1	2	3	4
2.	I am tense	1	2	3	4
3.	I feel upset	1	2	3	4
4.	I am relaxed	1	2	3	4
5.	I feel content	1	2	3	4
6.	I am worried	1	2	3	4

Please make sure that you have answered *all* the questions.

(Marteau & Bekker 1992)

EXP 05 10
Testing & Measures Pack v2017-04-08 1246

Trial block: Practice | | | | | |

Rotary motion: Zero Deceleration | Impulse Deceleration

Participant no.:

How you felt MOMENTS AGO, while you were COMPLETING the task

Rating scale for mental effort

Instructions

Please rate how much ***mental effort*** you exerted while performing the left-right judgement task **<u>during</u>** this latest practice trial **(tick one box)**:

Mentally At Rest	Minimal Mental Effort	Moderate Mental Effort	Maximal Mental Effort
☐	☐	☐	☐

To be the baseline marker for all subsequent ratings (as per Gardner et al 2016)

Perception of balance

Instructions

Please think back to when you were performing the task inside the enclosed cabin of the rotary chair. Now read each statement below and *circle* the most appropriate number to the right of the statement to indicate how you felt about your balance while you were **<u>completing the task</u>** in the chair. Once again, there are no right or wrong answers.

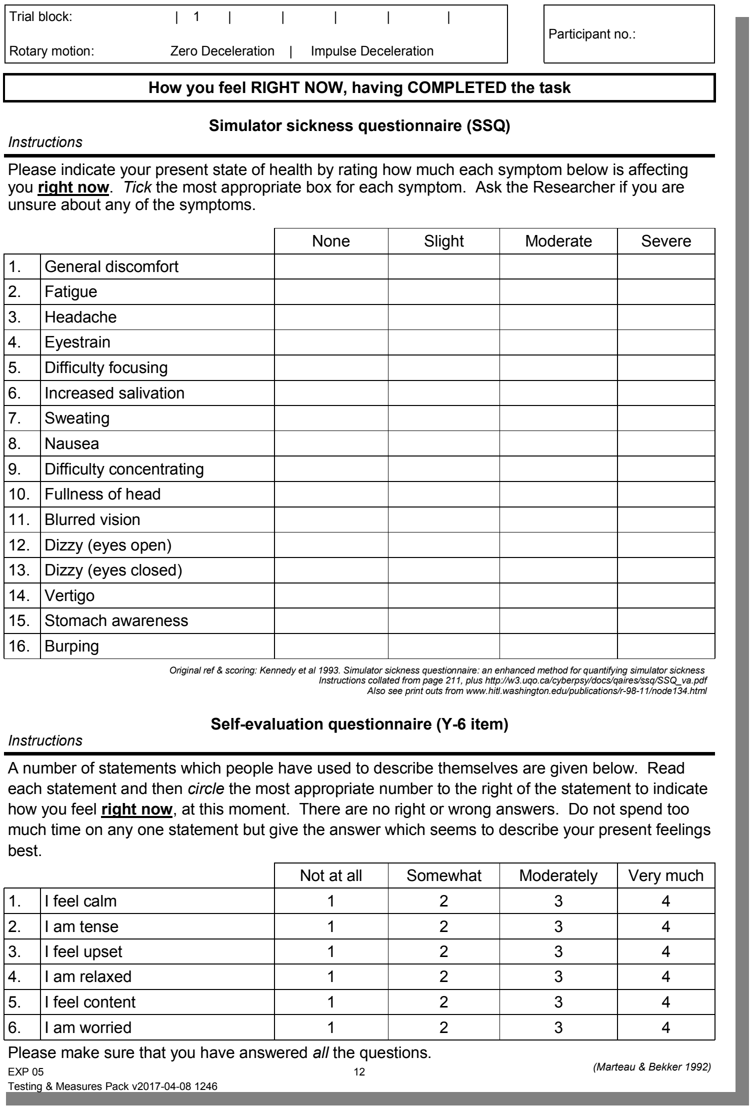
		Not at all	Somewhat	Moderately	Very much
1.	I felt balanced in the chair and could concentrate because of it	1	2	3	4
2.	I was unstable in the chair and was distracted because of it	1	2	3	4

Custom questionnaire

***

PHASE 3: Experimentation Phase

***



Trial block:	| 1 | | | | |	Participant no.:
Rotary motion:	Zero Deceleration | Impulse Deceleration	

How you feel RIGHT NOW, having COMPLETED the task

Simulator sickness questionnaire (SSQ)

Instructions

Please indicate your present state of health by rating how much each symptom below is affecting you **right now**. *Tick* the most appropriate box for each symptom. Ask the Researcher if you are unsure about any of the symptoms.

		None	Slight	Moderate	Severe
1.	General discomfort				
2.	Fatigue				
3.	Headache				
4.	Eyestrain				
5.	Difficulty focusing				
6.	Increased salivation				
7.	Sweating				
8.	Nausea				
9.	Difficulty concentrating				
10.	Fullness of head				
11.	Blurred vision				
12.	Dizzy (eyes open)				
13.	Dizzy (eyes closed)				
14.	Vertigo				
15.	Stomach awareness				
16.	Burping				

Original ref & scoring: Kennedy et al 1993. Simulator sickness questionnaire: an enhanced method for quantifying simulator sickness
Instructions collated from page 211, plus http://w3.uqo.ca/cyberpsy/docs/qaires/ssq/SSQ_va.pdf
Also see print outs from www.hitl.washington.edu/publications/r-98-11/node134.html

Self-evaluation questionnaire (Y-6 item)

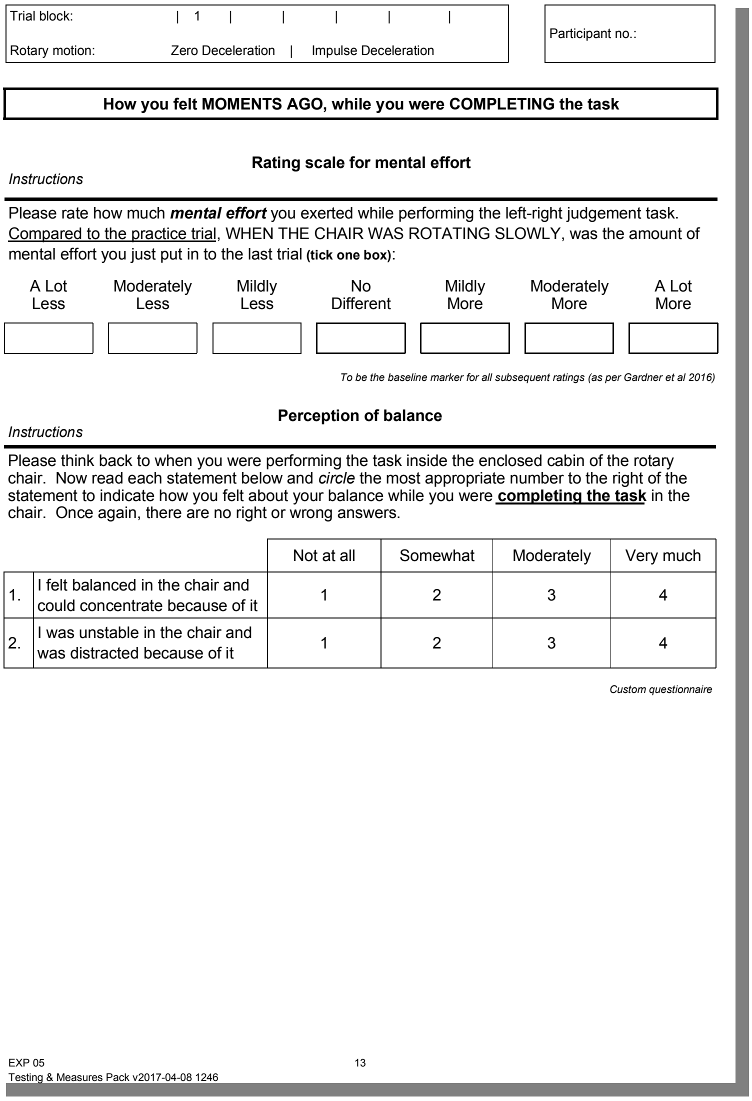
Instructions

A number of statements which people have used to describe themselves are given below. Read each statement and then *circle* the most appropriate number to the right of the statement to indicate how you feel **right now**, at this moment. There are no right or wrong answers. Do not spend too much time on any one statement but give the answer which seems to describe your present feelings best.

		Not at all	Somewhat	Moderately	Very much
1.	I feel calm	1	2	3	4
2.	I am tense	1	2	3	4
3.	I feel upset	1	2	3	4
4.	I am relaxed	1	2	3	4
5.	I feel content	1	2	3	4
6.	I am worried	1	2	3	4

Please make sure that you have answered *all* the questions.

(Marteau & Bekker 1992)



Trial block: | 1 | | | | |

Rotary motion: Zero Deceleration | Impulse Deceleration

Participant no.:

How you felt MOMENTS AGO, while you were COMPLETING the task

Rating scale for mental effort

Instructions

Please rate how much ***mental effort*** you exerted while performing the left-right judgement task. Compared to the practice trial, WHEN THE CHAIR WAS ROTATING SLOWLY, was the amount of mental effort you just put in to the last trial **(tick one box)**:

A Lot Less	Moderately Less	Mildly Less	No Different	Mildly More	Moderately More	A Lot More
☐	☐	☐	☐	☐	☐	☐

To be the baseline marker for all subsequent ratings (as per Gardner et al 2016)

Perception of balance

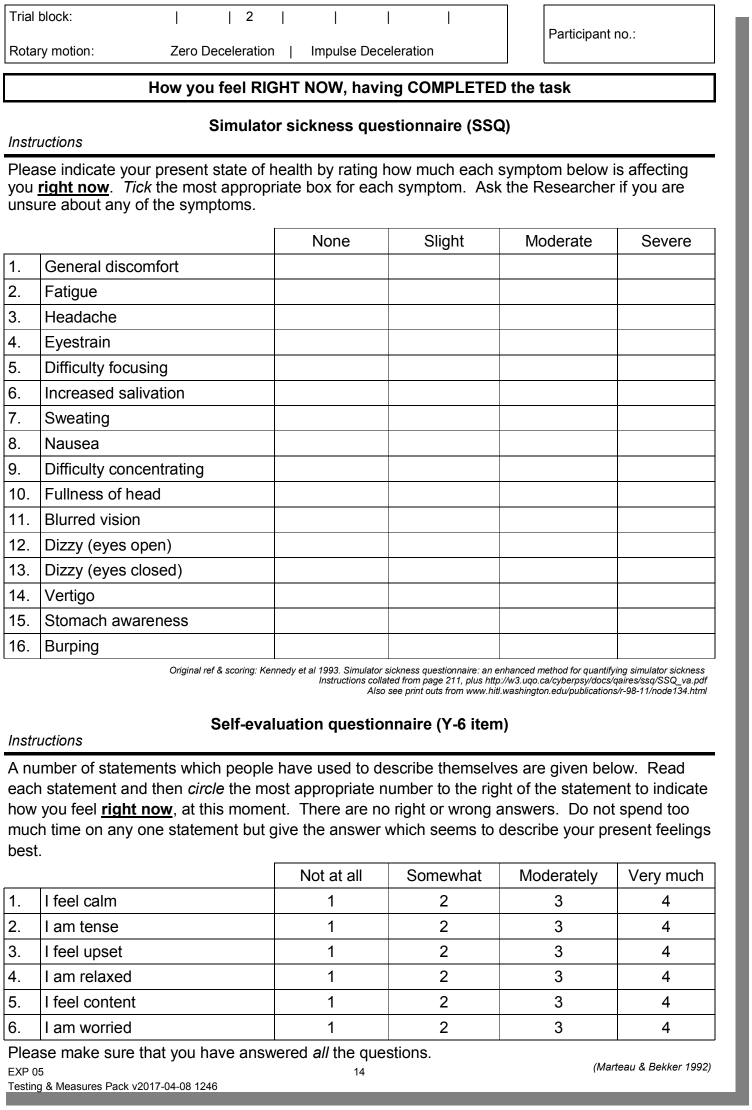
Instructions

Please think back to when you were performing the task inside the enclosed cabin of the rotary chair. Now read each statement below and *circle* the most appropriate number to the right of the statement to indicate how you felt about your balance while you were **completing the task** in the chair. Once again, there are no right or wrong answers.

		Not at all	Somewhat	Moderately	Very much
1.	I felt balanced in the chair and could concentrate because of it	1	2	3	4
2.	I was unstable in the chair and was distracted because of it	1	2	3	4

Custom questionnaire

EXP 05 13
Testing & Measures Pack v2017-04-08 1246



Trial block: | | 2 | | | |

Rotary motion: Zero Deceleration | Impulse Deceleration

Participant no.:

How you feel RIGHT NOW, having COMPLETED the task

Simulator sickness questionnaire (SSQ)

Instructions

Please indicate your present state of health by rating how much each symptom below is affecting you **right now**. *Tick* the most appropriate box for each symptom. Ask the Researcher if you are unsure about any of the symptoms.

		None	Slight	Moderate	Severe
1.	General discomfort				
2.	Fatigue				
3.	Headache				
4.	Eyestrain				
5.	Difficulty focusing				
6.	Increased salivation				
7.	Sweating				
8.	Nausea				
9.	Difficulty concentrating				
10.	Fullness of head				
11.	Blurred vision				
12.	Dizzy (eyes open)				
13.	Dizzy (eyes closed)				
14.	Vertigo				
15.	Stomach awareness				
16.	Burping				

Original ref & scoring: Kennedy et al 1993. Simulator sickness questionnaire: an enhanced method for quantifying simulator sickness
Instructions collated from page 211, plus http://w3.uqo.ca/cyberpsy/docs/qaires/ssq/SSQ_va.pdf
Also see print outs from www.hitl.washington.edu/publications/r-98-11/node134.html

Self-evaluation questionnaire (Y-6 item)

Instructions

A number of statements which people have used to describe themselves are given below. Read each statement and then *circle* the most appropriate number to the right of the statement to indicate how you feel **right now**, at this moment. There are no right or wrong answers. Do not spend too much time on any one statement but give the answer which seems to describe your present feelings best.

		Not at all	Somewhat	Moderately	Very much
1.	I feel calm	1	2	3	4
2.	I am tense	1	2	3	4
3.	I feel upset	1	2	3	4
4.	I am relaxed	1	2	3	4
5.	I feel content	1	2	3	4
6.	I am worried	1	2	3	4

Please make sure that you have answered *all* the questions.

(Marteau & Bekker 1992)

EXP 05 14
Testing & Measures Pack v2017-04-08 1246

Trial block:	| | 2 | | | |	Participant no.:
Rotary motion:	Zero Deceleration | Impulse Deceleration	

How you felt MOMENTS AGO, while you were COMPLETING the task

Rating scale for mental effort

Instructions

Please rate how much ***mental effort*** you exerted while performing the left-right judgement task. Compared to the practice trial, WHEN THE CHAIR WAS ROTATING SLOWLY, was the amount of mental effort you just put in to the last trial **(tick one box)**:

A Lot Less	Moderately Less	Mildly Less	No Different	Mildly More	Moderately More	A Lot More
☐	☐	☐	☐	☐	☐	☐

To be the baseline marker for all subsequent ratings (as per Gardner et al 2016)

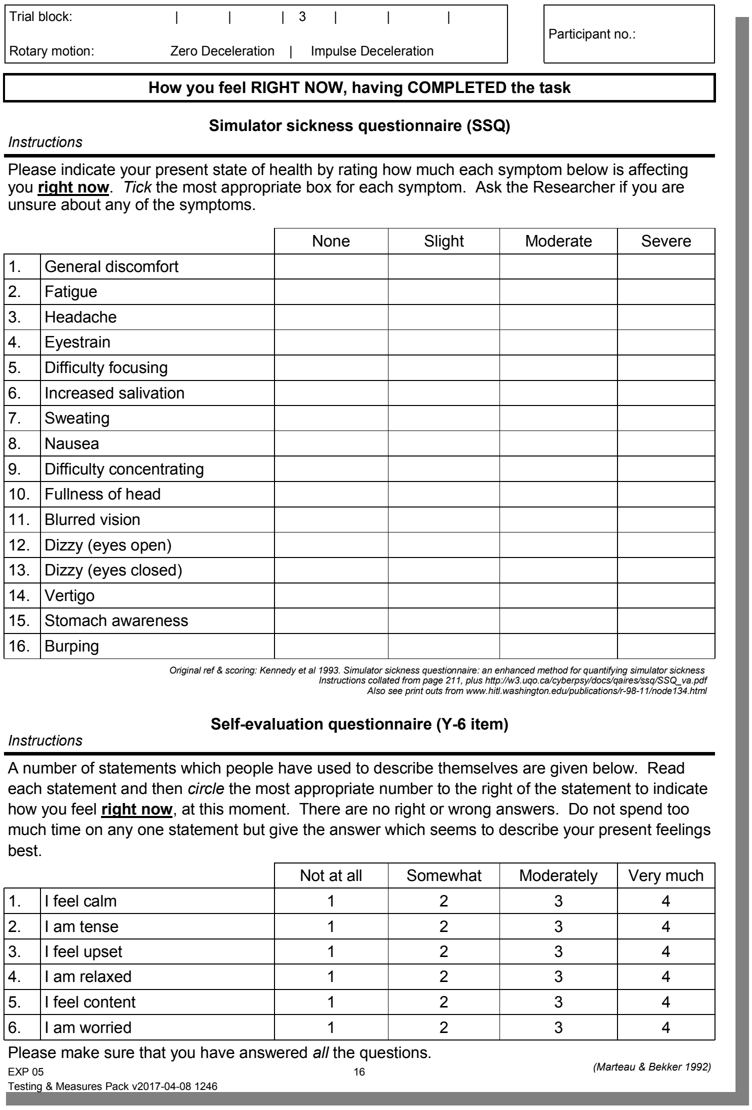
Perception of balance

Instructions

Please think back to when you were performing the task inside the enclosed cabin of the rotary chair. Now read each statement below and *circle* the most appropriate number to the right of the statement to indicate how you felt about your balance while you were **completing the task** in the chair. Once again, there are no right or wrong answers.

		Not at all	Somewhat	Moderately	Very much
1.	I felt balanced in the chair and could concentrate because of it	1	2	3	4
2.	I was unstable in the chair and was distracted because of it	1	2	3	4

Custom questionnaire



Trial block: | | | 3 | | |

Rotary motion: Zero Deceleration | Impulse Deceleration

Participant no.:

How you feel RIGHT NOW, having COMPLETED the task

Simulator sickness questionnaire (SSQ)

Instructions

Please indicate your present state of health by rating how much each symptom below is affecting you **right now**. *Tick* the most appropriate box for each symptom. Ask the Researcher if you are unsure about any of the symptoms.

		None	Slight	Moderate	Severe
1.	General discomfort				
2.	Fatigue				
3.	Headache				
4.	Eyestrain				
5.	Difficulty focusing				
6.	Increased salivation				
7.	Sweating				
8.	Nausea				
9.	Difficulty concentrating				
10.	Fullness of head				
11.	Blurred vision				
12.	Dizzy (eyes open)				
13.	Dizzy (eyes closed)				
14.	Vertigo				
15.	Stomach awareness				
16.	Burping				

Original ref & scoring: Kennedy et al 1993. Simulator sickness questionnaire: an enhanced method for quantifying simulator sickness
Instructions collated from page 211, plus http://w3.uqo.ca/cyberpsy/docs/qaires/ssq/SSQ_va.pdf
Also see print outs from www.hitl.washington.edu/publications/r-98-11/node134.html

Self-evaluation questionnaire (Y-6 item)

Instructions

A number of statements which people have used to describe themselves are given below. Read each statement and then *circle* the most appropriate number to the right of the statement to indicate how you feel **right now**, at this moment. There are no right or wrong answers. Do not spend too much time on any one statement but give the answer which seems to describe your present feelings best.

		Not at all	Somewhat	Moderately	Very much
1.	I feel calm	1	2	3	4
2.	I am tense	1	2	3	4
3.	I feel upset	1	2	3	4
4.	I am relaxed	1	2	3	4
5.	I feel content	1	2	3	4
6.	I am worried	1	2	3	4

Please make sure that you have answered *all* the questions.

(Marteau & Bekker 1992)

EXP 05
16
Testing & Measures Pack v2017-04-08 1246

Trial block: | | | 3 | | | Rotary motion: Zero Deceleration | Impulse Deceleration	Participant no.:

How you felt MOMENTS AGO, while you were COMPLETING the task

Rating scale for mental effort

Instructions

Please rate how much ***mental effort*** you exerted while performing the left-right judgement task. Compared to the practice trial, WHEN THE CHAIR WAS ROTATING SLOWLY, was the amount of mental effort you just put in to the last trial **(tick one box)**:

A Lot Less	Moderately Less	Mildly Less	No Different	Mildly More	Moderately More	A Lot More
☐	☐	☐	☐	☐	☐	☐

To be the baseline marker for all subsequent ratings (as per Gardner et al 2016)

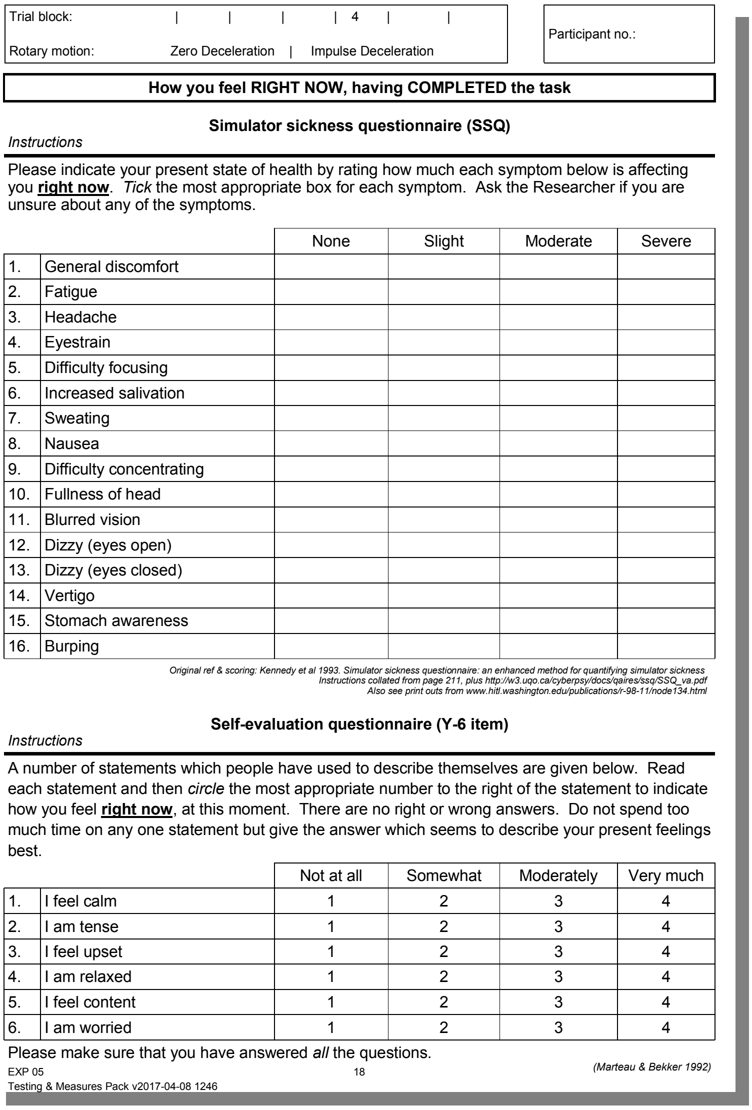
Perception of balance

Instructions

Please think back to when you were performing the task inside the enclosed cabin of the rotary chair. Now read each statement below and *circle* the most appropriate number to the right of the statement to indicate how you felt about your balance while you were **completing the task** in the chair. Once again, there are no right or wrong answers.

		Not at all	Somewhat	Moderately	Very much
1.	I felt balanced in the chair and could concentrate because of it	1	2	3	4
2.	I was unstable in the chair and was distracted because of it	1	2	3	4

Custom questionnaire



Trial block: | | | | 4 | |

Rotary motion: Zero Deceleration | Impulse Deceleration

Participant no.:

How you feel RIGHT NOW, having COMPLETED the task

Simulator sickness questionnaire (SSQ)

Instructions

Please indicate your present state of health by rating how much each symptom below is affecting you **right now**. *Tick* the most appropriate box for each symptom. Ask the Researcher if you are unsure about any of the symptoms.

		None	Slight	Moderate	Severe
1.	General discomfort				
2.	Fatigue				
3.	Headache				
4.	Eyestrain				
5.	Difficulty focusing				
6.	Increased salivation				
7.	Sweating				
8.	Nausea				
9.	Difficulty concentrating				
10.	Fullness of head				
11.	Blurred vision				
12.	Dizzy (eyes open)				
13.	Dizzy (eyes closed)				
14.	Vertigo				
15.	Stomach awareness				
16.	Burping				

Original ref & scoring: Kennedy et al 1993. Simulator sickness questionnaire: an enhanced method for quantifying simulator sickness
Instructions collated from page 211, plus http://w3.uqo.ca/cyberpsy/docs/qaires/ssq/SSQ_va.pdf
Also see print outs from www.hitl.washington.edu/publications/r-98-11/node134.html

Self-evaluation questionnaire (Y-6 item)

Instructions

A number of statements which people have used to describe themselves are given below. Read each statement and then *circle* the most appropriate number to the right of the statement to indicate how you feel **right now**, at this moment. There are no right or wrong answers. Do not spend too much time on any one statement but give the answer which seems to describe your present feelings best.

		Not at all	Somewhat	Moderately	Very much
1.	I feel calm	1	2	3	4
2.	I am tense	1	2	3	4
3.	I feel upset	1	2	3	4
4.	I am relaxed	1	2	3	4
5.	I feel content	1	2	3	4
6.	I am worried	1	2	3	4

Please make sure that you have answered *all* the questions.

(Marteau & Bekker 1992)

EXP 05 18

Testing & Measures Pack v2017-04-08 1246

Trial block:	| | | | 4 | |	Participant no.:
Rotary motion:	Zero Deceleration | Impulse Deceleration	

How you felt MOMENTS AGO, while you were COMPLETING the task

Rating scale for mental effort

Instructions

Please rate how much ***mental effort*** you exerted while performing the left-right judgement task. Compared to the practice trial, WHEN THE CHAIR WAS ROTATING SLOWLY, was the amount of mental effort you just put in to the last trial **(tick one box)**:

A Lot Less	Moderately Less	Mildly Less	No Different	Mildly More	Moderately More	A Lot More
☐	☐	☐	☐	☐	☐	☐

To be the baseline marker for all subsequent ratings (as per Gardner et al 2016)

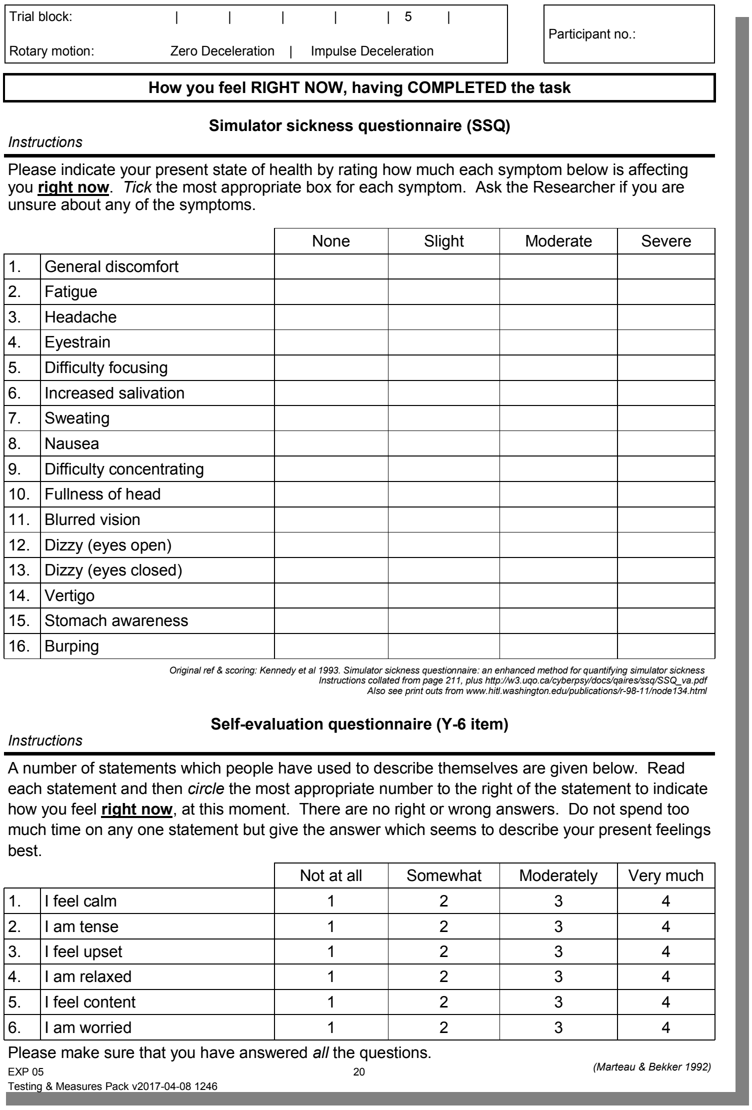
Perception of balance

Instructions

Please think back to when you were performing the task inside the enclosed cabin of the rotary chair. Now read each statement below and *circle* the most appropriate number to the right of the statement to indicate how you felt about your balance while you were **completing the task** in the chair. Once again, there are no right or wrong answers.

		Not at all	Somewhat	Moderately	Very much
1.	I felt balanced in the chair and could concentrate because of it	1	2	3	4
2.	I was unstable in the chair and was distracted because of it	1	2	3	4

Custom questionnaire



Trial block: | | | | | 5 |

Rotary motion: Zero Deceleration | Impulse Deceleration

Participant no.:

How you feel RIGHT NOW, having COMPLETED the task

Simulator sickness questionnaire (SSQ)

Instructions

Please indicate your present state of health by rating how much each symptom below is affecting you **right now**. *Tick* the most appropriate box for each symptom. Ask the Researcher if you are unsure about any of the symptoms.

		None	Slight	Moderate	Severe
1.	General discomfort				
2.	Fatigue				
3.	Headache				
4.	Eyestrain				
5.	Difficulty focusing				
6.	Increased salivation				
7.	Sweating				
8.	Nausea				
9.	Difficulty concentrating				
10.	Fullness of head				
11.	Blurred vision				
12.	Dizzy (eyes open)				
13.	Dizzy (eyes closed)				
14.	Vertigo				
15.	Stomach awareness				
16.	Burping				

Original ref & scoring: Kennedy et al 1993. Simulator sickness questionnaire: an enhanced method for quantifying simulator sickness
Instructions collated from page 211, plus http://w3.uqo.ca/cyberpsy/docs/qaires/ssq/SSQ_va.pdf
Also see print outs from www.hitl.washington.edu/publications/r-98-11/node134.html

Self-evaluation questionnaire (Y-6 item)

Instructions

A number of statements which people have used to describe themselves are given below. Read each statement and then *circle* the most appropriate number to the right of the statement to indicate how you feel **right now**, at this moment. There are no right or wrong answers. Do not spend too much time on any one statement but give the answer which seems to describe your present feelings best.

		Not at all	Somewhat	Moderately	Very much
1.	I feel calm	1	2	3	4
2.	I am tense	1	2	3	4
3.	I feel upset	1	2	3	4
4.	I am relaxed	1	2	3	4
5.	I feel content	1	2	3	4
6.	I am worried	1	2	3	4

Please make sure that you have answered *all* the questions.

(Marteau & Bekker 1992)

EXP 05 20
Testing & Measures Pack v2017-04-08 1246

Trial block:	| | | | | 5 |	Participant no.:
Rotary motion:	Zero Deceleration | Impulse Deceleration	

How you felt MOMENTS AGO, while you were COMPLETING the task

Rating scale for mental effort

Instructions

Please rate how much ***mental effort*** you exerted while performing the left-right judgement task. Compared to the practice trial, WHEN THE CHAIR WAS ROTATING SLOWLY, was the amount of mental effort you just put in to the last trial **(tick one box)**:

A Lot Less	Moderately Less	Mildly Less	No Different	Mildly More	Moderately More	A Lot More
☐	☐	☐	☐	☐	☐	☐

To be the baseline marker for all subsequent ratings (as per Gardner et al 2016)

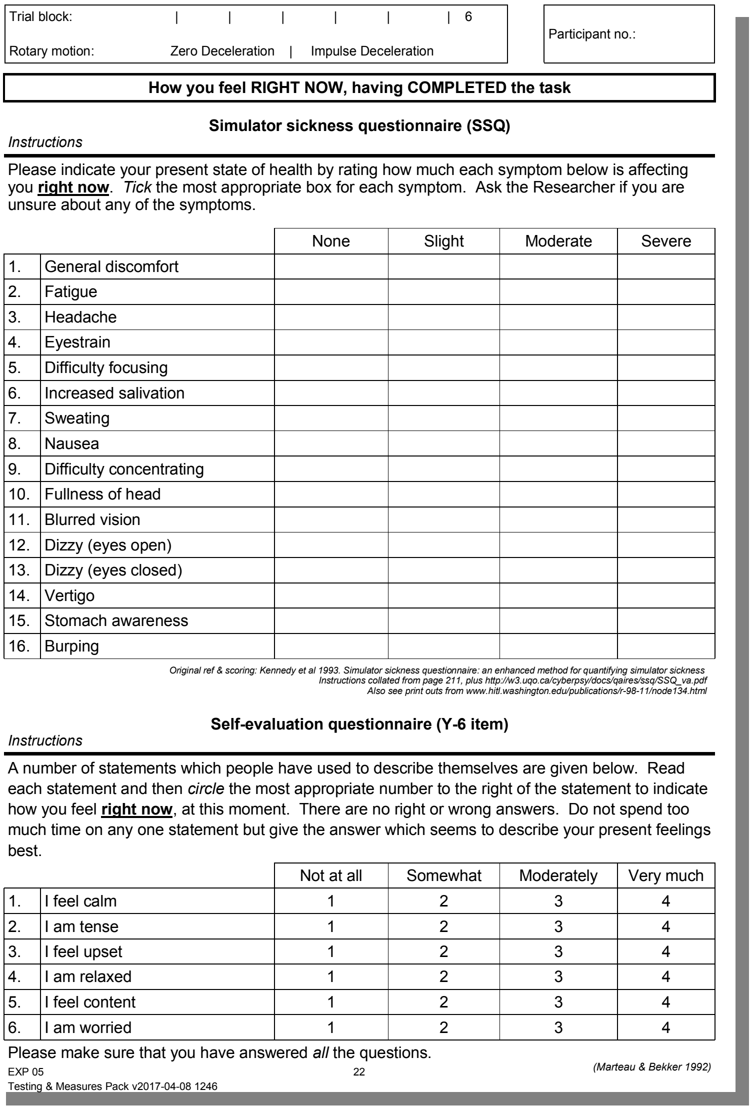
Perception of balance

Instructions

Please think back to when you were performing the task inside the enclosed cabin of the rotary chair. Now read each statement below and *circle* the most appropriate number to the right of the statement to indicate how you felt about your balance while you were **completing the task** in the chair. Once again, there are no right or wrong answers.

		Not at all	Somewhat	Moderately	Very much
1.	I felt balanced in the chair and could concentrate because of it	1	2	3	4
2.	I was unstable in the chair and was distracted because of it	1	2	3	4

Custom questionnaire



Trial block: | | | | | | 6

Rotary motion: Zero Deceleration | Impulse Deceleration

Participant no.:

How you feel RIGHT NOW, having COMPLETED the task

Simulator sickness questionnaire (SSQ)

Instructions

Please indicate your present state of health by rating how much each symptom below is affecting you **right now**. *Tick* the most appropriate box for each symptom. Ask the Researcher if you are unsure about any of the symptoms.

		None	Slight	Moderate	Severe
1.	General discomfort				
2.	Fatigue				
3.	Headache				
4.	Eyestrain				
5.	Difficulty focusing				
6.	Increased salivation				
7.	Sweating				
8.	Nausea				
9.	Difficulty concentrating				
10.	Fullness of head				
11.	Blurred vision				
12.	Dizzy (eyes open)				
13.	Dizzy (eyes closed)				
14.	Vertigo				
15.	Stomach awareness				
16.	Burping				

Original ref & scoring: Kennedy et al 1993. Simulator sickness questionnaire: an enhanced method for quantifying simulator sickness
Instructions collated from page 211, plus http://w3.uqo.ca/cyberpsy/docs/qaires/ssq/SSQ_va.pdf
Also see print outs from www.hitl.washington.edu/publications/r-98-11/node134.html

Self-evaluation questionnaire (Y-6 item)

Instructions

A number of statements which people have used to describe themselves are given below. Read each statement and then *circle* the most appropriate number to the right of the statement to indicate how you feel **right now**, at this moment. There are no right or wrong answers. Do not spend too much time on any one statement but give the answer which seems to describe your present feelings best.

		Not at all	Somewhat	Moderately	Very much
1.	I feel calm	1	2	3	4
2.	I am tense	1	2	3	4
3.	I feel upset	1	2	3	4
4.	I am relaxed	1	2	3	4
5.	I feel content	1	2	3	4
6.	I am worried	1	2	3	4

Please make sure that you have answered *all* the questions.

(Marteau & Bekker 1992)

EXP 05 22
Testing & Measures Pack v2017-04-08 1246

Trial block: | | | | | | 6

Rotary motion: Zero Deceleration | Impulse Deceleration

Participant no.:

How you felt MOMENTS AGO, while you were COMPLETING the task

Rating scale for mental effort

Instructions

Please rate how much ***mental effort*** you exerted while performing the left-right judgement task. Compared to the practice trial, WHEN THE CHAIR WAS ROTATING SLOWLY, was the amount of mental effort you just put in to the last trial **(tick one box)**:

A Lot Less	Moderately Less	Mildly Less	No Different	Mildly More	Moderately More	A Lot More
☐	☐	☐	☐	☐	☐	☐

To be the baseline marker for all subsequent ratings (as per Gardner et al 2016)

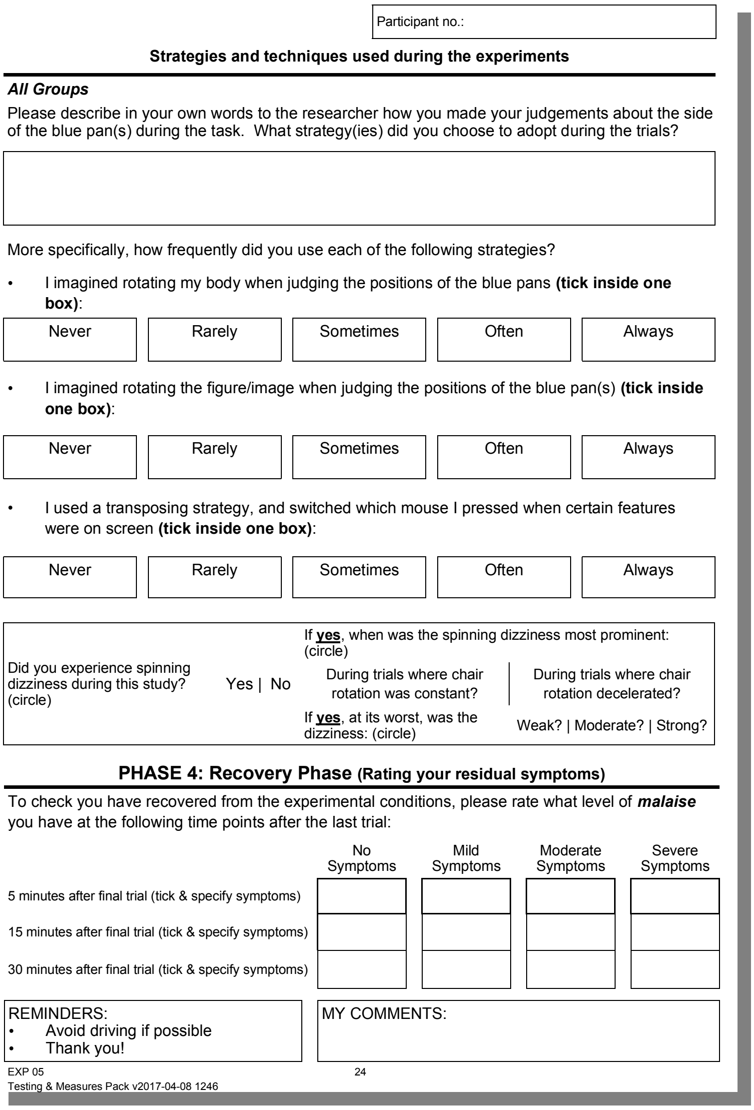
Perception of balance

Instructions

Please think back to when you were performing the task inside the enclosed cabin of the rotary chair. Now read each statement below and *circle* the most appropriate number to the right of the statement to indicate how you felt about your balance while you were **completing the task** in the chair. Once again, there are no right or wrong answers.

		Not at all	Somewhat	Moderately	Very much
1.	I felt balanced in the chair and could concentrate because of it	1	2	3	4
2.	I was unstable in the chair and was distracted because of it	1	2	3	4

Custom questionnaire



Participant no.:

Strategies and techniques used during the experiments

All Groups

Please describe in your own words to the researcher how you made your judgements about the side of the blue pan(s) during the task. What strategy(ies) did you choose to adopt during the trials?

More specifically, how frequently did you use each of the following strategies?

- I imagined rotating my body when judging the positions of the blue pans **(tick inside one box)**:

Never	Rarely	Sometimes	Often	Always

- I imagined rotating the figure/image when judging the positions of the blue pan(s) **(tick inside one box)**:

Never	Rarely	Sometimes	Often	Always

- I used a transposing strategy, and switched which mouse I pressed when certain features were on screen **(tick inside one box)**:

Never	Rarely	Sometimes	Often	Always

Did you experience spinning dizziness during this study? (circle)	Yes | No	If **yes**, when was the spinning dizziness most prominent: (circle) During trials where chair rotation was constant?	During trials where chair rotation decelerated?
		If **yes**, at its worst, was the dizziness: (circle)	Weak? | Moderate? | Strong?

PHASE 4: Recovery Phase **(Rating your residual symptoms)**

To check you have recovered from the experimental conditions, please rate what level of ***malaise*** you have at the following time points after the last trial:

	No Symptoms	Mild Symptoms	Moderate Symptoms	Severe Symptoms
5 minutes after final trial (tick & specify symptoms)				
15 minutes after final trial (tick & specify symptoms)				
30 minutes after final trial (tick & specify symptoms)				

REMINDERS:
- Avoid driving if possible
- Thank you!

MY COMMENTS:

EXP 05 24
Testing & Measures Pack v2017-04-08 1246

References

Acerbi, L., Dokka, K., Angelaki, D. E., & Ma, W. J. (2017). Bayesian comparison of explicit and implicit causal inference strategies in multisensory heading perception. *BioRxiv*, *150052*, 1080.

Adams, R. A., Stephan, K. E., Brown, H. R., Frith, C. D., & Friston, K. J. (2013). The computational anatomy of psychosis. *Frontiers in Psychiatry*, *4*(May), 1–26. https://doi.org/10.3389/fpsyt.2013.00047

Adkin, A. L., Frank, J. S., Carpenter, M. G., & Peysar, G. W. (2002). Fear of falling modifies anticipatory postural control. *Experimental Brain Research*, *143*(2), 160–170. https://doi.org/10.1007/s00221-001-0974-8

Agarwal, K., Bronstein, A. M., Faldon, M. E., Mandalà, M., Murray, K., & Silove, Y. (2012). Visual dependence and BPPV. *Journal of Neurology*, *259*(6), 1117–1124. https://doi.org/10.1007/s00415-011-6311-7

Aguilar, M., & Stiles, W. S. (1954). Saturation of the rod mechanism of the retina at high levels of stimulation. *Optica Acta: International Journal of Optics*, *1*(1), 59–65. https://doi.org/10.1080/09500347109696914

Aitchison, L., & Lengyel, M. (2017). With or without you: predictive coding and Bayesian inference in the brain. *Current Opinion in Neurobiology*, *46*, 219–227. https://doi.org/10.1016/j.conb.2017.08.010

Alais, D., & Burr, D. (2004). Ventriloquist effect results from near-optimal bimodal integration. *Current Biology*, *14*(3), 257–262. https://doi.org/10.1016/S0960-9822(04)00043-0

Allison, R. S., Howard, I. P., & Zacher, J. E. (1999). Effect of field size, head motion, and rotational velocity on roll vection and illusory self-tilt in a tumbling room. *Perception*, *28*(3), 299–306. https://doi.org/10.1068/p2891

Ambler, R. K., & Guedry, F. E. (1972). Assessment of reactions to vestibular disorientation stress for the purposes of aircrew selection. In *NATO AGARD* (pp. 1–8).

Andersen, G. J., & Dyre, B. P. (1989). Spatial orientation from optic flow in the central visual field. *Perception and Psychophysics*, *45*(4), 453–458. https://doi.org/10.3758/BF03210719

Angelaki, D. E., Gu, Y., & DeAngelis, G. C. (2011). Visual and vestibular cue integration for heading perception in extrastriate visual cortex. *Journal of Physiology*, *589*(4), 825–833. https://doi.org/10.1113/jphysiol.2010.194720

Ardid, S., Wang, X.-J., & Compte, A. (2007). An integrated microcircuit model of attentional processing in the neocortex. *Journal of Neuroscience*, *27*(32), 8486–8495. https://doi.org/10.1523/jneurosci.1145-07.2007

Arnold, N. R., Bröder, A., & Bayen, U. J. (2015). Empirical validation of the diffusion model for recognition memory and a comparison of parameter-estimation methods. *Psychological Research*, *79*(5), 882–898. https://doi.org/10.1007/s00426-014-0608-y

Arthur, J. C., Philbeck, J. W., & Chichka, D. (2007). Spatial memory enhances the precision of angular self-motion updating. *Experimental Brain Research*, *183*(4), 557–568. https://doi.org/10.1007/s00221-007-1075-0

Arthur, J. C., Philbeck, J. W., & Chichka, D. (2009). Non-sensory inputs to angular path integration. *Journal of Vestibular Research: Equilibrium and Orientation*, *19*(3–4), 111–125. https://doi.org/10.1021/nn300902w.Release

Arzy, S., Thut, G., Mohr, C., Michel, C. M., & Blanke, O. (2006). Neural basis of embodiment: distinct contributions of temporoparietal junction and extrastriate body area. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *26*(31), 8074–8081. https://doi.org/10.1523/JNEUROSCI.0745-06.2006

Balasubramaniam, R. (2004). Redundancy in the nervous system: Where internal models collapse. *Behavioral and Brain Sciences*, *27*(3), 396–397.

Baloh, R. W., Honrubia, V., & Kerber, K. A. (2011). *Baloh and Honrubia's clinical neurophysiology of the vestibular system* (4th ed.). Oxford.

Barmack, N. H. (2003). Central vestibular system: Vestibular nuclei and posterior cerebellum. *Brain Research Bulletin*, *60*(5–6), 511–541. https://doi.org/10.1016/S0361-9230(03)00055-8

Barra, J., Bray, A., Sahni, V., Golding, J. F., & Gresty, M. A. (2006). Increasing cognitive load with increasing balance challenge: Recipe for catastrophe. *Experimental Brain Research*, *174*, 734–745. https://doi.org/10.1007/s00221-006-0519-2

Barra, J., Marquer, A., Joassin, R., Reymond, C., Metge, L., Chauvineau, V., & Pérennou, D. (2010). Humans use internal models to construct and update a sense of verticality. *Brain*, *133*(12), 3552–3563. https://doi.org/10.1093/brain/awq311

Bartos, M., Alle, H., & Vida, I. (2011). Role of microcircuit structure and input integration in hippocampal interneuron recruitment and plasticity. *Neuropharmacology*, *60*(5), 730–739. https://doi.org/10.1016/j.neuropharm.2010.12.017

Benazet, M., Thénault, F., Whittingstall, K., & Bernier, P.-M. (2016). Attenuation of visual reafferent signals in the parietal cortex during voluntary movement. *Journal of Neurophysiology*, *116*(4), 1831–1839. https://doi.org/10.1152/jn.00231.2016

Benson, A. J., & Gedye, J. L. (1963). *Logical processes in the resolution of orientation conflict*. Farnborough, UK.

Berger, L., & Bernard-Demanze, L. (2011). Age-related effects of a memorizing spatial task in the adults and elderly postural control. *Gait and Posture*, *33*(2), 300–302. https://doi.org/10.1016/j.gaitpost.2010.10.082

Bermúdez Rey, M. C., Clark, T. K., Wang, W., Leeder, T., Bian, Y., & Merfeld, D. M. (2016). Vestibular perceptual thresholds increase above the age of 40. *Frontiers in Neurology*, *7*(OCT), 1–17. https://doi.org/10.3389/fneur.2016.00162

Bernstein, N. A. (1967). *The co-ordination and regulation of movements*. London.

Berthoz, A., Lacour, M., Soechting, J. F., & Vidal, P.-P. (1979). The role of vision in the control of posture during linear motion. *Progress in Brain Research*, *50*, 197–209.

Billman, G. E. (2013). The LF/HF ratio does not accurately measure cardiac sympatho-vagal balance. *Frontiers in Physiology*, *4*, 1–5. https://doi.org/10.3389/fphys.2013.00026

Bitzer, S., Park, H., Blankenburg, F., & Kiebel, S. J. (2014). Perceptual decision making: drift-diffusion model is equivalent to a Bayesian model. *Frontiers in Human Neuroscience*, *8*, 1–17. https://doi.org/10.3389/fnhum.2014.00102

Blake, R., & Logothetis, N. K. (2002). Visual competition. *Nature Reviews. Neuroscience*, *3*(1), 13–21. https://doi.org/10.1038/nrn701

Blanke, O., Mohr, C., Michel, C. M., Pascual-Leone, A., Brugger, P., Seeck, M., … Thut, G. (2005). Linking out-of-body experience and self processing to mental own-body imagery at the temporoparietal junction. *The Journal of Neuroscience*, *25*(3), 550–557. https://doi.org/10.1523/JNEUROSCI.2612-04.2005

Blanke, O., Thut, G., Landis, T., & Seeck, M. (2000). Simple and complex vestibular responses induced by electrical cortical stimulation of the parietal cortex in humans. *Journal of Neurology, Neurosurgery & Psychiatry*, *69*(4), 553–556. https://doi.org/10.1136/jnnp.69.4.553

Blazhenkova, O., & Kozhevnikov, M. (2008). The new Object-Spatial-Verbal Cognitive Style Model: Theory and measurement. *Applied Cognitive Psychology*, *23*, 638–663. https://doi.org/10.1002/acp

Bles, W., Bos, J. E., de Graaf, B., Groen, E., & Wertheim, A. H. (1999). Motion sickness: Only one provocative conflict? *Brain Research Bulletin*, *47*(5), 481–487.

Borst, A., & Euler, T. (2011). Seeing things in motion: Models, circuits, and mechanisms. *Neuron*, *71*(6), 974–994. https://doi.org/10.1016/j.neuron.2011.08.031

Bos, J. E. (2015). Less sickness with more motion and/or mental distraction. *Journal of Vestibular Research: Equilibrium and Orientation*, *25*(1), 23–33. https://doi.org/10.3233/VES-150541

Bos, J. E., MacKinnon, S. N., & Patterson, A. (2005). Motion sickness symptoms in a ship motion simulator: Effects of inside, outside, and no view. *Aviation Space and Environmental Medicine*, *76*(12), 1111–1118.

Bouffard, M., & Wall, A. E. (1990). A problem solving approach to movement skill acquisition: Implications for special populations. *Advances in Psychology*, *74*, 107–131. https://doi.org/10.1016/S0166-4115(08)61179-6

Bower, J. D., Bian, Z., & Andersen, G. J. (2012). Effects of retinal eccentricity and acuity on global motion processing. *Attention, Perception & Psychophysics*, *74*(5), 942–949. https://doi.org/10.3758/s13414-012-0283-2.Effects

Brandt, T. (2000). *Vertigo: Its multisensory syndromes* (2nd ed.). London.

Brandt, T., Bartenstein, P., Janek, A., & Dieterich, M. (1998). Reciprocal inhibitory visual – vestibular interaction: Visual motion stimulation deactivates the parieto-insular vestibular cortex, 1749–1758.

Brandt, T., Dichgans, J., & Koenig, E. (1973). Differential effects of central versus peripheral vision on egocentric and exocentric motion perception. *Experimental Brain Research*, *16*(5), 476–491.

Brandt, T., Kugler, G., Schniepp, R., Wuehr, M., & Huppert, D. (2015). Acrophobia impairs visual exploration and balance during standing and walking. *Annals of the New York Academy of Sciences*, *1343*(1), 37–48. https://doi.org/10.1111/nyas.12692

Brandt, T., Schautzer, F., Hamilton, D. a, Brüning, R., Markowitsch, H. J., Kalla, R., … Strupp, M. (2005). Vestibular loss causes hippocampal atrophy and impaired spatial memory in humans. *Brain : A Journal of Neurology*, *128*(Pt 11), 2732–2741. https://doi.org/10.1093/brain/awh617

Brandt, T., Strupp, M., & Dieterich, M. (2014). Towards a concept of disorders of "higher vestibular function." *Frontiers in Integrative Neuroscience*, *8*, 1–8. https://doi.org/10.3389/fnint.2014.00047

Bringoux, L., Scotto Di Cesare, C., Borel, L., Macaluso, T., & Sarlegna, F. R. (2016). Do visual and vestibular inputs compensate for somatosensory loss in the perception of spatial orientation? Insights from a deafferented patient. *Frontiers in Human Neuroscience*, *10*(April), 1–10. https://doi.org/10.3389/fn-hum.2016.00181

Brisinda, D., Venuti, A., Sorbo, A. R., Cataldi, C., Iantorno, E., & Fenici, R. (2013). Comparison between standard short-term, very-short and ultra-short-term heart rate variability analysis in healthy subjects during exercise testing. *European Heart Journal*, *34*(Suppl 1), 3384.

Britten, K. H. (2008). Mechanisms of self-motion perception. *Annual Review of Neuroscience*, *31*(1), 389–410. https://doi.org/10.1146/annurev.neuro.29.051605.112953

Bronstein, A. M. (1995). Visual vertigo syndrome: Clinical and posturography findings. *Journal of Neurology, Neurosurgery & Psychiatry*, *59*(5), 472–476.

Brooks, J. X., Carriot, J., & Cullen, K. E. (2015). Learning to expect the unexpected: Rapid updating in primate cerebellum during voluntary self-motion. *Nature Neuroscience*, *18*(9), 1310–1317. https://doi.org/10.1038/nn.4077

Bruya, B., & Tang, Y.-Y. (2018). Is attention really effort? Revisiting Daniel Kahneman's influential 1973 book Attention and Effort. *Frontiers in Psychology*, *9*, 1–10. https://doi.org/10.3389/fpsyg.2018.01133

Butler, J. S., Campos, J. L., & Bülthoff, H. H. (2015). Optimal visual-vestibular integration under conditions of conflicting intersensory motion profiles. *Experimental Brain Research*, *233*(2), 587–597. https://doi.org/10.1007/s00221-014-4136-1

Button, K. S., Ioannidis, J. P. A., Mokrysz, C., Nosek, B. A., Flint, J., Robinson, E. S. J., & Munafo, M. R. (2013). Power failure: Why small sample size undermines the reliability of neuroscience. *Nature Reviews Neuroscience*, *13*(5), 365–376. https://doi.org/10.1038/nrn3475

Candidi, M., Micarelli, A., Viziano, A., Aglioti, S. M., Minio-Paluello, I., & Alessandrini, M. (2013). Impaired mental rotation in benign paroxysmal positional vertigo and acute vestibular neuritis. *Frontiers in Human Neuroscience*, *7*, 1–11. https://doi.org/10.3389/fnhum.2013.00783

Carpenter, M. G., Adkin, A. L., Brawley, L. R., & Frank, J. S. (2006). Postural, physiological and psychological reactions to challenging balance: Does age make a difference? *Age and Ageing*, *35*(3), 298–303. https://doi.org/10.1093/ageing/afl002

Carpenter, R. H. S. (2003). *Neurophysiology* (Fourth Edi). London.

Carriot, J., Brooks, J. X., & Cullen, K. E. (2013). Multimodal integration of self-motion cues in the vestibular system: Active versus passive translations. *Journal of Neuroscience*, *33*(50), 19555–19566. https://doi.org/10.1523/jneurosci.3051-13.2013

Chukoskie, L., & Movshon, J. A. (2009). Modulation of visual signals in macaque MT and MST neurons during pursuit eye movement. *Journal of Neurophysiology*, *102*(6), 3225–3233. https://doi.org/10.1152/jn.90692.2008

Clifford, C. W. G., & Langley, K. (1996). Psychophysics of motion adaptation parallels insect electrophysiology. *Current Biology*, *6*(10), 1340–1342. https://doi.org/10.1016/S0960-9822(02)70721-5

Cochran, W. G. (1937). Problems arising in the analysis of a series of similar experiments. *Journal of the Royal Statistical Society*, *4(Suppl.)*(1), 102–118.

Colnaghi, S., Rezzani, C., Gnesi, M., Manfrin, M., Quaglieri, S., Nuti, D., … Versino, M. (2017). Validation of the Italian version of the dizziness handicap inventory, the situational vertigo questionnaire, and the activity-specific balance confidence scale for peripheral and central vestibular symptoms. *Frontiers in Neurology*, *8*, 1–7. https://doi.org/10.3389/fneur.2017.00528

Corballis, M. C. (1988). Recognition of disoriented shapes. *Psychological Review*, *95*(1), 115–123. https://doi.org/10.1037/0033-295X.95.1.115

Cousins, S., Kaski, D., Cutfield, N., Seemungal, B. M., Golding, J. F., Gresty, M. A., … Bronstein, A. M. (2013). Vestibular perception following acute unilateral vestibular lesions. *PLoS ONE*, *8*(5), 1–10. https://doi.org/10.1371/journal.pone.0061862

Creem-Regehr, S. H. (2010). Body mapping and spatial transformations. In F. L. Dolins & R. W. Mitchell (Eds.), *Spatial cognition, spatial perception: mapping the self and space* (pp. 422–438). Cambridge, UK.

Creem-Regehr, S. H., Gagnon, K. T., Geuss, M. N., & Stefanucci, J. K. (2013). Relating spatial perspective taking to the perception of other's affordances: providing a foundation for predicting the future behavior of others. *Frontiers in Human Neuroscience*, *7*(September), 1–14. https://doi.org/10.3389/fnhum.2013.00596

Creem-Regehr, S. H., & Kunz, B. R. (2010). Perception and action. *Wiley Interdisciplinary Reviews: Cognitive Science*, *1*(6), 800–810. https://doi.org/10.1002/wcs.82

Creem-Regehr, S. H., Neil, J. A., & Yeh, H. J. (2007). Neural correlates of two imagined egocentric transformations. *NeuroImage*, *35*(2), 916–927. https://doi.org/10.1016/j.neuroimage.2006.11.057

Cullen, K. E. (2016). Physiology of central pathways. In J. M. Furman & T. Lempert (Eds.), *Handbook of clinical neurology, Vol. 137* (pp. 17–40). Amsterdam.

Cullen, K. E. (2018). Multisensory integration and the perception of self-motion. *Oxford Research Encyclopedia of Neuroscience*. https://doi.org/10.1093/acrefore/9780190264086.013.91

Cullen, K. E., & Taube, J. S. (2017). Our sense of direction: Progress, controversies and challenges. *Nature Neuroscience*, *20*(11), 1465–1473. https://doi.org/10.1038/nn.4658

D'hemecourt, P. (2011). Subacute symptoms of sports-related concussion: outpatient management and return to play. *Clinics in Sports Medicine*, *30*(1), 63–72. https://doi.org/10.1016/j.csm.2010.08.008

Dallal, G. E. (1997). Randomization.com.

Davis, J. R., Campbell, A. D., Adkin, A. L., & Carpenter, M. G. (2009). The relationship between fear of falling and human postural control. *Gait & Posture*, *29*, 275–279. https://doi.org/10.1016/j.gaitpost.2008.09.006

de Haan, E. H. F., & Cowey, A. (2011). On the usefulness of "what" and "where" pathways in vision. *Trends in Cognitive Sciences*, *15*(10), 460–466. https://doi.org/10.1016/j.tics.2011.08.005

De Winkel, K. N., Katliar, M., & Bülthoff, H. H. (2015). Forced fusion in multisensory heading estimation. *PLoS ONE*, *10*(5), 1–20. https://doi.org/10.1371/journal.pone.0169676

De Winkel, K. N., Katliar, M., & Bülthoff, H. H. (2017). Causal inference in multisensory heading estimation. *PLoS ONE*, *12*(1), 1–20. https://doi.org/10.1371/journal.pone.0169676

De Winkel, K. N., Katliar, M., Diers, D., & Bülthoff, H. H. (2018). Causal inference in the perception of verticality. *Scientific Reports*, *8*(1), 1–12. https://doi.org/10.1038/s41598-018-23838-w

DeAngelis, G. C., & Angelaki, D. E. (2012). Visual – Vestibular integration for self motion perception. In M. M. Murray & M. T. Wallace (Eds.), *The neural bases of multisensory processes* (pp. 629–652). Boca Raton.

Debelak, R., Gittler, G., & Arendasy, M. (2014). On gender differences in mental rotation processing speed. *Learning and Individual Differences*, *29*, 8–17. https://doi.org/10.1016/j.lindif.2013.10.003

Deroualle, D., Borel, L., Devèze, A., & Lopez, C. (2015). Changing perspective: The role of vestibular signals. *Neuropsychologia*, *79*, 175–185. https://doi.org/10.1016/j.neuropsychologia.2015.08.022

Deroualle, D., & Lopez, C. (2014). Toward a vestibular contribution to social cognition. *Frontiers in Integrative Neuroscience*, *8*, 14–17. https://doi.org/10.3389/fnint.2014.00016

Diedrichsen, J., Shadmehr, R., & Ivry, R. B. (2010). The coordination of movement: Optimal feedback control and beyond. *Trends in Cognitive Sciences*, *14*(1), 31–39. https://doi.org/10.1016/j.tics.2009.11.004

Dieterich, M., & Brandt, T. (2015). The bilateral central vestibular system: its pathways, functions, and disorders. *Annals of the New York Academy of Sciences*, *1343*(1), 10–26. https://doi.org/10.1111/nyas.12585

Dilda, V., MacDougall, H. G., Curthoys, I. S., & Moore, S. T. (2012). Effects of galvanic vestibular stimulation on cognitive function. *Experimental Brain Research*, *216*(2), 275–285. https://doi.org/10.1007/s00221-011-2929-z

Douglas, R. H., & Lawnenson, J. G. (2016). Eye. In S. Standring, N. Anand, R. Birch, P. Collins, A. R. Crossman, M. Gleeson, … C. B. Wigley (Eds.), *Gray's anatomy: The anatomical basis of clinical practice*. New York.

Duchowski, A. T., Babu, V. S., Bertrand, J., & Krejtz, K. (2014). Gaze analytics pipeline for unity 3D integration: Signal filtering and analysis. In *CEUR Workshop Proceedings* (pp. 7–11). Vienna.

Dukelow, S. P., Desouza, J. F. X., Culham, J. C., Berg, V. D. A. V, Menon, R. S., & Vilis, T. (2001). Distinguishing subregions of the human MT+ complex using visual fields and pursuit eye movements. *Journal of Neurophysiology*, *86*, 1991–2000.

Dully, J., McGovern, D. P., & O'Connell, R. G. (2018). The impact of natural aging on computational and neural indices of perceptual decision making: A review. *Behavioural Brain Research*, 1–8. https://doi.org/10.1016/j.bbr.2018.02.001

Dutilh, G., Annis, J., Brown, S. D., Cassey, P., Evans, N. J., Grasman, R. P. P. P., … Donkin, C. (2018). The quality of response time data inference: A blinded, collaborative assessment of the validity of cognitive models. *Psychonomic Bulletin & Review*, 1–19. https://doi.org/10.17605/OSF.IO/S2X32

Dutilh, G., Wagenmakers, E.-J., Visser, I., & van der Maas, H. L. J. (2011). A phase transition model for the speed-accuracy trade-off in response time experiments. *Cognitive Science*, *35*, 211–250. https://doi.org/10.1111/j.1551-6709.2010.01147.x

Edwards, M. J., Adams, R. A., Brown, H., Pareés, I., & Friston, K. J. (2012). A Bayesian account of "hysteria." *Brain*, *135*(11), 3495–3512. https://doi.org/10.1093/brain/aws129

Efron, B., & Tibshirani, R. J. (1993). *An introduction to the bootstrap*. Boca Raton (FL).

Ehrenfried, T., Guerraz, M., Thilo, V. K., Yardley, L., & Gresty, M. A. (2003). Posture and mental task performance when viewing a moving visual field. *Cognitive Brain Research*, *17*(1), 140–153. https://doi.org/10.1016/S0926-6410(03)00088-0

Einstein, A. (1907). Über das Relativitätsprinzip und die aus demselben gezogenen Folgerungen. *Jahrbuch Der Radio-Aktivität Und Elektronik*, *4*, 411–462.

Ellis, A. W., & Mast, F. W. (2017). Toward a dynamic probabilistic model for vestibular cognition. *Frontiers in Psychology*, *8*, 1–7. https://doi.org/10.3389/fpsyg.2017.00138

Ellis, A. W., Schone, C. G., Vibert, D., Caversaccio, M. D., & Mast, F. W. (2018). Cognitive rehabilitation in bilateral vestibular patients : A computational perspective. *Frontiers in Neurology*, *9*(April), 1–7. https://doi.org/10.3389/fneur.2018.00286

Elzière, M., Devèze, A., Bartoli, C., & Levy, G. (2017). Post-traumatic balance disorder. *European Annals of Otorhinolaryngology, Head and Neck Diseases*, *134*(3), 171–175. https://doi.org/10.1016/j.anorl.2016.10.005

Engel, A. K., Maye, A., Kurthen, M., & König, P. (2013). Where's the action? The pragmatic turn in cognitive science. *Trends in Cognitive Sciences*, *17*(5), 202–209. https://doi.org/10.1016/j.tics.2013.03.006

Ernst, M. O. (2012). Optimal multisensory integration: Assumptions and limits. In B. E. Stein (Ed.), *The New Handbook of Multisensory Processes* (pp. 527–544). Cambridge.

Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature*, *415*, 429–433. https://doi.org/10.1038/415429a

Ernst, M. O., & Di Luca, M. (2011). Multisensory perception: From integration to remapping. In J. Trommershauser, K. P. Kording, & M. S. Landy (Eds.), *Sensory cue integration*. Oxford. https://doi.org/10.1093/acprof

Faisal, A. A., Selen, L. P. J., & Wolpert, D. M. (2008). Noise in the nervous system. *Nature Reviews Neuroscience*, *9*(4), 292–303. https://doi.org/10.1038/nrn2258.Noise

Falconer, C. J., & Mast, F. W. (2012). Balancing the mind: Vestibular induced facilitation of egocentric mental transformations. *Experimental Psychology*, *59*(6), 332–339. https://doi.org/10.1027/1618-3169/a000195

Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behaviour Research Methods*, *39*(2), 175–191. https://doi.org/10.3758/BF03193146

Fetsch, C. R., DeAngelis, G. C., & Angelaki, D. E. (2010). Visual-vestibular cue integration for heading perception: Applications of optimal cue integration theory.

European Journal of Neuroscience, *31*(10), 1721–1729. https://doi.org/10.1111/j.1743-6109.2008.01122.x.Endothelial

Fetsch, C. R., DeAngelis, G. C., & Angelaki, D. E. (2013). Bridging the gap between theories of sensory cue integration and the physiology of multisensory neurons. *Nature Reviews Neuroscience*, *14*(6), 1–28. https://doi.org/10.2217/nnm.12.167.Gene

Fetsch, C. R., Gu, Y., Deangelis, G. C., & Angelaki, D. E. (2011). Self-motion perception: Multisensory integration in extrastriate visual cortex. In J. Trommershauser, K. P. Kording, & M. S. Landy (Eds.), *Sensory cue integration*. Oxford. https://doi.org/10.1093/acprof

Fetsch, C. R., Pouget, A., Deangelis, G. C., & Angelaki, D. E. (2012). Neural correlates of reliability-based cue weighting during multisensory integration. *Nature Neuroscience*, *15*(1), 146–154. https://doi.org/10.1038/nn.2983

Fetsch, C. R., Turner, A. H., DeAngelis, G. C., & Angelaki, D. E. (2009). Dynamic reweighting of visual and vestibular cues during self-motion perception. *Journal of Neuroscience*, *29*(49), 15601–15612. https://doi.org/10.1523/JNEUROSCI.2574-09.2009

Field, A. (2013). *Discovering statistics using IBM SPSS Statistics* (4th ed.). London.

FitzGerald, T. H. B., Moran, R. J., Friston, K. J., & Dolan, R. J. (2015). Precision and neuronal dynamics in the human posterior parietal cortex during evidence accumulation. *NeuroImage*, *107*, 219–228. https://doi.org/10.1016/j.neuroimage.2014.12.015

Fitzpatrick, R. C., & Day, B. L. (2004). Probing the human vestibular system with galvanic stimulation. *Journal of Applied Physiology*, *96*, 2301–2316. https://doi.org/10.1152/japplphysiol.00008.2004

Floresco, S. B. (2016). Dopamine neurons, input integration, and reward prediction errors: E Pluribus Unum. *Neuron*, *91*(6), 1192–1194. https://doi.org/10.1016/j.neuron.2016.09.012

Forbes, P. A., Chien, A., & Blouin, J.-S. (2018). Sensorimotor control of standing balance. In B. L. Day & S. R. Lord (Eds.), *Handbook of clinical neurology, Vol. 139* (pp. 61–83). Amsterdam.

Friston, K. J. (2012). Prediction, perception and agency. *International Journal of Psychophysiology*, *83*(2), 248–252. https://doi.org/10.1016/j.ijpsycho.2011.11.014

Friston, K. J., Daunizeau, J., Kilner, J., & Kiebel, S. J. (2010). Action and behavior: A free-energy formulation. *Biological Cybernetics*, *102*(3), 227–260. https://doi.org/10.1007/s00422-010-0364-z

Frith, C. D., Blakemore, S.-J., & Wolpert, D. M. (2000). Explaining the symptoms of schizophrenia: Abnormal awareness of action. *Brain Research Reveiws*, *31*, 357–363.

Frith, C. D., & Dolan, R. J. (1996). The role of the prefrontal cortex in higher cognitive functions. *Cognitive Brain Research*, *5*, 175–181. https://doi.org/http://dx.doi.org/10.1016/S0926-6410(96)00054-7

Frith, C. D., & Frith, U. (2007). Social cognition in humans. *Current Biology*, *17*(16), R724–R732. https://doi.org/10.1016/j.cub.2007.05.068

Furman, J. M., Redfern, M. S., Fuhrman, S. I., & Jennings, J. R. (2012). Visual-vestibular stimulation influences spatial and non-spatial cognitive processing. *Journal of Vestibular Research : Equilibrium & Orientation*, *22*(5–6), 253–259. https://doi.org/10.3233/VES-2012-00460

Furness, D. N. (2016). Inner ear. In S. Standring, N. Anand, R. Birch, P. Collins, A. R. Crossman, M. Gleeson, … C. B. Wigley (Eds.), *Gray's anatomy: The anatomical basis of clinical practice*. New York.

Gardner, M. R., Brazier, M., Edmonds, C. J., & Gronholm, P. C. (2013). Strategy modulates spatial perspective-taking: evidence for dissociable disembodied and embodied routes. *Frontiers in Human Neuroscience*, *7*(August), 457. https://doi.org/10.3389/fnhum.2013.00457

Gardner, M. R., & Potts, R. (2011). Domain general mechanisms account for imagined transformations of whole body perspective. *Acta Psychologica*, *137*(3), 371–381. https://doi.org/10.1016/j.actpsy.2011.04.006

Gardner, M. R., Stent, C., Mohr, C., & Golding, J. F. (2017). Embodied perspective-taking indicated by selective disruption from aberrant self motion. *Psychological Research*, *81*(2), 480–489. https://doi.org/10.1007/s00426-016-0755-4

Geh, C. L. M., Beauchamp, M. R., Crocker, P. R. E., & Carpenter, M. G. (2011). Assessed and distressed: White-coat effects on clinical balance performance. *Journal of Psychosomatic Research*, *70*(1), 45–51. https://doi.org/10.1016/j.jpsychores.2010.09.008

Gibson, J. J. (1950). *The perception of the visual world*. Cambridge.

Gibson, J. J. (1958). Visually controlled locomotion and visual orientation in animals. *British Journal of Psychology*, *49*(3), 182–194.

Gibson, J. J. (1966). *The senses considered as perceptual systems*. Boston.

Gilaie-Dotan, S. (2016). Visual motion serves but is not under the purview of the dorsal pathway. *Neuropsychologia*, *89*, 378–392. https://doi.org/10.1016/j.neuropsychologia.2016.07.018

Gilbert, C. D., & Li, W. (2013). Top-down influences on visual processing. *Nature Reviews Neuroscience*, *14*(5), 350–363. https://doi.org/10.1038/nrn3476

Gillingham, K. K., & Wolfe, J. W. (1986). *Spatial orientation in flight*. Brooks Air Force Base, TX.

Gizzi, M., Zlotnick, M., Cicerone, K., & Riley, E. (2003). Vestibular disease and cognitive dysfunction. *Journal of Head Trauma Rehabilitation*, *18*(5), 398–407.

Goldberg, J. M., & Fernandez, C. (1984). The vestibular system. In V. B. Brooks (Ed.), *Supplement 3: Handbook of Physiology - The Nervous System, Sensory Processes* (pp. 977–1022). Oxford. https://doi.org/10.1016/j.cub.2005.07.053

Goldberg, J. M., Wilson, V. J., Cullen, K. E., Angelaki, D. E., Broussard, D. M., Buttner-Ennever, J. A., … Minor, L. B. (2012). *The vestibular system: A sixth sense*. Oxford.

Golding, J. F. (2006). Predicting individual differences in motion sickness susceptibility by questionnaire. *Personality and Individual Differences*, *41*(2), 237–248. https://doi.org/10.1016/j.paid.2006.01.012

Golding, J. F., & Gresty, M. A. (2016). Biodynamic hypothesis for the frequency tuning of motion sickness. *Aerospace Medicine and Human Performance*, *87*(1), 65–68. https://doi.org/10.3357/AMHP.4295.2016

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, *15*(1), 20–25. https://doi.org/10.1016/0166-2236(92)90344-8

Grabherr, L., Karmali, F., Bach, S., Indermaur, K., Metzler, S., & Mast, F. W. (2007). Mental own-body and body-part transformations in microgravity. *Journal of Vestibular Research : Equilibrium & Orientation*, *17*(5–6), 279–287.

Green, A. M., & Angelaki, D. E. (2010). Internal models and neural computation in the vestibular system. *Experimental Brain Research*, *200*, 197–222. https://doi.org/10.1007/s00221-009-2054-4

Gresty, M. A., & Golding, J. F. (2009). Impact of vertigo and spatial disorientation on concurrent cognitive tasks. *Annals of the New York Academy of Sciences*, *1164*, 263–267. https://doi.org/10.1111/j.1749-6632.2008.03744.x

Gresty, M. A., Golding, J. F., Le, H., & Nightingale, K. (2008). Cognitive impairment by spatial disorientation. *Aviation Space and Environmental Medicine*, *79*(2), 105–111. https://doi.org/10.3357/ASEM.2143.2008

Gresty, M. A., Waters, S., Bray, A., Bunday, K., & Golding, J. F. (2003). Impairment of spatial cognitive function with preservation of verbal performance during spatial disorientation. *Current Biology*, *28*(13(21)), R829–R830.

Gronholm, P. C., Flynn, M., Edmonds, C. J., & Gardner, M. R. (2012). Empathic and non-empathic routes to visuospatial perspective-taking. *Consciousness and Cognition*, *21*(1), 494–500. https://doi.org/10.1016/j.concog.2011.12.004

Gros, D. F., Antony, M. M., Simms, L. J., & McCabe, R. E. (2007). Psychometric propoerties of the State-Trait inventory for Cognitive and Somatic Anxiety (STICSA): Comparison to the State-Trait Anxiety Inventory (STAI). *Psychological Assessment*, *19*(4), 369–381. https://doi.org/10.1037/1040-3590.19.4.369

Grush, R. (2004). The emulation theory of representation: motor control, imagery, and perception. *The Behavioral and Brain Sciences*, *27*, 377–442. https://doi.org/10.1017/S0140525X04000093

Grusser, O. J., Pause, M., & Schreiter, U. (1990). Vestibular neurones in the parieto-insular cortex of monkeys (Macaca fascicularis): Visual and neck receptor responses. *Journal of Physiology*, *430*, 559–583.

Gu, Y., DeAngelis, G. C., & Angelaki, D. E. (2007). A functional link between area MSTd and heading perception. *Nature Neuroscience*, *10*(8), 1038–1047. https://doi.org/10.1038/jid.2014.371

Guedry, F. E. (1965). Orientation of the rotation-axis relative to gravity: Its influence on nystagmus and the sensation of rotation. *Acta Oto-Laryngologica*, *60*(1–6), 30–48. https://doi.org/10.3109/00016486509126986

Guerraz, M., & Bronstein, A. M. (2008). Mechanisms underlying visually induced body sway. *Neuroscience Letters*, *443*(1), 12–16. https://doi.org/10.1016/j.neulet.2008.07.053

Guerraz, M., Yardley, L., Bertholon, P., Pollak, L., Rudge, P., Gresty, M. A., & Bronstein, A. M. (2001). Visual vertigo: Symptom assessment, spatial orientation and postural control. *Brain : A Journal of Neurology*, *124*, 1646–1656.

Hauck, L. J., Carpenter, M. G., & Frank, J. S. (2008). Task-specific measures of balance efficacy, anxiety, and stability and their relationship to clinical balance performance. *Gait and Posture*, *27*, 676–682. https://doi.org/10.1016/j.gaitpost.2007.09.002

Hayes, A. F. (2013). *Introduction to mediation, moderation, and conditional process analysis: A regression-based approach*. New York.

Heil, M., & Rolke, B. (2002). Toward a chronopsychophysiology of mental rotation. *Psychophysiology*, *39*(4), 414–422. https://doi.org/10.1111/1469-8986.3940414

Hitier, M., Besnard, S., & Smith, P. F. (2014). Vestibular pathways involved in cognition. *Frontiers in Integrative Neuroscience*, *8*(July), 1–16. https://doi.org/10.3389/fnint.2014.00059

Howard, I. P. (1982). *Human visual orientation*. New York.

Howard, I. P., & Heckmann, T. (1989). Circular vection as a function of the relative sizes, distances, and positions of two competing visual displays. *Perception*, *18*(5), 657–665.

Huffman, J. L., Horslen, B. C., Carpenter, M. G., & Adkin, A. L. (2009). Does increased postural threat lead to more conscious control of posture? *Gait and Posture*, *30*, 528–532. https://doi.org/10.1016/j.gaitpost.2009.08.001

Inaba, N., Shinomoto, S., Yamane, S., Takemura, A., & Kawano, K. (2007). MST neurons code for visual motion in space independent of pursuit eye movements. *Journal of Neurophysiology*, *97*(5), 3473–3483. https://doi.org/10.1152/jn.01054.2006

Indovina, I., Riccelli, R., Staab, J. P., Lacquaniti, F., & Passamonti, L. (2014). Personality traits modulate subcortical and cortical vestibular and anxiety responses to sound-evoked otolithic receptor stimulation. *Journal of Psychosomatic Research*, *77*(5), 391–400. https://doi.org/10.1016/j.jpsychores.2014.09.005

Ionta, S., Heydrich, L., Lenggenhager, B., Mouthon, M., Fornari, E., Chapuis, D., … Blanke, O. (2011). Multisensory mechanisms in temporo-parietal cortex support self-location and first-person perspective. *Neuron*, *70*(2), 363–374. https://doi.org/10.1016/j.neuron.2011.03.009

Isableu, B., Ohlmann, T., Crémieux, J., & Amblard, B. (1997). Selection of spatial frame of reference and postural control variability. *Experimental Brain Research*, *114*(3), 584–589. https://doi.org/10.1007/PL00005667

Israël, I., Bronstein, A. M., Kanayama, R., Faldon, M., & Gresty, M. A. (1996). Visual and vestibular factors influencing vestibular "navigation." *Experimental Brain Research*, *112*, 411–419.

Israël, I., & Warren, W. H. (2005). Vestibular, proprioceptive, and visual influences on the perception of orientation and self-motion in humans. In S. I. Wiener & J. S. Taube (Eds.), *Head Direction Cells and the Neural Mechanisms of Spatial Orientation* (pp. 347–381). Cambridge.

Jacob, R. G., Lilienfeld, S. O., Furman, J. M., Durrant, J. D., & Turner, S. M. (1989). Panic disorder with vestibular dysfunction: Further clinical observations and description of space and motion phobic stimuli. *Journal of Anxiety Disorders*, *3*(1958), 117–130. https://doi.org/10.1016/0887-6185(89)90006-6

Jola, C., & Mast, F. W. (2005). Mental object rotation and egocentric body transformation: Two dissociable processes? *Spatial Cognition & Computation*, *5*(2&3), 217–237. https://doi.org/10.1207/s15427633scc052

Jørstad, E. C., Hauer, K., Becker, C., & Lamb, S. E. (2005). Measuring the psychological outcomes of falling: A systematic review. *Journal of the American Geriatrics Society*, *53*(3), 501–510. https://doi.org/10.1111/j.1532-5415.2005.53172.x

Jürgens, R., & Becker, W. (2006). Perception of angular displacement without landmarks: evidence for Bayesian fusion of vestibular, optokinetic, podokinesthetic, and cognitive information. *Experimental Brain Research*, *174*(3), 528–543. https://doi.org/10.1007/s00221-006-0486-7

Jürgens, R., & Becker, W. (2011). Human spatial orientation in non-stationary environments: Relation between self-turning perception and detection of surround motion. *Experimental Brain Research*, *215*(3–4), 327–344. https://doi.org/10.1007/s00221-011-2900-z

Kahneman, D. (1973). *Attention and Effort*. Englewood Cliffs, NJ.

Kaiser, S., Walther, S., Nennig, E., Kronmüller, K., Mundt, C., Weisbrod, M., … Vogeley, K. (2008). Gender-specific strategy use and neural correlates in a spatial perspective taking task. *Neuropsychologia*, *46*(10), 2524–2531. https://doi.org/10.1016/j.neuropsychologia.2008.04.013

Kaliuzhna, M., Prsa, M., Gale, S., Lee, S. J., & Blanke, O. (2015). Learning to integrate contradictory multisensory self-motion cue pairings. *Journal of Vision*, *15*(10), 1–15.

Kaltner, S., & Jansen, P. (2014). Emotion and affect in mental imagery: do fear and anxiety manipulate mental rotation performance? *Frontiers in Psychology*, *5*, 1–12. https://doi.org/10.3389/fpsyg.2014.00792

Kaltner, S., Riecke, B. E., & Jansen, P. (2014). Embodied mental rotation: a special link between egocentric transformation and the bodily self. *Frontiers in Psychology*, *5*, 1–11. https://doi.org/10.3389/fpsyg.2014.00505

Kaski, D., Malhotra, P. A., Bronstein, A. M., & Seemungal, B. M. (2012). Temporoparietal cortex affords self-location perception by a temporal integration of sensory signals of motion. *Journal of Neurology, Neurosurgery & Psychiatry*, *88*(Suppl 2), A2. https://doi.org/10.1136/jnnp-2012-304200a.9

Kaski, D., Quadir, S., Nigmatullina, Y., Malhotra, P. A., Bronstein, A. M., & Seemungal, B. M. (2016). Temporoparietal encoding of space and time during vestibular-guided orientation. *Brain*, *139*(2), 392–403. https://doi.org/10.1093/brain/awv370

Kennedy, R. S., Drexler, J. M., Compton, D. E., Stanney, K. M., Lanham, D. S., & Harm, D. L. (2003). Configural scoring of simulator sickness, cybersickness and space adaption syndrome, similarities and difference. In L. J. Hettinger & M. W. Haas (Eds.), *Virtual and Adaptive Environments: Applications, Implications, and Human Performance Issues* (pp. 247–278). Boca Raton. https://doi.org/10.1201/9781410608888.ch12

Kennedy, R. S., & Fowlkes, J. E. (1992). Simulator sickness is polygenic and polysymptomatic: Implications for research. *The International Journal of Aviation Psychology*, *2*(1), 23–38.

Kennedy, R. S., Lane, N. E., Berbaum, K. S., & Lilienthal, M. G. (1993). Simulator Sickness Questionnaire: An enhanced method for quantifying simulator sickness.

The International Journal of Aviation Psychology, *3*(3), 203–220. https://doi.org/10.1207/s15327108ijap0303

Kennedy, R. S., Lane, N. E., Lilienthal, M. G., Berbaum, K. S., & Hettinger, L. J. (1992). Profile analysis of simulator sickness symptoms: Application to virtual environment systems. *Presence: Teleoperators and Virtual Environments*, *1*(3), 295–301.

Kessler, K., & Thomson, L. A. (2010). The embodied nature of spatial perspective taking: Embodied transformation versus sensorimotor interference. *Cognition*, *114*(1), 72–88. https://doi.org/10.1016/j.cognition.2009.08.015

Kingma, H., & van de Berg, R. (2016). Anatomy, physiology, and physics of the peripheral vestibular system. In J. M. Furman & T. Lempert (Eds.), *Handbook of clinical neurology, Vol. 137* (pp. 1–16). Amsterdam.

Kirsch, V., Keeser, D., Hergenroeder, T., Erat, O., Ertl-Wagner, B., Brandt, T., & Dieterich, M. (2016). Structural and functional connectivity mapping of the vestibular circuitry from human brainstem to cortex. *Brain Structure and Function*, *221*(3), 1291–1308. https://doi.org/10.1007/s00429-014-0971-x

Kleinschmidt, A., Thilo, V. K., Büchel, C., Gresty, M. A., Bronstein, A. M., & Frackowiak, R. S. J. (2002). Neural correlates of visual-motion perception as object- or self-motion. *NeuroImage*, *16*(4), 873–882. https://doi.org/10.1006/nimg.2002.1181

Klingner, C. M., Axer, H., Brodoehl, S., & Witte, O. W. (2016). Vertigo and the processing of vestibular information: A review in the context of predictive coding. *Neuroscience and Biobehavioral Reviews*, *71*, 379–387. https://doi.org/10.1016/j.neubiorev.2016.09.009

Knill, D. C., & Saunders, J. A. (2003). Do humans optimally integrate stereo and texture information for judgments of surface slant? *Vision Research*, *43*(24), 2539–2558. https://doi.org/10.1016/S0042-6989(03)00458-9

Körding, K. P., & Wolpert, D. M. (2004). Bayesian integration in sensorimotor learning. *Nature*, *427*(6971), 244–247. https://doi.org/10.1038/nature02169

Kosslyn, S. M., DiGirolamo, G. J., Thompson, W. L., & Alpert, N. M. (1998). Mental rotation of objects versus hands: Neural mechanisms revealed by positron emission tomography. *Psychophysiology*, *35*(2), 151–161. https://doi.org/10.1017/S0048577298001516

Kozhevnikov, M., Kosslyn, S. M., & Shephard, J. (2005). Spatial versus object visualizers: A new characterization of visual cognitive style. *Memory and Cognition*, *33*(4), 710–726. https://doi.org/10.3758/BF03195337

Lackner, J. R., & DiZio, P. (2005). Vestibular, proprioceptive, and haptic contributions to spatial orientation. *Annual Review of Psychology*, *56*(1), 115–147. https://doi.org/10.1146/annurev.psych.55.090902.142023

Lamm, C., & Majdandžić, J. (2015). The role of shared neural activations, mirror neurons, and morality in empathy - A critical comment. *Neuroscience Research*, *90*, 15–24. https://doi.org/10.1016/j.neures.2014.10.008

Latash, M. L., Ferreira, S. S., Wieczorek, S. A., & Duarte, M. (2003). Movement sway: changes in postural sway during voluntary shifts of the center of pressure. *Experimental Brain Research*, *150*(3), 314–324. https://doi.org/10.1007/s00221-003-1419-3

Laurens, J., & Angelaki, D. E. (2011). The functional significance of velocity storage and its dependence on gravity. *Experimental Brain Research*, *210*(0), 407–422. https://doi.org/10.1007/s00221-011-2568-4.The

Laurens, J., & Angelaki, D. E. (2017). A unified internal model theory to resolve the paradox of active versus passive self-motion sensation. *ELife*, *6*, 1–45. https://doi.org/10.7554/elife.28074

Lee, D. N., & Aronson, E. (1974). Visual proprioceptive control of standing in human infants. *Perception & Psychophysics*, *15*(3), 529–532. https://doi.org/10.3758/BF03199297

Lenggenhager, B., Lopez, C., & Blanke, O. (2008). Influence of galvanic vestibular stimulation on egocentric and object-based mental transformations. *Experimental Brain Research*, *184*(2), 211–221. https://doi.org/10.1007/s00221-007-1095-9

Lin, H. W., & Bhattacharyya, N. (2012). Balance disorders in the elderly: Epidemiology and functional impact. *The Laryngoscope*, *122*, 1858–1861. https://doi.org/10.1002/lary.23376

Lopez, C., & Blanke, O. (2011). The thalamocortical vestibular system in animals and humans. *Brain Research Reviews*, *67*(1–2), 119–146. https://doi.org/10.1016/j.brainresrev.2010.12.002

Lopez, C., Schreyer, H.-M., Preuss, N., & Mast, F. W. (2012). Vestibular stimulation modifies the body schema. *Neuropsychologia*, *50*(8), 1830–1837. https://doi.org/10.1016/j.neuropsychologia.2012.04.008

Lovibond, P. F., & Lovibond, S. H. (1995). The structure of negative emotional states: Comparison of the Depression Anxiety Stress Scales (DADD) with the Beck Depression and Anxiety Inventories. *Behaviour Research and Therapy*, *33*(3), 335–343. https://doi.org/10.1016/0005-7967(94)00075-U

Lowenstein, O. (1975). The peripheral neuron. In R. Naunton (Ed.), *The vestibular system* (pp. 99–108). New York.

Lowry, R. (2001, January 9). Significance of the difference between two correlation coefficients. Retrieved from http://vassarstats.net/rdiff.html

Lubeck, A. J. A., Bos, J. E., & Stins, J. F. (2016). Framing visual roll-motion affects postural sway and the subjective visual vertical. *Attention, Perception, and Psychophysics*, *78*(8), 2612–2620. https://doi.org/10.3758/s13414-016-1150-3

Lucas, J. W. (2003). Theory testing, generalization, and the problem of external validity. *Sociological Theory*, *21*(3), 236–253. https://doi.org/10.1111/1467-9558.00187

Luxon, L. M. (2004). Evaluation and management of the dizzy patient. *Journal of Neurology, Neurosurgery, and Psychiatry*, *75*(Suppl IV), iv45-iv52. https://doi.org/10.1136/jnnp.2004.055285

Luxon, L. M., & Bamiou, D.-E. (2007). Vestibular system disorders. In A. Schapira (Ed.), *Neurology and Clinical Neuroscience* (p. 337). Philadelphia, PA.

Ma, W. J., Beck, J., & Pouget, A. (2011). A neural implementation of optimal cue integration. In J. Trommershauser, K. P. Kording, & M. S. Landy (Eds.), *Sensory cue integration*. Oxford. https://doi.org/10.1093/acprof

Mach, E. (1875). *Grundlinien der Lehre von den Bewegungsempfindungen*. Leipzig.

Malliani, A., Pagani, M., Lombardi, F., & Cerutti, S. (1991). Cardiovascular neural regulation explored in the frequency domain. *Circulation*, *84*(2), 482–492. https://doi.org/10.1161/01.CIR.84.2.482

Marteau, T. M., & Bekker, H. (1992). The development of a six item form of the state scale of the Spielberger State Trait Anxiety Inventory (STAI). *British Journal of Clinical Psychology*, *31*(3), 301–306. https://doi.org/10.1111/j.2044-8260.1992.tb00997.x

Mast, F. W., & Ellis, A. W. (2015). Internal models, vestibular cognition, and mental imagery: Conceptual considerations. *Multisensory Research*, *28*(5–6), 443–460. https://doi.org/10.1163/22134808-00002503

Mast, F. W., Merfeld, D. M., & Kosslyn, S. M. (2006). Visual mental imagery during caloric vestibular stimulation. *Neuropsychologia*, *44*(1), 101–109. https://doi.org/10.1016/j.neuropsychologia.2005.04.005

Mast, F. W., Preuss, N., Hartmann, M., & Grabherr, L. (2014). Spatial cognition, body representation and affective processes: the role of vestibular information beyond ocular reflexes and control of posture. *Frontiers in Integrative Neuroscience*, *8*, 1–14. https://doi.org/10.3389/fnint.2014.00044

Matsangas, P., Mccauley, M. E., & Becker, W. (2014). The effect of mild motion sickness and sopite syndrome on multitasking cognitive performance. *Human Factors*, *56*(6), 1124–1135. https://doi.org/10.1177/0018720814522484

May, M. (2004). Imaginal perspective switches in remembered environments: Transformation versus interference accounts. *Cognitive Psychology*, *48*(2), 163–206. https://doi.org/10.1016/S0010-0285(03)00127-0

May, M., & Wendt, M. (2013). Visual perspective taking and laterality decisions: Problems and possible solutions. *Frontiers in Human Neuroscience*, *7*, 549. https://doi.org/10.3389/fnhum.2013.00549

Mayer, R. E. (2013). Problem solving. In D. Reisberg (Ed.), *The Oxford Handbook of Cognitive Psychology* (pp. 769–778). Oxford.

Merfeld, D. M., Park, S., Gianna-Poulin, C., Black, F. O., & Wood, S. (2005). Vestibular perception and action employ qualitatively different mechanisms. II. VOR and perceptual responses during combined tilt&translation. *Journal of Neurophysiology*, *94*(1), 199–205. https://doi.org/10.1152/jn.00905.2004

Mergner, T., & Rosemeier, T. (1998). Interaction of vestibular, somatosensory and visual signals for postural control and motion. *Brain Research Reveiws*, *21*, 118–135.

Mergner, T., Rumberger, A., & Becker, W. (1996). Is perceived angular displacement the time integral of perceived angular velocity? *Brain Research Bulletin*, *40*(5–6), 467–471. https://doi.org/10.1016/0361-9230(96)00143-8

Miall, R. C., & Wolpert, D. M. (1996). Forward models for physiological motor control. *Neural Networks*, *9*(8), 1265–1279.

Michelon, P., & Zacks, J. M. (2006). Two kinds of visual perspective taking. *Perception & Psychophysics*, *68*(2), 327–337. https://doi.org/10.3758/BF03193680

Moè, A. (2009). Are males always better than females in mental rotation? Exploring a gender belief explanation. *Learning and Individual Differences*, *19*(1), 21–27. https://doi.org/10.1016/j.lindif.2008.02.002

Molenaar, D., Tuerlinckx, F., & van der Maas, H. L. J. (2015). Fitting diffusion item response theory models for responses and response times using the R-package diffIRT. *Journal of Statistical Software*, *66*(4), 1–35. https://doi.org/10.18637/jss.v080.b01

Money, J., Alexander, D., & Walker, H. T. (1965). *A standardized road-map test of direction sense: Manual*. Baltimore.

Montello, D. R., & Raubal, M. (2013). Functions and applications of spatial cognition. In D. Waller & L. Nadel (Eds.), *Handbook of spatial cognition.* (pp. 249–264). https://doi.org/10.1037/13936-014

Montoya, A. K., & Hayes, A. F. (2017). Two-condition within-participant statistical mediation analysis: A path-analytic framework. *Psychological Methods*, *22*(1), 6–27. https://doi.org/10.1037/met0000086

Mooradian, T. A., Davis, M. H., & Matzler, K. (2011). Dispositional empathy and the hierarchical structure of personality. *American Journal of Psychology*, *124*(1), 99–109. https://doi.org/10.5406/amerjpsyc.124.1.0099

Moore, D. S., & Ellis, R. (2008). Measurement of fall-related psychological constructs among independent-living older adults: A review of the research literature. *Aging and Mental Health*, *12*(6), 684–699. https://doi.org/10.1080/13607860802148855

Nesti, A., De Winkel, K., & Bülthoff, H. H. (2017). Accumulation of inertial sensory information in the perception of whole body yaw rotation. *PLoS ONE*, *12*(1), 1–14. https://doi.org/10.1371/journal.pone.0170497

Nigmatullina, Y., Hellyer, P. J., Nachev, P., Sharp, D. J., & Seemungal, B. M. (2015). The neuroanatomical correlates of training-related perceptuo-reflex uncoupling in dancers. *Cerebral Cortex*, *25*(2), 554–562. https://doi.org/10.1093/cercor/bht266

Nooij, S. A. E., Pretto, P., & Bülthoff, H. H. (2018). More vection means more velocity storage activity: A factor in visually induced motion sickness? *Experimental Brain Research*, 1–11. https://doi.org/10.1007/s00221-018-5340-1

Northoff, G. (2016). Is the self a higher-order or fundamental function of the brain? The "basis model of self-specificity" and its encoding by the brain's spontaneous activity. *Cognitive Neuroscience*, *7*(1–4), 203–222. https://doi.org/10.1080/17588928.2015.1111868

Nunan, D., Gay, D., Jakovljevic, D. G., Hodges, L. D., Sandercock, G. R. H., & Brodie, D. A. (2009). Validity and reliability of short-term heart-rate variability from the Polar S810. *Medicine and Science in Sports and Exercise*, *41*(1), 243–250. https://doi.org/10.1249/MSS.0b013e318184a4b1

O'Callaghan, C., Hall, J. M., Tomassini, A., Muller, A. J., Walpola, I. C., Moustafa, A. A., … Lewis, S. J. G. (2017). Visual hallucinations are characterized by impaired sensory evidence accumulation: Insights from hierarchical drift diffusion modeling in Parkinson's disease. *Biological Psychiatry, Cognitive Neuroscience and Neuroimaging*, *2*(8), 680–688.

Okada, T., Grunfeld, E. A., Shallo-Hoffmann, J., & Bronstein, A. M. (1999). Vestibular perception of angular velocity in normal subjects and in patients with congenital nystagmus. *Brain*, *122*(7), 1293–1303. https://doi.org/10.1093/brain/122.7.1293

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia*, *9*, 97–113.

Oswald, W. D., & Roth, E. (1978). *Der Zahlen-Verbindungs-Test (ZVT): Ein sprachfreier Intelligenz-Schnell-Test*. Gottingen.

Parsons, L. M. (1987). Imagined spatial transformations of one's hands and feet. *Cognitive Psychology*, *19*, 178–241.

Parsons, T. D., Larson, P., Kratz, K., Thiebaux, M., Bluestein, B., Buckwalter, J. G., & Rizzo, A. A. (2004). Sex differences in mental rotation and spatial rotation in a virtual environment. *Neuropsychologia*, *42*(4), 555–562. https://doi.org/10.1016/j.neuropsychologia.2003.08.014

Pavlou, M., Davies, R. A., & Bronstein, A. M. (2006). The assessment of increased sensitivity to visual stimuli in patients with chronic dizziness. *Journal of Vestibular Research : Equilibrium & Orientation*, *16*(4–5), 223–231.

Peterka, R. J. (2002). Sensorimotor integration in human postural control. *Journal of Neurophysiology*, *88*(3), 1097–1118. https://doi.org/10.1152/jn.2002.88.3.1097

Peterson, R. A., & Merunka, D. R. (2014). Convenience samples of college students and research reproducibility. *Journal of Business Research*, *67*(5), 1035–1041. https://doi.org/10.1016/j.jbusres.2013.08.010

Pezzulo, G., Donnarumma, F., Iodice, P., Maisto, D., & Stoianov, I. (2017). Model-based approaches to active perception and control. *Entropy*, *19*(6), 1–21. https://doi.org/10.3390/e19060266

Pfeiffer, C. (2015). Multisensory spatial mechanisms of the bodily self and social cognition - a commentary on Vittorio Gallese and Valentina Cuccio. *Open Mind*, *14*, 1–14. https://doi.org/10.15502/9783958570450

Popkirov, S., Staab, J. P., & Stone, J. (2017). Persistent postural-perceptual dizziness (PPPD): a common, characteristic and treatable cause of chronic dizziness. *Practical Neurology*, practneurol-2017-001809. https://doi.org/10.1136/practneurol-2017-001809

Post, R. B. (1988). Circular vection is independent of stimulus eccentricity. *Perception*, *17*(6), 737–744.

Preuss, N., Harris, L. R., & Mast, F. W. (2013). Allocentric visual cues influence mental transformation of bodies. *Journal of Vision*, *13*(12), 1–10. https://doi.org/10.1167/13.12.14.doi

Proctor, R. W., & Vu, K.-P. L. (2006). *Stimulus-response compatibility principles: Data, theory, and application*. Boca Raton (FL).

Purves, D., Augustine, G. J., Fitzpatrick, D., Hall, W. C., LaMantia, A.-S., & White, L. E. (2012). *Neuroscience* (Fifth Edit). Sunderland.

Rabbitt, R. D., Breneman, K. D., King, C., Yamauchi, A. M., Boyle, R., & Highstein, S. M. (2009). Dynamic displacement of normal and detached semicircular canal cupula. *JARO - Journal of the Association for Research in Otolaryngology*, *10*(4), 497–509. https://doi.org/10.1007/s10162-009-0174-y

Ratcliff, R., & Tuerlinckx, F. (2002). Estimating parameters of the diffusion model: Approaches to dealing with contaminant reaction times and parameter variability. *Psychonomic Bulletin and Review*, *9*(3), 438–481. https://doi.org/10.3758/BF03196302

Raudies, F., & Neumann, H. (2013). Modeling heading and path perception from optic flow in the case of independently moving objects. *Frontiers in Behavioral Neuroscience*, *7*, 1–19. https://doi.org/10.3389/fnbeh.2013.00023

Redfern, M. S., Talkowski, M. E., Jennings, J. R., & Furman, J. M. (2004). Cognitive influences in postural control of patients with unilateral vestibular loss. *Gait and Posture*, *19*(2), 105–114. https://doi.org/10.1016/S0966-6362(03)00032-8

Rees, G. (2008). The anatomy of blindsight. *Brain*, *131*(6), 1414–1415. https://doi.org/10.1093/brain/awn089

Riccio, G. E., & Stoffregen, T. A. (1991). An ecological theory of motion sickness and postural instability. *Ecological Psychology*, *3*(3), 195–240. https://doi.org/10.1207/s15326969eco0303

Richardson, J. T. E. (2011). Eta squared and partial eta squared as measures of effect size in educational research. *Educational Research Review*, *6*(2), 135–147. https://doi.org/10.1016/j.edurev.2010.12.001

Rinkenauer, G., Osman, A., Ulrich, R., Müler-Gethmann, H., & Mattes, S. (2004). On the locus of speed-accuracy trade-off in reaction time: Inferences from the lateralized readiness potential. *Journal of Experimental Psychology: General*, *133*(2), 261–282. https://doi.org/10.1037/0096-3445.133.2.261

Roach, N. W., Heron, J., & McGraw, V. P. (2006). Resolving multisensory conflict: A strategy for balancing the costs and benefits of audio-visual integration. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1598), 2159–2168. https://doi.org/10.1098/rspb.2006.3578

Roberts, R. E., Bronstein, A. M., & Seemungal, B. M. (2013). Visual-vestibular interaction: Basic science to clinical relevance. *Advances in Clinical Neuroscience and Rehabilitation*, *13*(5), 8–12.

Rohe, T., & Noppeney, U. (2018). Reliability-weighted integration of audiovisual signals can be modulated by top-down control. *Eneuro*, *5*, 1–20. https://doi.org/10.1523/ENEURO.0315-17.2018

Rokszin, A., Márkus, Z., Braunitzer, G., Berényi, A., Benedek, G., & Nagy, A. (2010). Visual pathways serving motion detection in the mammalian brain. *Sensors*, *10*(4), 3218–3242. https://doi.org/10.3390/s100403218

Roy, J. E., & Cullen, K. E. (2001). Selective processing of vestibular reafference during self-generated head motion. *The Journal of Neuroscience*, *21*(6), 2131–2142. https://doi.org/10.1523/jneurosci.21-06-02131.2001

Salahuddin, L., Cho, J., Gi Jeong, M., & Kim, D. (2007). Ultra short term analysis of heart rate variability for monitoring mental stress in mobile settings. In *Proceedings of the 29th Annual International Conference of the IEEE EMBS* (pp. 4656–4659). Lyon, France. https://doi.org/10.1109/IEMBS.2007.4353378

Salmaso, D., & Longoni, A. M. (1985). Problems in the assessment of hand preference. *Cortex*, *21*(4), 533–549. https://doi.org/10.1016/S0010-9452(58)80003-9

Samaan, C. (2016). Calculation of COPx and COPy. *Personal communication*.

Scherer, H., & Clarke, A. H. (1985). The caloric vestibular reaction in space: Physiological considerations. *Acta Oto-Laryngologica*, *100*(5–6), 328–336. https://doi.org/10.3109/00016488509126556

Schmidt, R. A., & Lee, T. D. (2011). *Motor control and learning: A behavioral emphasis* (Fifth edit). Champaign.

Schneider, W., Eschman, A., & Zuccolotto, A. (2002). *E-Prime: User's guide*. Pittsburgh, PA.

Sears, D. O. (1986). College sophomores in the laboratory: Influences of a narrow database on social-psychology's view of human nature. *Journal of Personality and Social Psychology*, *51*(3), 515–530. https://doi.org/10.1037//0022-3514.51.3.515

Seemungal, B. M. (2014). The cognitive neurology of the vestibular system. *Current Opinion in Neurology*, *27*, 125–132. https://doi.org/10.1097/WCO.0000000000000060

Seemungal, B. M., Green, D. A., Bronstein, A. M., Golding, J. F., & Gresty, M. A. (2009). Autonomic reactivity in "dizzy patients": Motion sickness susceptibility and cardio-vascular and respiratory responses to caloric irrigation. *British Society of Neuro-Otology Meeting.*

Seemungal, B. M., Gunaratne, I. A., Fleming, I. O., Gresty, M. A., & Bronstein, A. M. (2004). Perceptual and nystagmic thresholds of vestibular function in yaw. *Journal of Vestibular Research : Equilibrium & Orientation*, *14*(6), 461–466.

Seriès, P., & Seitz, A. R. (2013). Learning what to expect (in visual perception). *Frontiers in Human Neuroscience*, *7*(October), 1–14. https://doi.org/10.3389/fnhum.2013.00668

Shaikh, A. G., Palla, A., Marti, S., Olasagasti, I., Optican, L. M., Zee, D. S., & Straumann, D. (2013). Role of cerebellum in motion perception and vestibulo-ocular reflex - similarities and disparities. *Cerebellum*, *12*(1), 97–107. https://doi.org/10.1007/s12311-012-0401-7.Role

Shepard, N. T., Janky, K., & Eggers, S. D. Z. (2013). The role of vestibular laboratory testing. In A. M. Bronstein (Ed.), *Oxford textbook of vertigo and imbalance* (pp. 145–156). Oxford.

Shepard, R. N., & Cooper, L. A. (1982). *Mental images and their transformations*. Cambridge.

Shepard, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science, New Series*, *171*(3972), 701–703. https://doi.org/10.1126/science.171.3972.701

Sherrington, C. S. (1907). On the proprio-ceptive system, especially in its reflex aspect. *Brain*, *29*(4), 467–482.

Shumway-cook, A., & Woollacott, M. H. (2007). *Motor control: Translating research into clinical practice* (3rd ed.). Philadelphia.

Singh, R., Chen, F., & Wegener, D. T. (2014). The similarity-attraction link: Sequential versus parallel multiple-mediator models involving inferred attraction, respect, and positive affect. *Basic and Applied Social Psychology*, *36*(4), 281–298. https://doi.org/10.1080/01973533.2014.912583

Singh, T., Perry, C. M., & Herter, T. M. (2016). A geometric method for computing ocular kinematics and classifying gaze events using monocular remote eye tracking in a robotic environment. *Journal of NeuroEngineering and Rehabilitation*, *13*(1), 1–17. https://doi.org/10.1186/s12984-015-0107-4

Smith, P. F., & Zheng, Y. (2013). From ear to uncertainty: vestibular contributions to cognitive function. *Frontiers in Integrative Neuroscience*, *7*(November), 1–13. https://doi.org/10.3389/fnint.2013.00084

Smith, P. F., Zheng, Y., Horii, A., & Darlington, C. L. (2005). Does vestibular damage cause cognitive dysfunction in humans? *Journal of Vestibular Research : Equilibrium & Orientation*, *15*(1), 1–9.

Smith, R. E., Smoll, F. L., & Schutz, R. W. (1990). Measurement and correlates of sport-specific cognitive and somatic trait anxiety: The sport anxiety scale. *Anxiety Research*, *2*(4), 263–280. https://doi.org/10.1080/08917779008248733

Spielberger, C. D. (1983). *Manual for the State-Trait Anxiety Inventory (Form Y)*. Palo Alto, CA.

Squire, R. F., Noudoost, B., Schafer, R. J., & Moore, T. (2013). Prefrontal contributions to visual selective attention. *Annual Review of Neuroscience*, *36*(1), 451–466. https://doi.org/10.1146/annurev-neuro-062111-150439

Staab, J. P., Eckhardt-Henn, A., Horii, A., Jacob, R. G., Strupp, M., Brandt, T., & Bronstein, A. M. (2017). Diagnostic criteria for persistent postural-perceptual dizziness (PPPD): Consensus document of the committee for the classification of vestibular disorders of the barany society. *Journal of Vestibular Research: Equilibrium and Orientation*, *27*(4), 191–208. https://doi.org/10.3233/VES-170622

Stephan, T., Deutschländer, A., Nolte, A., Schneider, E., Wiesmann, M., Brandt, T., & Dieterich, M. (2005). Functional MRI of galvanic vestibular stimulation with alternating currents at different frequencies. *NeuroImage*, *26*(3), 721–732. https://doi.org/10.1016/j.neuroimage.2005.02.049

Stoffregen, T. A. (1986). The role of optical velocity in the control of stance. *Perception & Psychophysics*, *39*(5), 355–360.

Stoffregen, T. A., & Riccio, G. E. (1990). Responses to optical looming in the retinal center and periphery. *Ecological Psychology*, *2*(3), 251–274. https://doi.org/10.1207/s15326969eco0203

Stoffregen, T. A., Yoshida, K., Villard, S., Scibora, L., & Bardy, B. G. (2010). Stance width influences postural stability and motion sickness. *Ecological Psychology*, *22*(3), 169–191. https://doi.org/10.1080/10407413.2010.496645

Stott, J. R. R. (2013). Orientation and disorientation in aviation. *Extreme Physiology & Medicine*, *2*(1), 2. https://doi.org/10.1186/2046-7648-2-2

Surtees, A., Apperly, I., & Samson, D. (2013). Similarities and differences in visual and spatial perspective-taking processes. *Cognition*, *129*(2), 426–438. https://doi.org/10.1016/j.cognition.2013.06.008

Tadi, T., Overney, L. S., & Blanke, O. (2009). Three sequential brain activations encode mental transformations of upright and inverted human bodies: A high resolution evoked potential study. *Neuroscience*, *159*(4), 1316–1325. https://doi.org/10.1016/j.neuroscience.2009.02.012

Tanahashi, S., Ujike, H., Kozawa, R., & Ukai, K. (2007). Effects of visually simulated roll motion on vection and postural stabilization. *Journal of Neuroengineering and Rehabilitation*, *4*, 39. https://doi.org/10.1186/1743-0003-4-39

Task Force of the European Society of Cardiology and the North American Society of Pacing and Electrophysiology. (1996). Heart rate variability: Standards of measurement, physiological interpretation, and clinical use. *Circulation*, *93*(5), 1043–1065.

Taube, J. S. (2007). The head direction signal: Origins and sensory-motor integration. *Annual Review of Neuroscience*, *30*(1), 181–207. https://doi.org/10.1146/annurev.neuro.29.051605.112854

Teichert, T., Ferrera, V. P., & Grinband, J. (2014). Humans optimize decision-making by delaying decision onset. *PLoS ONE*, *9*(3), 1–22. https://doi.org/10.1371/journal.pone.0089638

Teichert, T., Grinband, J., & Ferrera, V. P. (2016). The importance of decision onset. *Journal of Neurophysiology*, *115*(2), 643–661. https://doi.org/10.1152/jn.00274.2015

Thilo, V. K., Kleinschmidt, A., & Gresty, M. A. (2003). Perception of self-motion from peripheral optokinetic stimulation suppresses visual evoked responses to central stimuli. *Journal of Neurophysiology*, *90*(2), 723–730. https://doi.org/10.1152/jn.00880.2002

Tikidji-Hamburyan, A., Reinhard, K., Storchi, R., Dietter, J., Seitter, H., Davis, K. E., … Münch, T. A. (2017). Rods progressively escape saturation to drive visual responses in daylight conditions. *Nature Communications*, *8*(1). https://doi.org/10.1038/s41467-017-01816-6

Townsend, J. T., & Ashby, F. G. (1978). Methods of modeling capacity in simple processing systems. In N. J. Castellan Jr & F. Restle (Eds.), *Cognitive theory (Volume 3)* (pp. 199–239). Hillsdale. https://doi.org/10.1163/_q3_SIM_00374

Tribukait, A., & Eiken, O. (2006). Changes in the perceived head transversal plane and the subjective visual horizontal induced by Coriolis stimulation during gondola centrifugation. *Journal of Vestibular Research : Equilibrium & Orientation*, *16*(3), 105–116.

Trutoiu, L. C., Mohler, B. J., Schulte-Pelkum, J., & Bülthoff, H. H. (2009). Circular, linear, and curvilinear vection in a large-screen virtual environment with floor projection. *Computers and Graphics*, *33*(1), 47–58. https://doi.org/10.1016/j.cag.2008.11.008

Valk, P. J. L., Munnoch, K., & Bos, J. E. (2008). Human performance at sea: Effects on vigilance and complex task performance. In *International Maritime Conference*. Sydney, Australia.

Valko, Y., Lewis, R. F., Priesol, A. J., & Merfeld, D. M. (2012). Vestibular labyrinth contributions to human whole-body motion discrimination. *Journal of Neuroscience*, *32*(39), 13537–13542. https://doi.org/10.1109/TMI.2012.2196707.Separate

van Dam, N. T., Gros, D. F., Earleywine, M., & Antony, M. M. (2013). Establishing a trait anxiety threshold that signals likelihood of anxiety disorders. *Anxiety, Stress and Coping*, *26*(1), 70–86. https://doi.org/10.1080/10615806.2011.631525

van Elk, M., & Blanke, O. (2014). Imagined own-body transformations during passive self-motion. *Psychological Research*, *78*(1), 18–27. https://doi.org/10.1007/s00426-013-0486-8

van Elk, M., Duizer, M., Sligte, I., & van Schie, H. (2017). Transcranial direct current stimulation of the right temporoparietal junction impairs third-person perspective taking. *Cognitive, Affective and Behavioral Neuroscience*, *17*(1), 9–23. https://doi.org/10.3758/s13415-016-0462-z

van Ravenzwaaij, D., Dutilh, G., & Wagenmakers, E.-J. (2012). A diffusion model decomposition of the effects of alcohol on perceptual decision making. *Psychopharmacology*, *219*(4), 1017–1025. https://doi.org/10.1007/s00213-011-2435-9

Van Wassenbergh, S. (2007). butfilt2.

Vandenberg, S. G., & Kuse, A. R. (1978). Mental rotations, a group test of three-dimensional spatial visualization. *Perceptual and Motor Skills*, *47*, 599–604.

Verhaeghen, P. (2014). *The elements of cognitive aging*. Oxford.

Vernon, P. A. (1993). Der Zahlen-Verbindungs-Test Correlates and other trail-making correlates of general intelligence. *Personality and Individual Differences*, *14*(1), 35–40.

Vingerhoets, G., Lannoo, E., & Bauwens, S. (1996). Analysis of the Money Road-Map Test performance in normal and brain-damaged subjects. *Archives of Clinical Neuropsychology*, *11*(1), 1–9. https://doi.org/10.1016/0887-6177(95)00055-0

Voskullen, C., Ratcliff, R., Fennell, A., & McKoon, G. (2017). Diffusion models of memory and decision making. In J. H. Byrne (Ed.), *Learning and memory: A comprehensive reference* (pp. 213–242). Oxford.

Voss, A., Nagler, M., & Lerche, V. (2013). Diffusion models in experimental psychology: A practical introduction. *Experimental Psychology*, *60*(6), 385–402. https://doi.org/10.1027/1618-3169/a000218

Voss, A., Rothermund, K., & Voss, J. (2004). Interpreting the parameters of the diffusion model: An empirical validation. *Memory and Cognition*, *32*(7), 1206–1220. https://doi.org/10.3758/BF03196893

Voyer, D., Voyer, S., & Philip, B. M. (1995). Magnitude of sex differences in spatial abilities: A meta-analysis and consideration of critical variables. *Psychological Bulletin*, *117*(2), 250–270.

Wagenmakers, E.-J., van der Maas, H. L. J., & Grasman, R. P. P. P. (2007). An EZ-diffusion model for response time and accuracy. *Psychonomic Bulletin & Review*, *14*(1), 3–22. https://doi.org/10.3758/BF03194023

Walsh, E. G. (1961). Role of the vestibular apparatus in the perception of motion on a parallel swing. *Journal of Physiology*, *155*, 506–513.

Walther, L. E. (2017). Current diagnostic procedures for diagnosing vertigo and dizziness. *GMS Current Topics in Otorhinolaryngology, Head and Neck Surgery*, *16*, 1–29. https://doi.org/10.3205/cto000141

Warren, W. H., & Kurtz, K. J. (1992). The role of central and peripheral vision in perceiving the direction of self-motion. *Perception & Psychophysics*, *51*(5), 443–454. https://doi.org/10.3758/BF03211640

Wei, K., & Kording, K. P. (2011). Causal inference in sensorimotor learning and control. In J. Trommershauser, K. P. Kording, & M. S. Landy (Eds.), *Sensory cue integration*. Oxford. https://doi.org/10.1093/acprof

Wertheim, A. H. (1994). Motion perception during self-motion: The direct versus inferential controversy revisited. *Behavioural and Brain Sciences*, *17*(2), 293–355.

Wexler, M., Kosslyn, S. M., & Berthoz, A. (1998). Motor processes in mental rotation. *Cognition*, *68*(1), 77–94. https://doi.org/10.1016/S0010-0277(98)00032-8

Winter, D. A. (1995). Human balance and posture standing and walking control during. *Gait & Posture*, *3*(4), 193–214.

Witkin, H. A. (1959). The perception of the upright. *Scientific American*, *200*(2), 50–57.

Wohlschläger, A., & Wohlschläger, A. (1998). Mental and Manual Rotation. *Journal of Experimental Psychology. Human Perception and Performance*, *24*(2), 397–412.

Wolpert, D. M. (2007). Probabilistic models in human sensorimotor control. *Human Movement Science*, *26*, 511–524. https://doi.org/10.1016/j.humov.2007.05.005

Wolpert, D. M., & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nature Neuroscience*, *3*, 1212–1217. https://doi.org/10.1038/81497

Wraga, M., Thompson, W. L., Alpert, N. M., & Kosslyn, S. M. (2003). Implicit transfer of motor strategies in mental rotation. *Brain and Cognition*, *52*(2), 135–143. https://doi.org/10.1016/S0278-2626(03)00033-2

Yakusheva, T. A., Shaikh, A. G., Green, A. M., Blazquez, P. M., Dickman, J. D., & Angelaki, D. E. (2007). Purkinje cells in posterior cerebellar vermis encode motion in an inertial reference frame. *Neuron*, *54*(6), 973–985. https://doi.org/10.1016/j.neuron.2007.06.003

Yakushin, S. B., Raphan, T., & Cohen, B. (2017). Coding of velocity storage in the vestibular nuclei. *Frontiers in Neurology*, *8*, 1–19. https://doi.org/10.3389/fneur.2017.00386

Yardley, L., Gardner, M. R., Bronstein, A. M., Davies, R. A., Buckwell, D., & Luxon, L. M. (2001). Interference between postural control and mental task performance in patients with vestibular disorder and healthy controls. *Journal of Neurology, Neurosurgery, and Psychiatry*, *71*(1), 48–52.

Zacks, J. M., & Michelon, P. (2005). Transformations of visuospatial images. *Behavioral and Cognitive Neuroscience Reviews*, *4*(2), 96–118. https://doi.org/10.1177/1534582305281085

Zacks, J. M., Mires, J., Tversky, B., & Hazeltine, E. (2002). Mental spatial transformations of objects and perspective. *Spatial Cognition and Computation*, *2*, 315–332. https://doi.org/10.1023/A:1015584100204

Zacks, J. M., Rypma, B., Gabrieli, J. D. E., Tversky, B., & Glover, G. H. (1999). Imagined transformation of bodies: an fMRI investigation. *Neuropsychologia*, *37*(9), 1029–1040.

Zacks, J. M., & Tversky, B. (2005). Multiple systems for spatial imagery: transformations of objects and bodies. *Spatial Cognition and Computation*, *5*(4), 271–306. https://doi.org/10.1207/s15427633scc0504

Zaidel, A., Turner, A. H., & Angelaki, D. E. (2011). Multisensory calibration is independent of cue reliability. *Journal of Neuroscience*, *31*(39), 13949–13962. https://doi.org/10.1523/JNEUROSCI.2732-11.2011

Zimmerman, D. W. (1986). Tests of significance of correlation coefficients in the absence of bivariate normal populations. *Journal of Experimental Education*, *54*(4), 223–227. https://doi.org/10.1080/00220973.1986.10806425

Zu Eulenburg, P., Caspers, S., Roski, C., & Eickhoff, S. B. (2012). Meta-analytical definition and functional connectivity of the human vestibular cortex. *NeuroImage*, *60*(1), 162–169. https://doi.org/10.1016/j.neuroimage.2011.12.032