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Review

How is working memory content consciously experienced? The ‘conscious copy’ model of WM introspection

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ABSTRACT

We address the issue of how visual information stored in working memory (WM) is introspected. In other words, how do we become aware of WM content in order to consciously examine or manipulate it? Influential models of WM have suggested that WM representations are either conscious by definition, or directly accessible for conscious inspection. We propose that WM introspection does not operate on the actual memory trace but rather requires a new representation to be created for the conscious domain. This conscious representation exists in addition and in parallel to the actual memory representation. The existence of such a separate representation is revealed by and reflected in the qualitatively different functional characteristics between the actual memory trace and its conscious experience, and their distinct interactions within external visual input. Our model differs from state-based models in that WM introspection does not involve a change in the state of WM content, but rather involves the creation of a new, second representation existing in parallel to the original memory trace.

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1. Introduction

Working memory (WM) refers to short-term maintenance of information in service of goal-directed behavior (e.g. Baddeley, 1992a; Cowan, 1998). In WM, information is stored in an online fashion, allowing its contents to be easily accessed by other cognitive processes. In addition to the storage of perceptual input, WM is also involved in the retrieval of episodic memories from long-term memory (Ericsson and Kintsch, 1995). Some of the behavioral consequences of WM operations occur automatically, without the need for conscious utilization of WM content. For example, WM can automatically guide attention in a visual search context (Soto et al., 2005, 2006). Nonetheless, a key feature of WM is that its content can be consciously accessed, manipulated and examined (i.e. introspected).

Here, we address the question of how such introspection takes place. We will focus particularly on WM operations in the visual domain, i.e. on visual short-term memory (VSTM). While previous research and theoretical discussion has focused on whether WM operations can take place outside of awareness (cf. Hassin et al., 2009), and whether subliminal visual information can reach WM (Rosenthal et al., 2010; Soto and Silvanto, 2014; Soto et al., 2011), here we focus on how visual information can be consciously accessed and experienced, *after* it has been committed to WM. On the basis of recent empirical evidence and theoretical considerations, we propose that we do not consciously experience the actual memory representation. Rather, in order for memory content to be phenomenally experienced, a new representation needs to be created for the conscious domain. This representation, which exists in addition and parallel to the actual memory representation, forms the basis of the conscious experience of memory content. The need to create a separate representation for introspection is a consequence of the distinct functional characteristics and roles of conscious perception and certain aspects of WM.

2. Conventional views of how WM content reaches consciousness

One may argue that in many VSTM tasks, it is not necessary to bring the memory item into conscious experience at all. Memory accuracy is often assessed using forced-choice measures, which do not necessarily require conscious inspection of the memory item. There is ample evidence that forced-choice tasks can be performed on visual stimuli which are outside of conscious experience (Lau and Passingham, 2006; VanRullen and Koch, 2003; Weiskrantz, 1986). This has also been found to be the case for VSTM (Soto et al., 2011). Furthermore, many behavioral consequences of WM occur automatically (for example, attentional guidance (Soto et al., 2005, 2006), and are thus unlikely to require conscious inspection of memory content. However, a key feature of WM is that its content can be consciously scrutinized and manipulated (i.e. introspected). Below we describe and evaluate two influential viewpoints on the relationship between WM content and its conscious experience.

2.1. Viewpoint 1: All WM content is by definition conscious

In the psychological literature, there is a long tradition of equating WM processes with conscious experience (see Fig. 1a). The gist of this view, originating in the 19th century, is that the original memory trace is needed for conscious experience:

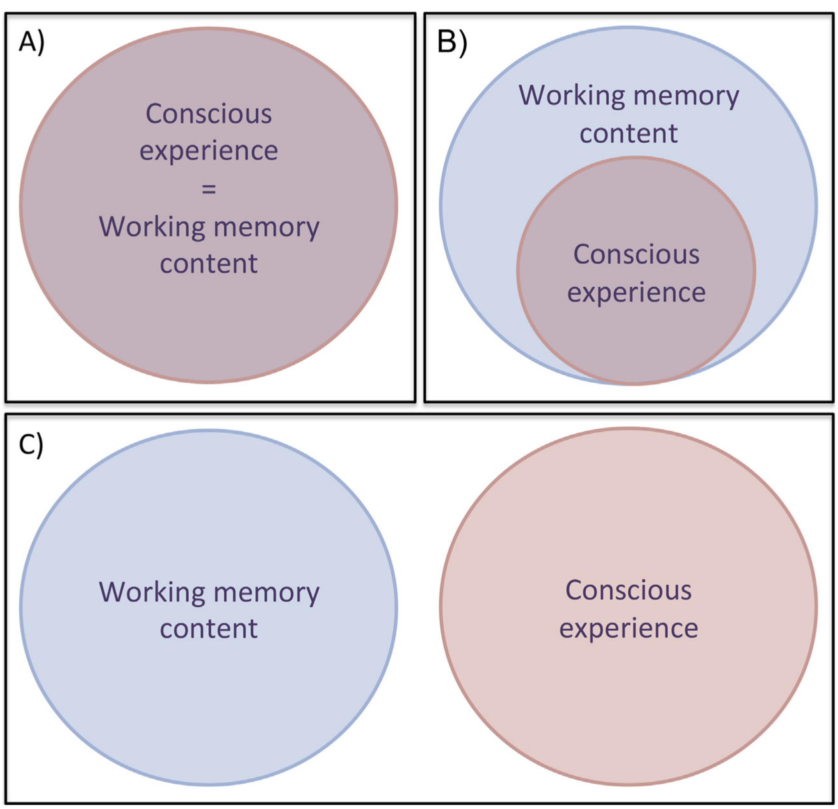

Fig. 1. Possibilities of the relationship between WM content and its conscious experience. The representation of all WM content is reflected by the blue circles, whereas the red circle depicts the representations currently in consciousness: (A) WM content is always conscious. (B) WM content is not automatically conscious, but with the aid of attention, a memory representation can be consciously experienced. The area of overlap between the two circles reflects the zone of direct access. (Note conscious experience is depicted here as part of WM. One might argue that there can be conscious experience outside of WM, but as the figure concerns the conscious experience of WM content, rather than consciousness in general, for reasons of clarity this view is not depicted here.) (C) Our proposal that the actual memory representation is never directly consciously experienced. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

"Without memory no conscious sensation, without memory no consciousness" (Richet, 1886). Almost a century later, Atkinson and Shiffrin (1968) proposed a multi-store model of the memory system consisting of three components: sensory memory, short-term store (STS), and long-term store. The STS resembles the concept of WM in the sense that, apart from passive storage, the information in STS is also used for active processes, like decision-making and problem solving. STS content was proposed to correspond to the contents of conscious experience (Atkinson and Shiffrin, 1971).

Subsequently, Baddeley developed a multiple component model of WM in which a visuospatial and a verbal slave system are controlled by a central executive (Baddeley and Hitch, 1974). Similar to the Atkinson and Shiffrin model, information in certain components of the model was assumed to automatically reach awareness. The earlier versions of his model proposed that all WM input, output, and voluntary operations are conscious (Baddeley, 1992b). Later models introduced the so-called episodic buffer, which plays a particularly important role in feature binding and awareness (Baddeley, 2000).

Furthermore, the study of subliminal processing has demonstrated that the human information processing system is selective as to which elements reach consciousness, and WM has been consistently implicated in theories of consciousness as the mechanism through which this selection takes place. For example, in certain versions of Global Workspace Theory (Baars, 1988), WM serves as a global workspace, the contents of which become conscious experiences (Baars and Franklin, 2003; Baars, 2002).

2.2. Viewpoint 2: WM content remains unconscious until focused attention selects the representation for conscious inspection

The gist of this second influential view is that WM content is not equal to conscious experience, allowing for the possibility that, at any given time, there are items in WM that are not conscious (see Fig. 1b). However, attention can bring the original memory trace into consciousness. The influential theory of Cowan states that WM can be conceived of as a zone of direct access, which can retain an unlimited number of activated representations in parallel, but only representations in the focus of internal attention can be accessed directly (Cowan, 1988). Focused attention is supposedly capacity-limited, with a maximum of four items within the focus of attention at any given time. According to this model, not all WM content is consciously accessible: the corresponding representation needs to be activated and placed within the focus of internal attention for this to occur. Oberauer (2002) developed this model further by introducing an unlimited store of reactivated long-term memory representations, a capacity-limited short-term store (or zone of direct access), and a process of focused attention with a maximal storage capacity of a single item only (Oberauer, 2009, 2002). The key feature shared by both Cowan's and Oberauer's models is that placing the original memory representation in the center of focused attention enables conscious access.

3. Evaluating conventional views in the light of recent evidence

In the following sections, these two models are evaluated in light of recent studies, which have directly examined the relationship between conscious experience and WM.

3.1. Working memory can operate upon unconscious content

In Viewpoint 1, conscious experience is equated with WM content. Therefore, empirical evidence demonstrating dissociations between WM content and conscious experience would refute this position. In fact, a number of studies have found such dissociations, either by using subliminal stimuli or by embedding implicit spatial patterns in supraliminal stimuli (Hassin et al., 2009; Pan et al., 2013; Rosenthal et al., 2010; Soto et al., 2011). For example, Hassin et al. (2009) demonstrated that WM processes required for pattern extraction, such as the keeping track of objects' sequential spatial positions, can take place incidentally without participants' awareness of them. Subsequently, in a series of experiments Soto et al. (2011) consistently demonstrated above-chance performance on a delayed discrimination task, even when participants reported no conscious awareness of the memory cues at encoding. The finding that subliminal stimuli can be encoded into and maintained in VSTM, and that a range of WM operations can take place without participants' awareness, contradicts views which equate WM with consciousness.

3.2. WM contents and their conscious experience can be dissociated

According to Viewpoint 2, WM content is not always consciously experienced. However, when it is (via allocation of attention to the WM representation), the content of the conscious experience is based on the actual memory trace (Cowan, 1988). Consistent with the view that the actual memory representation is consciously accessed, measures of memory performance and confidence generally tend to correlate quite strongly (Rademaker et al., 2012; Vandenbroucke et al., 2014), which is intuitive, given that conscious access to invalid information would have little behavioral relevance.

Nevertheless, there is evidence to indicate that metacognition of higher-level cognitive processes is sometimes inaccurate (see e.g. Nisbett and Wilson, 1977; Koriat, 2007 for review). Furthermore, a recent study by Scott et al. (2014) showed the reverse phenomenon: above chance metacognitive performance in the absence of decision accuracy, which they labeled 'blind insight'. Thus metacognition and actual objective task performance do not always go hand-in-hand and this has been shown to be case also for WM.

In a recent study by Bona et al. (2013), WM accuracy and conscious experience of the memory item (as assessed with vividness ratings) were found to be differently affected by the presentation of a distracter during the retention period. Memory accuracy for the orientation of a Gabor patch was impaired by both visible and invisible distracter stimuli that differed from the original memory cue by 40°, but not by smaller angle differences. In contrast, memory vividness was reduced by distracters of all orientations, but only when they were rendered invisible. This double dissociation suggests that introspection is a distinct process from the use of memory content in order to perform a forced-choice behavioral task. The key finding was the existence of a condition in which VSTM accuracy was impaired whilst memory vividness was unaffected. If introspection was merely a "conscious window" into the actual memory trace, then manipulations which affect the integrity of that trace should *always* affect its conscious experience. However, this was not the case.

The findings described above seem inconsistent with the view that introspection involves direct and accurate access to the actual memory trace. Rather, the double dissociation suggests that memory maintenance and introspection rely on separate representations. One might argue that dissociations between memory accuracy and introspection result from the latter requiring additional attentional processes, rendering it more vulnerable to distracter interference. However, even if this is the case, it does not explain the double dissociation found by Bona et al. (2013), and specifically the condition in which the memory trace was impaired but vividness was unaffected, because in all views in which introspection is directly based on the memory trace, anything that affects the integrity of the WM trace should also affect its conscious experience. In a recent study, memory accuracy and WM experience were also dissociated when confidence ratings rather than memory vividness were used as a measure of VSTM experience (Bona and Silvanto, 2014).

3.3. *VSTM and its conscious experience interact with external visual input in a qualitatively different fashion*

Consciousness of sensory information generally takes the form of a phenomenally experienced image, even when the experience is internally generated from WM or long-term memory. Such an 'internal conscious percept' is referred to as a mental image (Kosslyn, 1994). As mental imagery can be defined as conscious experience of memory content, studies on its cognitive and neural underpinnings are relevant to the question of how WM content is phenomenally experienced.

Conscious experience of WM content in the form of visual imagery is known to interfere with performance in various concurrently performed visual tasks. The Perky effect refers to the phenomenon in which mental imagery hampers the perception of simultaneously presented visual information (Perky, 1910). For example, when participants are asked to form a mental image of a previously presented feature (the mental imagery thus reflecting VSTM content), the mental image impairs the detection of an external item presented in the same location of visual space, regardless of their featural similarity. This effect resembles interference by an external visual mask and is believed to be primarily sensory in nature, mimicking a reduction in target energy, rather than merely resulting from attentional effects (Craver-Lemley and Reeves, 1987). Thus the consciously experienced memory content has an inhibitory relationship with external input at the level of the visual representation. The functional role of this masking effect may be to suppress visual input in order to prevent the mental image from being overwritten (Craver-Lemley and Reeves, 1992). Furthermore, a suppressive effect also occurs in the other direction. As discussed earlier, Bona et al. (2013) found that unconscious visual distracters interfered with reported vividness of WM, even when the distracter matched memory content. The key point is that internally generated percepts and external visual input have a mutually inhibitory relationship, likely to reflect competition for access to consciousness.

While mental imagery suppresses external input, the impact of WM on the encoding of incoming visual information is more complex. Attention is allocated to stimuli which match VSTM content, at the cost of stimuli which are incongruent with the items held in VSTM (e.g. Carlisle and Woodman, 2011; Downing, 2000; Gayet et al., 2013; Pan and Soto, 2010; Soto et al., 2005). Furthermore, access to consciousness is facilitated for perceptual inputs which match VSTM content, whereas consciousness for incongruent input is inhibited (Pan et al., 2013). Thus, VSTM has an interactive relationship with external input; it acts as a 'gatekeeper', guiding attention and conscious access on the basis of current memory states. These effects are also sensory in nature, occurring in the visual cortex where the VSTM storage takes place (Soto et al., 2007). In addition, while subliminal visual input impairs conscious experience of WM content even when the two are congruent (Bona et al., 2013), it has no such effect on VSTM accuracy; if anything, there is a slight facilitation of WM performance (Silvanto and Soto, 2012). This dissociation indicates that conscious experience of WM and the actual memory content are based on representations with very different functional characteristics.

4. Emerging view: WM storage and introspection of WM content are based on distinct representations

The behavioral evidence reviewed above challenges the view that WM content and its conscious experience are intrinsically coupled. First, demonstrations of unconscious WM functions are inconsistent with the view that WM content needs to be inherently conscious (Hassin et al., 2009; Soto et al., 2011). Second, the double dissociation between WM content and its conscious experience is inconsistent with the view that the latter is directly based on the actual memory representation (Bona and Silvanto, 2014; Bona et al., 2013). Third, consciously experienced memory content has a different impact on external visual input than WM content not being introspected (Craver-Lemley and Reeves, 1992; Pan et al., 2013; Perky, 1910), indicating that the consciously experienced representation has different functional characteristics than the WM trace on which it is based.

To account for these findings, we propose a novel view according to which WM representations are intrinsically unconscious, and introspecting them requires the creation of a new representation into the conscious domain (see Fig. 1c). This "conscious copy" has different functional properties from the underlying WM representation, which gives rise to the dissociations described above. Contrary to the positions depicted in Fig. 1a and b, the actual memory trace is never consciously experienced, and thus cannot be the subject of introspection. Wilful manipulation of the conscious copy can however feed back to the original memory trace, allowing memory contents to be updated and modulated.

Prior models have suggested mental imagery and VSTM to be distinct in the sense that they are different cognitive operations. However, in these models, both processes act on a single representation and rely on the same memory store (Baddeley and Logie, 1999; Logie, 2011, 2003, 1995). In our view, read-out during introspection involves the creation of a new representation which exists independently and in parallel to the actual memory trace (see Fig. 2a). Moreover, a key feature of the conscious copy is that, even though it reflects memory content, its functional properties are more similar to those of other types of conscious percepts (whether internally generated or externally induced) than to those of memory representations.

5. The need for separation: Distinct functions and characteristics of WM and conscious perception

We propose that the need for a separate representation for introspection of WM content is a consequence of the distinct functional characteristics and roles of conscious perception and certain functions of WM. After external input has been analyzed by the visual system, WM maintains relevant information and keeps it readily available for cognitive systems for guiding behavior. One important function of WM is to allocate attention to and bias the processing of incoming visual information. For example, as was discussed above, WM facilitates access to consciousness for matching perceptual inputs (Pan et al., 2013) and allocates attention to matching external stimuli (Soto et al., 2006). WM thus acts as a "gatekeeper" of visual perception (see Fig. 2b).

In contrast, during conscious experience (whether internally generated or externally induced), the interaction between different sources of visual information serves a different function. A critical aspect of conscious perception is that the source of the percept needs to be ascertained; confusion of internal and external sources of information results in the experience of hallucinations, as is the case in psychosis (Frith and Done, 1988). Therefore, when any kind of visual information is consciously perceived, contamination from other sources needs to be avoided. In the case of WM introspection,

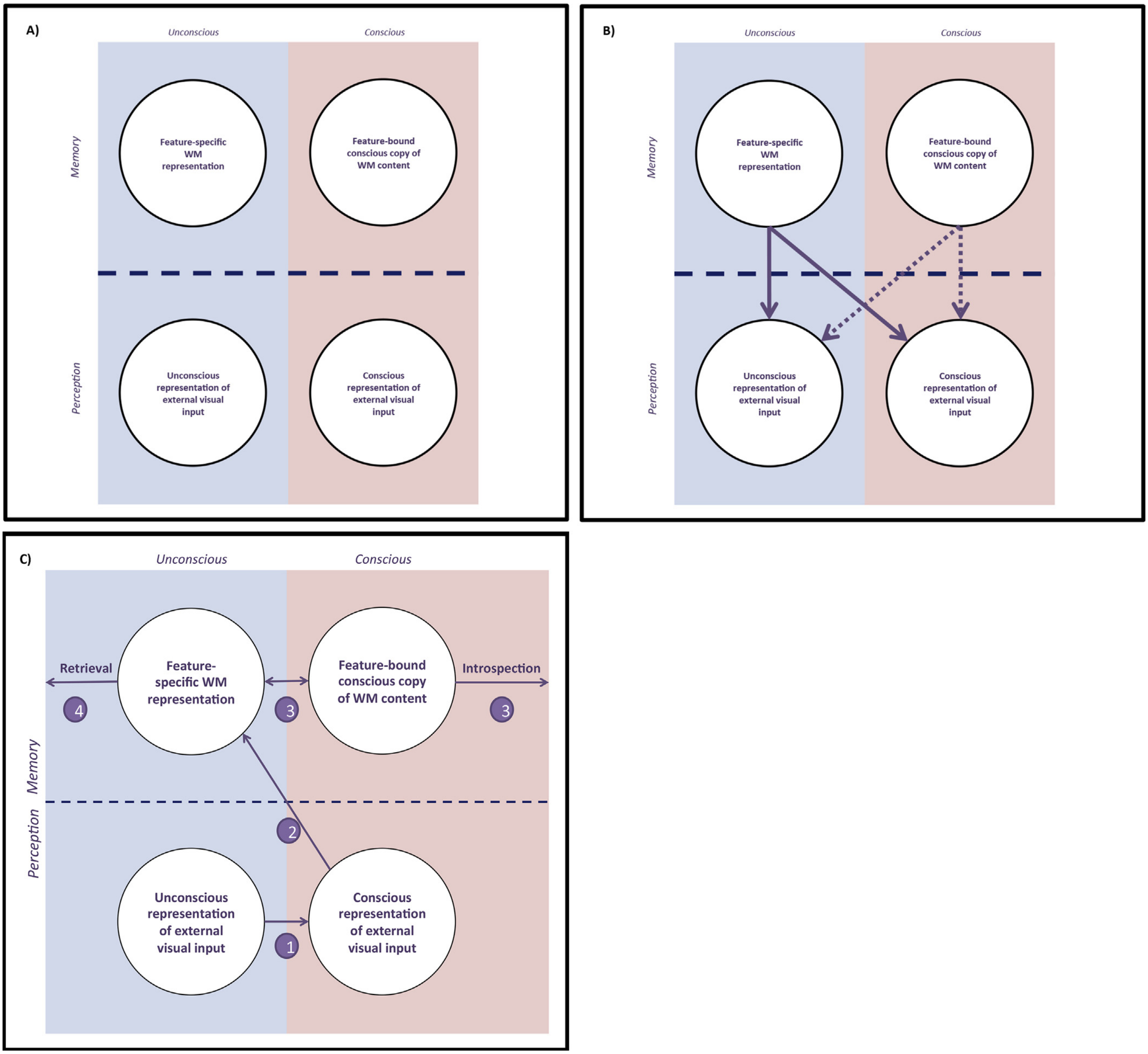

Fig. 2. "Conscious copy" model of WM introspection. The main gist of this model is that the conscious experience of WM content is not based on the actual memory representation. Rather, a new representation is created for the conscious domain (A). VSTM content and the conscious representation of that content interact differentially with external input. Conscious experience of VSTM content suppresses the encoding of concurrent visual information (dashed lines), whether matching or not (i.e. Perky effect). In contrast, WM content can facilitate the encoding and awareness of matching visual input (solid lines) (B). According to the model we present here, information passes through the following stages in a standard WM task (C): (1) The external, to-be-remembered stimulus is consciously experienced. There is some evidence that suggests that unconscious features of external input may reach consciousness (Soto and Silvanto, 2014), however in most circumstances information will first be consciously experiences before it enters into WM store. (2) The item is then transmitted to the WM store, at which point it is no longer conscious. Thus, it passes from phenomenal awareness to an unconscious form, which is consistent with Cowan's model (1988, 1998) according to which not all WM content is consciously accessible. (3) If introspection is required, a conscious copy of the original WM content is created for this purpose. Any manipulations carried out on the conscious copy can then be stored in unconscious WM (either as a new memory trace or by modifying the original memory trace). (4) If introspection is not required, retrieval without introspection based on the original memory representation can take place (e.g. in forced-choice tasks).

where the conscious experience is internally generated, intrusion of external input needs to be prevented. To accomplish this, incoming visual information is suppressed whenever an internal percept is experienced (see Fig. 2b). Conversely, when the aim is to consciously perceive the external world, internally generated percepts must be inhibited from reaching awareness. Thus the "conscious copy" is a representation competing for conscious access, rather than a representation guiding visual processing at the early levels of processing.

The proposed idea of a 'conscious copy' of a WM representation is somewhat analogous to what in the science of motor behavior is known as the efference copy; a copy of an original motor program is created and fed back to the system as a means to predict the sensory consequences of the programed, to–be-executed action (Cullen, 2004). This allows the observer to distinguish between incoming sensory information as a consequence of voluntary behavior, and sensory information from external sources. The purpose of the copied WM content might be similar, in the sense that it allows the system to distinguish between content within the memory systems that is externally generated, such as visual sensory input, and internally generated content, such as mental imagery. In fact, defective functioning of efference copies has been suggested to play a role in psychosis and schizophrenia (Brebion et al., 2008; Simons et al., 2006).

6. WM: Conscious or unconscious?

Of course, not all WM processes occur unconsciously. When we actively rehearse information in order to facilitate retention, we are performing this action with full awareness. Indeed, consciousness may be important for working memory for the same reasons that sensory input may benefit from conscious experience. Issues such as flexibility, integration of information, and dealing with input of great complexity have been put forward to explain the need for consciousness (see Seth, 2009 for review), and they may apply to WM as well. Furthermore, since much of the research described here has been performed with simple visual stimuli, we cannot exclude that although awareness might not be a prerequisite for specific WM operations on these stimuli, consciousness is necessary when the stimuli and the associated WM processes are more complex. However, multiple higher-level cognitive functions (i.e. visual search, word recognition, reading, and arithmetic) that rely on WM functions such as its executive component (e.g. Fürst and Hitch, 2000) have been shown to operate successfully in the absence of consciousness (Maljkovic and Martini, 2005; McKone, 1995; Sklar et al., 2012). More research on higher-level WM processes is required to fully establish the extent of implicit WM for higher-level cognitive operations, but the above studies provide the first promising results to indicate that conscious experience is not always a prerequisite, not even for semantic processes.

It is important to point out however that even when WM operations are conscious, this does not imply that that they require conscious access to *WM content*, and vice versa. For example, successful extraction of patterns from visual stimuli and their encoding into WM appears to require conscious experience of the memory cue (Hsieh and Colas, 2012), but no conscious experience of engaging into pattern extraction and maintenance (Hassin et al., 2009). Furthermore, subliminally presented orientation information can be encoded into WM when participants are knowingly engaged in WM encoding and maintenance (Soto et al., 2011). WM involves various components, some of which might be conscious in any given situation while others are unconscious. In this context, a key distinction needs to be made between awareness of WM operations (cf. Hassin et al., 2009), awareness of stimuli to be encoded (Soto et al., 2011), and awareness of the actual memory content once it has been encoded into WM. Previous research has shown that the first two of these can occur unconsciously. Here we focus on the latter issue and propose that the actual WM content is never consciously experienced, and that its conscious inspection requires the creation of a new representation in the conscious domain.

7. Feature-bound introspection versus feature-specific WM

The dissociation between WM content and its conscious experience entails that the conscious copy is in some respects different from the original memory trace, and that the copying process is, in that sense, imperfect. This may partly result from introspection involving bound percepts whereas WM can operate at the level of features. A clue to this issue is offered by the study of Bona et al. (2013), in which subjective vividness of WM content suffered from any type of (unconscious) visual distracter, whereas WM accuracy was impaired only when its orientation was sufficiently different from the memory item. The lack of sensitivity to individual stimulus features speaks in favor of viewing the conscious copy as a feature-bound percept. In fact, it seems impossible to imagine any single feature (for example, the orientation of a line) fully independently of other features, such as luminance or contrast, which provide surface properties to the percept. Our conscious experience, whether internally generated or externally induced, always consists of whole objects or scenes, rather than of individual features. In contrast, WM maintenance can be feature-specific and can rely on orientation and spatial frequency channels in the early visual cortex (e.g. Magnussen et al., 1991). Of course, WM can also store conjunctions of features and whole objects. Nevertheless, the point is that, unlike the conscious copy, it can operate at the level of individual features.

A possibility arising from this is that introspection does not require the creation of a new copy for conscious inspection, but rather, involves accessing an object-level representation which may not incorporate all aspects of feature-level memory traces. In this view, the key issue is not whether a representation is consciously accessed, but rather its featural complexity. However this view cannot account for all the evidence discussed here. For example, facilitation of visual processing by working memory (as discussed in Section 5) is also found when WM content involves representations at object-level. In the study by Soto et al. (2005), WM maintenance of a colored circle facilitated the detection of matching objects and impaired the detection of incongruent objects. In contrast, conscious experience (in the form of imagery) of objects held in WM always inhibits concurrent visual input, regardless of congruency (cf. Perky effect discussed in Section 3.3). Thus, it appears to be the extent of conscious experience rather than the complexity of the memory representation that explains the functional differences.

8. A new perspective on the link between VSTM, imagery and visual awareness: Summary of the “conscious copy” model (see Fig. 2c)

Below we summarize the main features of the proposed ‘conscious copy’ model on WM introspection. Some of its aspects are based on recent empirical evidence, others on theoretical considerations. We acknowledge that some components require empirical testing and that certain aspects may be considered speculative. However, its main gist, namely that WM content during the maintenance period in WM tasks is fundamentally unconscious, and that its introspection requires the creation of a conscious copy of the WM content, is supported by empirical evidence.

The model has the following tenets:

1. **The content of WM during maintenance is unconscious. For WM content to be introspected, a new representation must be created for the conscious domain**. Without entering the conscious domain, WM can act in an automatic fashion to guide behavior (e.g. by directing attention). The “conscious copy” enables phenomenal awareness of memory content and is required for willful inspection and manipulation of memory content.
2. **The WM trace and the conscious copy are independent representations,** such that they can be differentially influenced and modulated (e.g. by distracting information). Once the conscious copy has been created, disruption to the original memory trace does not compromise introspection. The outcome of any conscious manipulation can feed back to and modulate the original memory trace. Separate representations are needed due to the different functional demands of conscious perception and WM guidance of visual processing.

3. **The WM representation and the conscious copy interact differently with incoming visual information.** WM acts as a gatekeeper, guiding the encoding of incoming sensory information. It can either enhance or suppress the detection of external signals, depending on congruency and current goals. In contrast, the conscious representation has a mutually suppressive relationship with external sensory input, which is required to be able to adequately distinguish internal and external percepts.
4. **WM can be feature-specific; the conscious representation involves a bound object.** We cannot consciously experience an individual feature in isolation of other features. Thus, the conscious copy is by definition of feature-bound objects or conjunctions, perhaps based on the episodic memory of having perceived the stimulus at the beginning of the trial.

9. Neural underpinning of the "conscious copy": Different cognitive representations imply different neural representations

Separate mental representations need to be supported by distinct neural representations. The behavioral studies discussed above have identified quantifiable aspects consistent with current neuroscientific knowledge that can help to link our cognitive model to neurophysiology. For example, the impact of visual input on WM depends on featural similarity (e.g. cue-distracter orientation difference), consistent with low-level orientation channels being involved (see also Magnussen et al., 1991). In contrast, conscious experience WM content is impaired by all distracting visual input, independently of its featural similarity with memory content (Bona et al., 2013). This shows that VSTM maintenance can engage feature-specific mechanisms (such as orientation channels in early visual cortex), whereas the conscious copy does not seem to be sensitive to such factors, indicating a qualitative difference in the structure of the two representations.

Below we will give an overview of the neuroscientific evidence on the neural signature of WM retention and mental imagery. Unfortunately, there is currently a lack of neuroscientific evidence comparing neural activity associated with WM retention and WM introspection, and the few studies that have attempted this might have issues that complicate their interpretation, as will be discussed below.

According to *sensory recruitment hypothesis*, maintained sensory information is a form of "lingering" neural activity in sensory brain areas involved in perceptual processing (D'Esposito, 2007; Pasternak and Greenlee, 2005). Indeed, early visual cortex has been shown to be involved in VSTM (van de Ven et al., 2012), and the reactivation of modality-specific sensory brain regions has been linked with memory retrieval (Barsalou, 2008). Recent multivariate analyses of neuroimaging data have further supported this view by showing that the way in which early visual areas represent visual information is very similar across VSTM and visual perception (Harrison and Tong, 2009; LaRocque et al., 2013; Lewis-Peacock and Postle, 2012; Serences et al., 2009).

In order to investigate the neural underpinnings of state-based models of WM, Lewis-Peacock and Postle (Emrich et al., 2013; LaRocque et al., 2013; Lewis-Peacock and Postle, 2012; Lewis-Peacock et al., 2012; Riggall and Postle, 2012) performed multivariate analyses during the delay period of a WM task in brain areas responsive to the currently attended as well as the currently unattended memory item. They found no evidence for WM content being represented in frontal and parietal brain areas which showed a load-dependent, sustained delay-period increase in brain activity. In contrast, decoding from sensory brain areas responsive to the initial visual stimulus, but not activated during the delay period, did yield above chance decoding accuracies, which were load-dependent and correlated with participants' behavioral memory precision (Emrich et al., 2013; Riggall and Postle, 2012). This suggests that parietal attentional mechanisms guide the read-out of memory content from occipital visual areas.

In addition, Lewis-Peacock and Postle (2012) found increased decoding accuracies for attended versus unattended items, which they interpret as evidence for an active neural representation of WM content, which is within the focus of attention (FoA). In contrast, the unattended WM content could not be decoded from the BOLD signal, providing neural evidence for distinct states within WM. The "inactive" neural state associated with the unattended item could be reactivated when that item re-entered the FoA. As these studies did not assess conscious experience of the retro-cued item, they do not directly speak to the issue of how WM content is introspected. Specifically, it is not known whether retro-cueing evoked not only an "attended" state but also conscious experience of the memory item. Further studies using this paradigm, combined with manipulations/assessment of the level of conscious experience of the retro-cued items, could be used to examine neural representations associated with consciously experience memory content and to test our model directly.

If VSTM content and its conscious experience in the form of imagery rely on the same underlying representation, then one would expect them to have similar characteristics at the neuronal level. For example, if there is a neuronal code that is associated with stimulus maintenance (e.g. a specific firing pattern of orientation-selective neurons when maintaining the orientation of a grating), then that neural code should be associated also with imagery. Indeed, neuroimaging work has shown that mental imagery and visual perception activate overlapping areas in the early visual cortices (e.g. Barsalou, 2008; Kosslyn and Thompson, 2003; Kosslyn et al., 1995). Furthermore, overlapping neural structures for VSTM and imagery have been identified (Slotnick et al., 2012), and a recent study showed that the content of VSTM, imagery, and visual perception can be decoded from the pattern of brain activity in early visual areas (Albers et al., 2013).

From this, one might conclude that VSTM and imagery rely on the same regions and even neural representations in the visual cortex. As discussed in previous sections, the behavioral evidence is inconsistent with this view, as the impact of VSTM and imagery on external input differs. From the neural perspective, there is a confound in the literature which may explain this neural overlap, as pointed out by Kaas et al. (2010). In most studies on mental imagery, participants are instructed to imagine (a manipulated version of) a stimulus presented at the start of each trial. The neural correlates of imagery as observed in these studies might therefore reflect memory for the stimulus on which visual imagery is based, i.e. the original memory trace, rather than being a neural marker of the mental image, and thus its phenomenal experience, per se. To overcome this confound, Kaas et al. (2010) used a motion imagery paradigm in which participants based their mental image on static stimuli. Kaas et al. (2010) found increased activation in hMT+/V5, whereas critically the BOLD signal in early visual areas was decreased during imagery (indicating that external visual input was suppressed during mental imagery, as discussed above). In contrast, those early visual areas show an increased BOLD signal during WM maintenance of motion information (Goebel et al., 1998; Slotnick et al., 2005). This is consistent with our proposal that the conscious representation involves a bound object (thus more likely to be represented at higher extrastriate levels) whereas memory content can be feature-specific.

Even if the same visual areas are involved in mental imagery, VSTM and visual perception, the neural code may still differ across the three processes. The neural representation underlying each of them is still under debate. With respect to VSTM, sustained neuronal activity in feature-selective neurons of prefrontal areas was traditionally believed to represent WM content during retention (Goldman-Rakic, 1995). This hypothesis has been challenged and various alternatives have been suggested. Rather than the fixed selectivity of single neurons, the relative activity across a neuronal population could represent memory content (Jun et al., 2010). This population code has been suggested to be static (i.e. the population activity that codes for the memory stays the same throughout the entire delay) or dynamic (i.e. the population code corresponding to the memory dynamically changes over the duration of the delay interval) (Sreenivasan et al., 2014). Alternatively, synaptic changes rather than metabolically inefficient action potentials could be a way to encode WM content, and in this context presynaptic residues of calcium ions have been proposed to facilitate reactivation of the original, encoded signal (Mongillo et al., 2008). All of these potential ways in which the brain could represent WM content during the maintenance interval rely on empirical data from human and monkey prefrontal areas. Only the static population coding concept is supported by neuroimaging data acquired in human visual brain regions, namely by those fMRI studies that have applied multivariate analysis techniques as described earlier. Nevertheless, as there is no empirical evidence on the matter, we cannot rule out the possibility that any of the suggested neural mechanisms play a role in visual cortices as well. Resolving the question of whether and how the neural bases of VSTM content and mental imagery differ requires studies which compare VSTM and imagery in a non-confounded manner; the current evidence is inconclusive.

10. Multiple memory states/processes versus multiple memory representations

In various memory models, sometimes referred to as state-based models (Larocque et al., 2014), memory representations can be in different states of attentional and access prioritization. For example, in Oberauer's (2002) model, a subset of items can be held in the region of direct access, and within this region, one item can be selected for processing by the focus of attention and is consciously accessible. In other words, focused attention selects the WM representation for conscious inspection and allows WM content conscious access.

According to these models, there is a single representation for a specific WM content (i.e. the actual memory trace), which can be either in a conscious or unconscious state. Attention serves as the window granting us conscious access, in other words, placing the memory trace in a state in which it is consciously accessed. Introspection thus involves observation of current WM content, exactly as it is held in memory. This is analogous to passively sitting in front a window looking at what happens behind it, without altering what is being observed.

The most fundamental difference to state-based models is that in our model the introspection of WM content does not involve a change in the state of the memory trace, but rather the creation of a new representation *which co-exists together with the original WM trace*. Introspection is rather like a painting of the scene that is occurring behind the window; it captures most of that scene, but is not identical to it. The proposed conscious copy is not a precise duplicate of the original working memory trace, but rather contains qualitatively different information; namely feature-bound visual information placed within a context. Cognitive processes operating on the original memory trace thus utilize different information from those operating on the conscious copy. The experimental evidence presented in the sections above is in accordance with the existence of multiple memory representations. For example, the findings of Bona et al. (2013), Bona and Silvanto (2014) suggest that the conscious experience and the actual memory trace co-exist. To accommodate existing state-based models, one would need to postulate that a memory item can exist in two states at the same time.

Alternatively, one could consider forced-choice WM performance and introspection as reflecting two distinct processes operating on a single representation in the occipital cortex, implemented by parietal attentional mechanisms. In other words, instead of two distinct representations, there might be two different ways of accessing a single representation. This would be analogous to finding a book in a library through different search methods. For example, the books may be organized by call number, but at the same time the librarian may possess a list which contains information about the content and location of each book. The critical point about the library analogy is that, no matter through which route one finds the book, it is unreadable if its pages are missing. In other words, regardless of the search method, the original book needs to be found; disruption of the original memory representation will lead to failure to access, whatever the search strategy. What speaks against this possibility is the finding that introspective ratings can be unaffected even when the actual memory trace is impaired (Bona et al., 2013). One could argue that the distracter causing this effect could have interfered with the process of the WM maintenance rather than with the actual memory trace itself. However, we consider this explanation unlikely, as the orientation-specific distracter effect indicates that the distracter operates on the same perceptual channels which are also involved in initial encoding (Magnussen et al., 1991), and which thus represent the visual content.

Furthermore, there is much neuropsychological evidence indicating that internally generated conscious experience (in the form of visual imagery) relies most heavily on regions such as the inferotemporal cortex and can even function in the absence of early visual areas (see Bartolomeo, 2002 for review), inconsistent with the idea of lower level occipital regions acting as the source of "read-out" for introspection. However, the prior literature has mainly focused on imagery based on long-term memory; whether this applies to WM introspection remains to be directly tested.

The library analogy is interesting in that it raises the question of what exactly is a memory representation. Let us say the librarian's records contain a summary of each book. Albeit perhaps incomplete and condensed, the librarian's list would nevertheless be a version of the information contained in the book; thus it could be described as a second representation, or copy, of that information. In this view, numerous representations of the original book would exist. The essence of our model is that such multiple representations exist in working memory.

Finally, one may ask whether there is need for another model of WM function. In our view, the growing evidence for dissociation of WM and consciousness (see Soto and Silvanto, 2014, for review) raise unavoidable questions about how consciously experienced memory contents might differ from those that are not being introspected. Furthermore, the evidence that VSTM content and its conscious experience interact with external visual input in a qualitatively different manner indicates that these differences are of functional significance. There is thus need for a model which specifically address the subjective, introspective aspects of WM.

There is always a danger of new cognitive models being analogies at best and semantics at worst, if not accompanied by testable predictions and proposals of putative neural underpinnings. Is our model guilty of this? We would argue this not to be the case because our model generates specific predictions that are different from those derived from other theories. As stated above, the key feature of our proposal which sets it apart from prior models is the *co-existence of two representations—the memory trace and the conscious copy*. This leads to the prediction that both the conscious copy and the actual memory trace should differ in their neural bases (for example in terms of their cortical locus or their signature of oscillatory activity), when manipulation and assessment of conscious experience of WM content is built into the study design. In contrast, state-based models would not predict the existence of multiple memory representations.

11. Conclusion

We propose that for WM content to be introspected, a new representation must be created for the conscious domain. The WM representation and the conscious representation exist in parallel, such that once the "conscious copy" has been created, the two representations can be independently influenced and modulated. Willful manipulation of memory content occurs via the conscious copy and its outcome can feed back to and modulate the original memory trace. Separate representations are needed due to the different functional demands of conscious perception and WM guidance of visual processing. During conscious experience, confusion of internally generated and externally induced percepts must be avoided; thus consciously experienced memory content must have an inhibitory relationship with other items competing for conscious access. In contrast, nonconscious WM content acts as a gatekeeper, sometimes facilitating the encoding of incoming sensory information.

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