VISUAL COGNITION
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How visual working memory handles distraction: cognitive mechanisms and electrophysiological correlates

Heinrich R. Liesefeld[a,b], Anna M. Liesefeld[a], Paul Sauseng[a], Simon N. Jacob[c] and Hermann J. Müller[a]

[a]Department Psychologie, Ludwig-Maximilians-Universität München, München, Germany; [b]Munich Center for Neurosciences – Brain & Mind, Ludwig-Maximilians-Universität München, München, Germany; [c]Department of Neurosurgery, Technische Universität München, München, Germany

ABSTRACT
The ability to selectively encode relevant information (*filtering ability*) is crucial to make best use of the severely limited space that *visual working memory (VWM)* provides. This review considers why filtering ability is important, how it is measured, and it discusses how filtering might be implemented computationally at the cognitive and neuronal level. Based on theoretical considerations, we explore the possibility that filtering ability involves not only the suppression of irrelevant, but also the enhancement of relevant information – functions that might be implemented by different brain mechanisms; and we review behavioural and electrophysiological data in light of the various resulting model versions. We also highlight that filtering is better understood as coordinated brain network activity, rather than being the function of a single region. Broadcasting of control signals from prefrontal cortex appears critical in upholding information in posterior cortical areas in the absence of distractors. The very same ability might also support selective processing of relevant information in the presence of distractors. These ideas provide a novel explanation for the relation between filtering ability and VWM capacity and thereby (re-)establish a central role of filtering ability in general VWM functioning.

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VWM is a heavily restricted commodity (in terms of a flexible resource or as a quantised capacity; Cowan, 2001; Liesefeld & Müller, 2019a; Luck & Vogel, 2013; Ma, Husain, & Bays, 2014). Typically developed individuals can hold on average (with a reasonable resolution) only about three to four individual objects in mind (or even fewer, see Liesefeld, Liesefeld, & Müller, 2019). Given this severe capacity limitation and the important role VWM generally plays in cognition, the ability to selectively encode only relevant information into VWM (*filtering ability*) is a crucial cognitive function.[1]

In particular, there is strong variation in VWM capacity across individuals and this variation appears related to general intelligence, academic performance and many other important skills and life outcomes (e.g., Cowan et al., 2005; Fukuda, Vogel, Ulrich, Awh, 2010; Luck & Vogel, 2013; Unsworth, Fukuda, Awh, & Vogel, 2014). As reviewed below, a large part of this variation might actually stem from variation in filtering ability (e.g., Fukuda & Vogel, 2009, 2011; Liesefeld, Liesefeld, & Zimmer, 2014; McNab & Klingberg, 2008; Vogel, McCollough, & Machizawa, 2005). At first, it seems surprising that a simple measure such as VWM capacity is predictive of general cognitive performance and life outcomes. Consider, though, that rather than being just a passive store, VWM acts more like a versatile buffer for all kinds of mental operations working on visual information held temporarily, whether this information is/was physically present or retrieved from long-term memory (Aagten-Murphy & Bays, 2018; Fukuda & Woodman, 2017; Liesefeld & Müller, 2019a; Liesefeld, Fu, & Zimmer, 2015; Tsubomi, Fukuda, Watanabe, & Vogel, 2013). On this background, filtering ability in VWM is the general ability to selectively process visual information from the present moment or the (recent and more distant) past.

In the lab, VWM filtering ability can be examined in a task as exemplified in Figure 1a (Fukuda & Vogel, 2009; Liesefeld et al., 2014). In this example, participants are to store the colour of the squares (*targets*)

CONTACT Heinrich R. Liesefeld Heinrich.Liesefeld@psy.lmu.de Department Psychologie and Munich Center for Neurosciences – Brain & Mind, Ludwig-Maximilians-Universität München, München, Germany

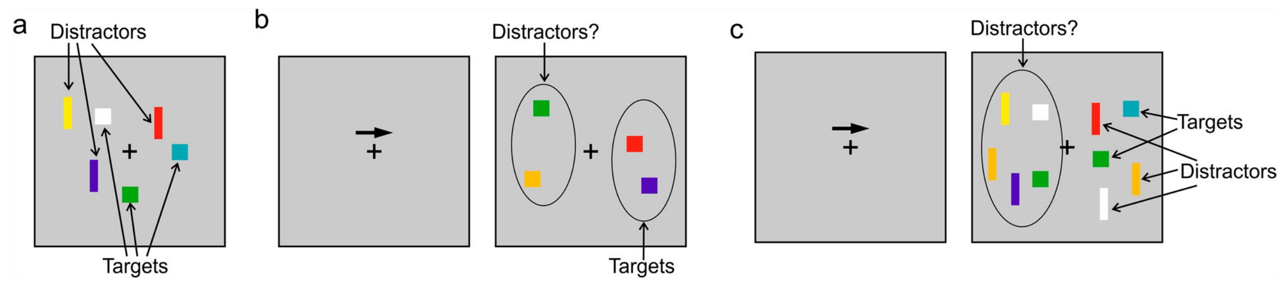

Figure 1. Three examples of typical VWM displays used to examine distraction during VWM encoding. In (a) participants are to remember the colours of the squares and ignore the rectangles. In (b) participants are to remember the colours of the squares on the right side of the display (as indicated by the preceding arrow) and ignore the squares on the left side. This type of task is used to extract the contralateral delay activity (CDA) by subtracting activity measured ipsilateral to the relevant side (*here:* over right electrode sites) from activity measured contralateral to the relevant side (*here:* over left electrode sites). The objects on the irrelevant side were originally introduced to balance visual stimulation, but they might also act as distractors (therefore the question mark). In (c) participants are to remember only the colours of the squares on the right side of the display.

and ignore the rectangles (*distractors*). Of course, various different combinations of features that discriminate targets and distractors (*here:* shape or, more, specifically, aspect ratio) and that have to be remembered (*here:* colour) can be and have been used. After a retention interval, memory is probed, most typically by having observers detect a change in one of the targets.

Cognitive mechanisms to implement filtering

In principle, filtering can be implemented in a number of ways (Figure 2): The probably most obvious and typically focused-on possibility is that all physically available information funnels into working memory automatically and filtering ability consists of keeping irrelevant information out (*distractor suppression*). This idea was most vividly illustrated by Awh and Vogel (2008), who suggested that VWM is an exclusive night club and filtering ability is comparable to a bouncer tasked to keep unwanted guests (i.e., irrelevant information) out. Alternatively, one could argue that VWM is not such an attractive place for stimuli outside and filtering ability is more comparable to nightclub staff selectively approaching wanted guests in the street. However, even the most desperate night-club owners have to solve a selection problem: they will need to decide which kind of customer they want to actively invite entering the club (and who better to leave out). There is no a-priori reason to exclude the possibility that both functions are actually in place: wanted guests are actively invited and unwanted guests actively discouraged from entering a moderately attractive night club (for similar ideas, see, e.g., Dube, Emrich, & Al-Aidroos, 2017; Feldmann-Wüstefeld & Vogel, 2019; Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005; Salahub, Lockhart, Dube, Al-Aidroos, & Emrich, 2019). By assuming that the different ways of selecting information (inviting and discouraging) are performed by different actors (brain mechanisms), we will explain some apparent discrepancies in the literature.

Both filtering functions can be seamlessly implemented in a biased-competition framework (Desimone & Duncan, 1995). The general idea of biased competition is that each stimulus has a certain, inherent affordance to be processed (its bottom-up saliency; general inclination to visit nightclubs); and the various stimuli therefore "compete" for access to VWM (see also Bundesen, Habekost, & Kyllingsbaek, 2011). Indeed, stimulus saliency has huge effects on VWM performance (Constant & Liesefeld, 2019). However, the visual system is not simply at the mercy of the environment, but saliency can be modulated by task goals and experiences (inviting and discouraging) and this top-down modulation might be based on the stimuli's attributes or their locations. Thus, top-down modulations bias bottom-up saliency signals, resulting in a map (i.e., a spatial representation of the visual scene) coding for behavioural relevance at each location (*priority map*). Notably, the priority map is the result of a massively parallel processing of the whole scene before attentional or VWM resources are committed (i.e., it is a pre-attentive representation guiding the deployment of scarce cognitive resources).

Within this framework, there are two general classes of distractor handling: down-weighting

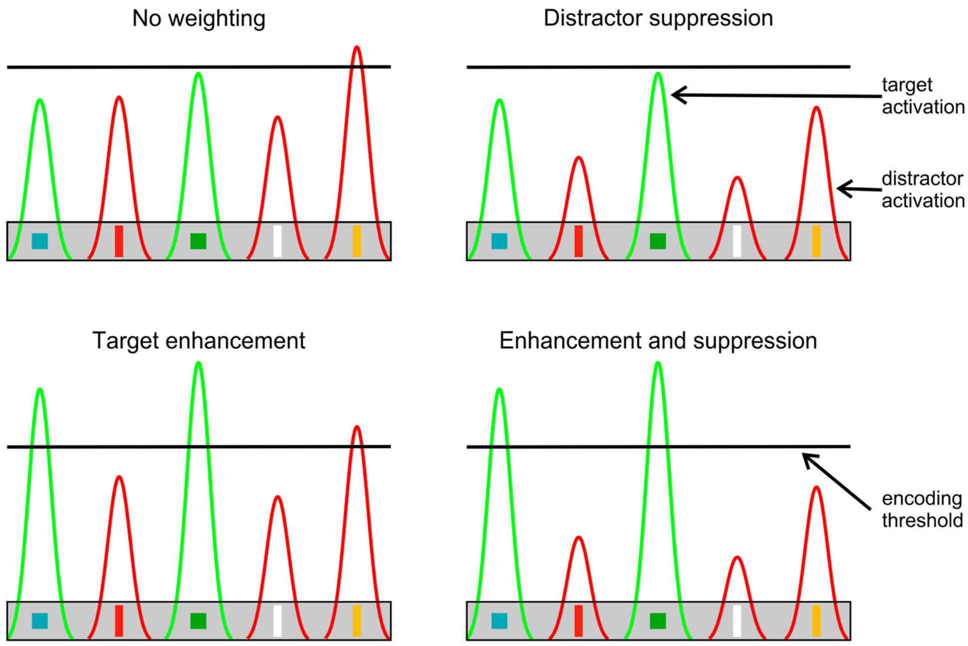

Figure 2. Potential implementations of filter mechanisms within a biased-competition framework. Each curve represents activation on the priority map (motivation to go out, in terms of the night-club metaphor of VWM), with green curves standing for targets and red curves for distractors. If no (top-down) weighting is applied, differences in activation are purely due to bottom-up features of the items, such as (uncontrolled) variation in saliency (this inter-item variation is fixed across panels in this example). Filtering can be implemented by distractor suppression, target enhancement or both. A threshold is depicted for those who believe in threshold models of VWM encoding (slot models); it marks the amount of activation required to enter VWM. Note that neither the activations nor the threshold represent VWM slots (which are not illustrated here), but only the mechanism deciding whether a particular item is encoded into VWM; competition between items could be implemented, for instance, as an activation-dependent race towards a fixed threshold that terminates once VWM is filled or the information is no longer present (see Bundesen et al., 2011). Alternatively, activation could also directly translate to how much of a flexible resource is assigned to each individual object. Note how targets must be actively encouraged to enter the night club, and how the distractor on the right (the orange bar) will be stopped from entering only when actively discouraged by the bouncer.

distractors and up-weighting targets. Both mechanisms can achieve a bias towards processing the targets, because both will increase relative target priority and decrease relative distractor priority (see Figure 2).

Despite influencing the same outcome (relative target priority), up- and down-weighting might be influenced by various, fundamentally different mechanisms. It could be a direct increase/decrease in the gain of task-relevant/-irrelevant features (Olivers, Peters, Houtkamp, & Roelfsema, 2011; Wolfe, 2007) or of all features within a dimension (Liesefeld, Liesefeld, Pollmann, & Müller, 2018; Liesefeld & Müller, 2020). Alternatively or in addition, filtering might be performed in a fashion that maximises the difference between target and distractor gain, rather than the target gain directly (Geng & Witkowski, 2019), or that (also) improves the precision of weighting the specific target feature (sharpening of tuning functions, Ling, Liu, & Carrasco, 2009). In any case, the outcome would be the same: targets attain the edge over distractors in terms of relative (target) priority and are therefore selected for encoding into VWM. VWM limitations might be genuinely due to restricted storage space or emerge from limitations of (some of) these mechanisms.

Note that target up-weighting and distractor down-weighting might be difficult to disentangle: that more suppression (down-weighting) might have to be applied when there are more objects to be suppressed is immediately apparent. In a biased-competition framework, the up-weighting of targets, too, might depend on the number of distractors: with more distractors, chances increase that one of them (e.g., due uncontrolled variation in saliency) attains a higher priority than a target and is therefore processed instead of the target (Zehetleitner, Koch, Goschy, & Müller, 2013). To counteract the stochastic increase in maximal distractor priority with the number of distractors, the targets would have to be up-weighted in accordance with the number of distractors.

Electrophysiology provides online measures of filtering performance

An obvious approach to measure filtering ability is to compare behavioural performance on trials with and without distractors. However, behaviour does not provide the most straight-forward measure of filtering ability for various reasons: on the one hand, distractor processing would harm performance only if VWM capacity is exceeded, so that distractors displace relevant information (or reduce the precision of relevant information to a degree that a change is no longer detected). On the other hand, it has been shown that distractors are typically not processed when VWM is filled with relevant information (Konstantinou, Beal, King, & Lavie, 2014; Lavie, 2005). Thus, in situations that make distractor processing likely (below capacity), encoding distractors might have no or only little effect on performance.

Furthermore, it is well established that individuals differ in the amount of relevant information they can store in VWM. Capturing this interindividual variation with behavioural indices might also be difficult: if a given individual's performance is not affected by adding distractors to displays containing an intermediate number of targets (e.g., 3), this might be due to the individual's good filtering ability (not letting distractors in) or its high storage space (letting distractors in still leaves enough space for all three targets).

Electrophysiology provides more direct measures of how much irrelevant information has entered VWM. In addition to avoiding the problem with behavioural measures illustrated above, electrophysiological measures have the additional advantage of tracking the evolution of VWM content during a trial (Balaban & Luria, 2017; Liesefeld & Zimmer, 2013; Vogel et al., 2005; see also section on Delayed Distractor Suppression below). An influential electrophysiological measure of filtering performance was derived from the contralateral delay-activity (CDA) component of the event-related potential (ERP) elicited by lateralised memory displays, as shown in Figure 1b and c. The CDA is a negativity contralateral to the hemifield in which remembered (or processed) items are shown, and its amplitude tracks the number of items that are concurrently kept in VWM (Feldmann-Wüstefeld, Vogel, & Awh, 2018; Vogel & Machizawa, 2004; this component is also known as sustained posterior contralateral negativity, SPCN: Robitaille et al., 2010; Robitaille & Jolicoeur, 2006; or contralateral negative slow wave: Klaver, Talsma, Wijers, Heinze, & Mulder, 1999; for a review, see Luria, Balaban, Awh, & Vogel, 2017). It is best isolated by subtracting delay activity ipsilateral of the relevant side from delay activity contralateral to the relevant side. As CDA amplitude is affected by processed distractors as well as processed targets, it can be exploited to derive a measure of distractor processing (Arend & Zimmer, 2012; Fukuda & Vogel, 2009; Liesefeld et al., 2014; Vogel et al., 2005). This is achieved by comparing the CDA between displays with and without distractors. Any extra activity on distractor-present compared to distractor-absent trials likely reflects distractor processing. Thus, *unnecessary storage* of distractor information is reflected in the difference in CDA amplitude for displays with distractors minus displays without distractors that contain the same number of targets.

Based on pioneering work by Vogel et al. (2005), distractors in CDA studies are typically spatially intermixed with the targets and defined by one of their features (Figure 1a,c). Alternatively, distractors can be defined by their position in space (e.g., at pre-cued positions) or time (e.g., objects presented during retention). In fact, even the objects on the irrelevant side of standard lateralised VWM displays (that Vogel & Machizawa, 2004, introduced originally to balance visual stimulation rather than to distract) can be conceived as distractors (Figure 1b). This raises the question how much of the CDA measured in the standard task design is actually influenced by "distractor" processing. Independently manipulating the number of objects on the relevant and irrelevant side of a lateralised VWM task and separately analysing ipsi- and contralateral delay activity, Arend and Zimmer (2011) found that the number of objects on the irrelevant side modulated delay activity ipsilateral to the targets (contralateral to the distractors) only for a memory load of one. Thus, if there is not much competition for VWM space anyway (only one target), individuals probably spare the effort of blocking irrelevant information from the other side of the display (see also Konstantinou et al., 2014; Lavie, 2005).

Using the same distractor definition in lateralised VWM displays (Figure 1b), another measure of distractor processing was suggested by Sauseng et al. (2009). Suppression of unwanted information is thought to be related to increases in alpha activity (e.g., Bonnefond & Jensen, 2012; Klimesch, Sauseng, & Hanselmayr, 2007; Roux & Uhlhaas, 2014; but see Foster & Awh, 2019). Sauseng et al. indeed found an increase in induced alpha with an increase in the number of distractors on the irrelevant side (that goes along with an increase in memory load on the relevant side) in a typical lateralised VWM task (Figure 1b). In line with common VWM capacity estimates, this alpha activity levelled off at three items. Furthermore, when manipulating the number of targets and distractors independently in a follow-up experiment (similar to Arend & Zimmer, 2011), Sauseng et al. found that induced lateralised alpha power mainly tracks the number of distractors. In line with a functional role of alpha, repetitive transcranial magnetic stimulation (rTMS) at parietal sites in the alpha frequency range increased performance when applied ipsilateral to the targets (thus potentially suppressing the distractors) and decreased performance when applied contralateral to the targets (thus potentially suppressing the targets). This effect was stimulation-site and frequency specific to 10 Hz (alpha) rTMS at parietal sites and did not occur with 15 Hz (beta) rTMS at parietal sites or 10 Hz rTMS at centroparietal sites. Recently, very similar findings have been reported by Riddle et al. (2020). Compared to arrhythmic rTMS, parietal stimulation in the alpha frequency range ipsilateral to targets (i.e., contralateral to distractors) increased VWM capacity.

Despite the similarity in design, the findings of Sauseng et al. (2009) and Arend and Zimmer (2011) seem incompatible at first: Sauseng et al.'s alpha activity increased with the number of distractors for all load conditions (within capacity), whereas the delay activity of Arend and Zimmer was sensitive to the number of distractors only when VWM load was low. This might indicate that induced oscillatory activity and ERPs tap into different aspects of VWM storage and filtering. One possibility is that one reflects the actual VWM storage and the other the weighting of targets and/or distractors.

In line with different roles for event-related delay activity and induced alpha, Fukuda, Mance, and Vogel (2015) observed that the two electrophysiological correlates of VWM processing are dissociable and explain unique portions of interindividual variance in behaviourally measured VWM capacity even in a task without distraction (see also de Vries, van Driel, & Olivers, 2017; Hakim, Feldmann-Wüstefeld, Awh, & Vogel, 2019; van Driel, Gunseli, Meeter, & Olivers 2017).

Chain of events in distractor handling

Processing of distractor information in VWM as measured in parietal activity is only the end result of (failed) distractor handling and likely depends on outcomes from earlier processing stages. Thus, unnecessary storage is not the reason for, but rather a consequence of individual filtering (in)ability. Various cognitive processes are involved in successful filtering and, even though the focus of research has been on unnecessary storage (the end result), electrophysiological markers have been identified for some of these precursors. Electrophysiology is particularly suited to reveal such chains of events, because it provides the high temporal resolution necessary to differentiate the various sub-processes involved in a given task and gain information about their relative timing and, consequently, about the likely causal relationships (Liesefeld, 2018).

The temporal dynamics of various events involved in successful VWM filtering were investigated by Liesefeld et al. (2014): searching for ERP components sensitive to distractor presence, they identified a posterior distractor-related activity peaking at around 230 ms after onset of the stimulus array, likely signalling the presence of distractors (*distractor-detection component*). The amplitude of this positive component was increased when distractors were present relative to pure-target displays. The latency of the distractor-detection component was predictive of both the strength and the latency of a subsequent distractor-related activity over frontal electrode sites peaking at 265 ms, likely reflecting the initiation of an active filtering process (*pre-frontal bias signal*). The strength of this pre-frontal signal, in turn, was predictive of filtering success as measured in subsequent, persistent delay activity (unnecessary storage). Both the distractor-detection component and the prefrontal bias signal were sensitive to the presence of distractors, but not modulated by the number of distractors, indicating that they reflect cognitive processes involved in triggering distractor handling, but not the up- or down-weighting of individual objects (which should be load-dependent).

Based on this spatio-temporal ERP pattern and the observed correlation between ERP components (i.e., the amplitude and/or latency of one ERP component predicted the amplitude of a subsequent component measured at other electrode sites), Liesefeld et al. (2014) argued that filtering during VWM encoding involves the following chain of cognitive events: (i) the presence of distractor features is detected by (accordingly tuned[2]) posterior areas; next, (ii) this information is communicated to prefrontal areas, where, in turn, (iii) filtering is initiated, resulting in the avoidance of distractor processing in posterior areas where VWM representations reside (e.g., D'Esposito & Postle, 2015). The neurocognitive mechanisms reflected by the distractor-detection component and the prefrontal bias signal complement each other as PFC has no direct access to visual information and visual posterior areas cannot interpret visual input with respect to task rules; therefore only together can prefrontal and posterior areas detect the presence of distractors and initiate the appropriate reaction (see also Lara & Wallis, 2015; Salazar, Dotson, Bressler, & Gray, 2012).

The central role of a prefrontal bias signal in VWM processing fits well with the well-examined relation between executive control and prefrontal-lobe function (Bari & Robbins, 2013; Corbetta & Shulman, 2002; Miller & Cohen, 2001), in particular, the role of PFC in filtering task-irrelevant information and controlling distractor suppression (Bichot, Heard, DeGennaro, & Desimone, 2015; Egner et al., 2008; Shimamura, 2000). In fact, it would be highly surprising if any type of cognitive control did not involve prefrontal cortical areas and if any component emerging in posterior areas (e.g., induced alpha or the P_D, see below) did reflect executive control *per se*. Likewise, prefrontal theta activity, rather than posterior alpha activity, has been associated with cognitive control processes (e.g., Sauseng, Griesmayr, Freunberger, & Klimesch, 2010).

Liesefeld et al.'s (2014) data provide further insight into how interindividual variation in filtering performance determines variation in measured VWM capacity (Awh & Vogel, 2008): the various electrophysiological measures of cognitive processes involved in distractor handling – namely, latency of distractor detection, amplitude of the prefrontal bias signal and amount of unnecessary storage – all predicted VWM capacity as measured on trials without distractors. Given the intercorrelations of the components, one wonders how they mutually mediate the relation to VWM capacity. For example, is the relation between prefrontal bias signal and behaviourally measured VWM capacity mediated by unnecessary storage? In contrast to this intuitive hypothesis, a re-analysis of the Liesefeld et al. (2014) data using path analysis indicated that the prefrontal bias signal is most directly related to VWM capacity and mediates the correlation between VWM capacity and the other two components (Emrich & Busseri, 2015). Thus, the prefrontal bias signal might reflect a process at the core of interindividual variability in filtering ability and VWM capacity.

The functional role of the prefrontal cortex

The potential important role of the prefrontal bias signal for VWM capacity and filtering ability calls for more detailed investigations into the nature of the cognitive process this signal reflects. It is often assumed that PFC is the storage site of VWM representations (D'Esposito & Postle, 2015; Goldman-Rakic, 1987; Miller & Cohen, 2001; Baddeley, 2003). This hypothesis is based on observations of persistent delay activity in prefrontal neurons that is specific to the remembered stimulus (e.g., Levy & Goldman-Rakic, 2000) and is less influenced by task-irrelevant information (Miller et al., 1996; Rainer et al., 1998; Katsuki & Constantinidis, 2012; Suzuki & Gottlieb, 2013). Furthermore, PFC lesions result in severe VWM deficits (Fuster & Alexander, 1971; Levy & Goldman-Rakic, 2000; Voytek & Knight, 2010).

More recently, an intense and yet unsettled debate has spun as to whether prefrontal delay activity reflects VWM storage per se or "merely" the control signal responsible for upholding information in more posterior areas (Christophel et al., 2017; Curtis & D'Esposito, 2003; D'Esposito & Postle, 2015; Lara & Wallis, 2015; Riley & Constantinidis, 2016). In other words, active frontal involvement might be needed to uphold information even in the absence of distractors. In line with our speculations above, upholding information might work via target enhancement. That is, upholding information and filtering (by target enhancement) would (in part) rely on the same mechanism implemented in prefrontal areas, namely drawing (and keeping) wanted guests in our moderately attractive night club called VWM.

There is indeed neuronal evidence that prefrontal areas counteract the encoding of distractor information by target enhancement. Jacob and Nieder (2014) and Jacob, Stalter, and Nieder (2016) found that populations of single neurons in the PFC of rhesus monkeys trained to resist interference in a visual working-memory task transiently encoded distractors (in contrast to Miller et al., 1996; Rainer et al., 1998) and then quickly restored target information that was no longer physically present. By contrast, single neurons in ventral intraparietal cortex robustly encoded target information throughout. Of note, the strength of restored target information in PFC was predictive of task performance, arguing more in favour of a role of PFC in target enhancement, rather than in distractor suppression. Parthasarathy et al. (2017, 2019) also reported a significant impact of distractors on coding of target information in the monkey PFC. Using machine-learning techniques, they found that presentation of distractors morphed the population code of the memorized target stimulus (i.e., decoders trained to decode the target from the pre-distractor epoch perform very poorly when tested on the post-distractor epoch).

Neuronal evidence for distractor suppression?

An ERP component potentially reflecting distractor suppression (P_D) can be measured using displays in which only distractors are lateralised and targets are presented on the midline (Gaspar & McDonald, 2014; Hickey, Di Lollo, & McDonald, 2009; Jannati, Gaspar, & McDonald, 2013). Objects on the midline (*here:* targets) will not contribute any lateralised activity, so that the difference wave between electrodes contralateral minus ipsilateral to the distractors isolates distractor-related activity and the P_D component in particular. Being the first to isolate the P_D in a VWM task, Feldmann-Wüstefeld and Vogel (2019) indeed found evidence of distractor suppression: In particular, a P_D emerged whose amplitude was modulated by the number of distractors; furthermore, across participants, P_D amplitude correlated with VWM capacity measured in a task without distractors. These findings indicate that distractors are actively suppressed in VWM tasks and that the ability to efficiently suppress distractors contributes to VWM capacity per se.

Further evidence for a role of distractor suppression – and the P_D in particular – comes from a visual-search study (where the P_D is usually examined). Gaspar et al. (2016) presented a salient distractor on some trials of an easy (pop-out) visual search task (*additional-singleton task*; for recent reviews on this paradigm, see Chelazzi et al., 2019; Gaspelin & Luck, 2018, 2019; Liesefeld & Müller, 2019b; van Moorselaar & Slagter, 2020). Of note, P_D amplitude again correlated with VWM capacity. It is remarkable that VWM capacity is predicted even by filtering ability measured in a classical attention task (visual search; see also Luria & Vogel, 2011), given that the two types of task may appear to differ substantially in their requirements, and connecting the two paradigms (e.g., via the biased-competition framework as done here) opens up interesting avenues for future research aimed at understanding the specific mechanisms involved in filtering in both paradigms.

Fukuda and Vogel (2009) cued the location of an upcoming search target and then used the dot-probe technique to determine where attention was 100 ms after search-display onset. In particular, they analysed the ERP elicited by task-irrelevant dot-probe stimuli at either the target or distractor positions. As stimuli (*here:* the dot-probes) occurring at attended locations produce higher P1/N1 amplitudes, the amplitude differences for probes at target vs. distractor positions was taken to reflect the efficiency of attention allocations. This measure was also predictive of VWM capacity. In line with Feldmann-Wüstefeld and Vogel (2019), they interpreted this finding as showing that low-capacity individuals are less able to handle distraction. However, given that the employed measure quantified the difference in attentional enhancement between target and distractor positions, it is equally plausible to assume that the relationship with VWM capacity is due to the ability to enhance targets.

Further evidence for a role of distractor suppression in VWM filtering comes from a set of experiments by Allon and Luria (2017). They found that cueing the distractor locations reduces distractor costs only if distractor locations change from trial to trial or when location cueing is coupled with a temporal warning cue. They concluded that VWM filtering can be implemented via suppression of distractor locations, but only if filter settings are reactivated shortly before distractor onset. In a follow-up ERP study, Allon and Luria (2019) differentiated between target and distractor processing using a similar technique as described above for Fukuda and Vogel (2009). In particular, they also probed attention allocations toward distractor and target locations and found that successful filtering resulted in decreased attention allocation towards distractors, rather than increased attention allocation towards the targets.

Given the evidence for distractor suppression reviewed in this section, it is important to reiterate that distractor suppression and target enhancement are not mutually exclusive, so that evidence for the one does not rule out the other. It is also important to point out that the degree to which suppression or enhancement are involved likely depends on the specific circumstances. In Allon and Luria (2019), for example, participants only received information about distractor locations and not about target locations, so that they did not get the chance to enhance processing at target locations in advance. Also, clustering many distractors in one region of the display in Feldmann-Wüstefeld and Vogel (2019) or having identical distractors (Vissers, Gulbinaite, van den Bos, & Slagter, 2017) might promote specific and particularly efficient grouping- or region-based suppression mechanisms (see, e.g., Goschy, Bakos, Müller, & Zehetleitner, 2014; Sauter, Liesefeld, & Müller, 2019; Sauter, Liesefeld, Zehetleitner, & Müller, 2018).

Finally, it is worth noting that the P_D component Feldmann-Wüstefeld and Vogel (2019) and Gaspar et al. (2016) focused on is only a relatively recently discovered and not yet well-validated component. Also, there is dispute regarding its functional interpretation, with some evidence suggesting that it might be related to target enhancement, rather than to distractor suppression (Livingstone, Christie, Wright, & McDonald, 2017; see also Kerzel & Burra, 2020; but see Gaspelin & Luck, 2019).

Delayed distractor suppression

An interesting aspect of the delay-activity pattern as reported by Liesefeld et al. (2014) is that, in an early period, delay activity did not discriminate between targets and distractors. Rather, its amplitude reflected the total number of objects during an early time window (around 290–350 ms after memory-display onset) and decreased for distractor-present trials only later. This might indicate that distractors initially entered VWM, but were suppressed only later. This initial distractor processing can be avoided (in young, but not in old adults) by pre-cueing the target positions (Schwarzkopp, Mayr, & Jost, 2016). Further evidence for delayed distractor suppression comes from Fukuda and Vogel (2011). Following up on their earlier study described above (Fukuda & Vogel, 2009), they showed that the relationship between attention allocation towards non-targets and VWM capacity changes depended on when attention was probed: this correlation occurred only for probes presented 100 ms after search-display onset, but not for probes presented 50 ms or 150 ms after onset. This indicates that the filtering process they measured does not generally differ between high- and low-capacity individuals, but that individuals differ in the time it takes them to implement filtering. This raises the interesting possibility that variation in filtering ability and the related variation in VWM capacity reflects variation in temporal efficiency, rather than in some absolute resource.

In any case, the observation of delayed suppression and the observed effects of pre-cueing (Allon & Luria, 2017, 2019; Schwarzkopp et al., 2016) add another interesting layer to the question of distractor handling: filtering ability might be implemented by preparing for upcoming distraction or by reacting to distraction that is already taking place. These two types of distractor handling are referred to as pro- vs. reactive control (Braver, 2012; Geng, 2014; Visser, Driel, & Slagter, 2016), and they might be implemented by fundamentally different, but complementary mechanisms. Based on a comparison between results from Liesefeld, Liesefeld, Töllner, and Müller (2017) and other studies on distraction in visual search (e.g., Gaspar & McDonald, 2014; Jannati et al., 2013), Liesefeld and Müller (2019b), for example, argued that pro-active control is often implemented by a selective weighting of feature dimensions in favour of target processing. This weighting can happen long before the display comes up, if target and distractor features are known in advance. Re-active control might come into play when pro-active control is not sufficient and might be implemented by suppressing the specific distractor locations on each trial (as reflected by the P_D component reviewed above; Gaspar & McDonald, 2014; Gaspelin & Luck, 2018, 2019; Liesefeld et al., 2017). Note though, that this relation between pro-active control and feature-based filtering on the one and re-active control and space-based filtering on the other hand might be due to idiosyncrasies of the typical filtering tasks (Figure 2c): object positions are unpredictable, whereas the features discriminating targets and distractors are predictable.

Concurrent target enhancement and distractor suppression

There is convincing recent evidence for parallel distractor suppression and target enhancement influencing VWM capacity. In addition to the findings discussed above, namely that parietal brain activity can be associated with suppression of distracting information, de Vries and colleagues have demonstrated slow oscillatory activity in the theta and delta frequency range over prefrontal areas to be involved in prioritisation of target information in VWM (de Vries, van Driel, Karacaoglu, & Olivers, 2018; de Vries, Savran, van Driel, & Olivers, 2019; de Vries, Slagter, & Olivers, 2020). This is well supported by recent findings suggesting prefrontal theta phase controlling posterior neuronal activity (Berger et al., 2019). The idea that prefrontal theta activity is involved in target prioritisation/enhancement while posterior alpha activity reflects a mechanism of distractor suppression is supported by a recent study providing causal evidence for these parallel mechanisms (Riddle et al., 2020): rTMS was used to entrain alpha or theta oscillations. When alpha activity was enhanced at parietal brain areas processing distractors, an increase of VWM capacity was observed (similar to the findings reported by Sauseng et al., 2009). In addition, Riddle and colleagues showed that VWM capacity was also enhanced when prefrontal cortex (PFC) was stimulated at theta frequency. In contrast to that, prefrontal alpha or posterior theta rTMS led to decreased VWM performance. This supports the idea of posterior alpha activity (over distractor processing brain regions) being associated with suppression of distractors, while at the same time prefrontal theta activity is responsible for the enhancement of target information; and both processes contribute to VWM capacity (Sauseng & Liesefeld, 2020).

Measuring distractor handling at the cellular and network level

Liesefeld et al. (2014) argued that the various distractor-related processes form a causal chain of events based on the observed timing and correlational pattern of ERP components measured at the scalp (see also, McEvoy, Pellouchoud, Smith, & Gevins, 2001; Sauseng et al., 2005, 2004). These are, of course, relatively indirect measures of neuronal communication. More direct evidence can be derived from measuring synchronisation in oscillatory signals between brain regions using invasive methods. Due to the methodological difficulties involved in measuring neuronal activity at a sufficient temporal resolution and with sufficient precision in multiple brain areas concurrently, studies directly measuring neuronal intercommunication at the level of single cells and their long-range networks are rare for VWM in general (but see, Liebe et al., 2012; Mendoza-Halliday et al., 2014; Salazar et al., 2012) and for distractor handling in VWM in particular (but see Jacob, Hähnke, & Nieder, 2018). Liebe et al. (2012) recorded single-neuron activity and local field potentials in monkey V4 and PFC during the delay period of a VWM task without distractors. Synchronisation between these regions was significantly enhanced in the theta band with the phase of PFC oscillations leading those in V4 by about 15 ms. This effect was stronger on correct trials than on error trials. Together, synchronisation, temporal (phase) pattern, and relation to behavioural performance would indicate that PFC is causally involved in modulating activity in V4 and that this modulation is relevant for successful VWM storage.

Jacob et al. (2018) recorded local field potentials in prefrontal and parietal cortex (area VIP, ventral intraparietal cortex) during the match-to-numerosity working-memory task also employed by Jacob and Nieder (2014) discussed above. Using the phase-slope index (Johnson et al., 2017; Nolte et al., 2008) and Wiener-Granger causality (Bressler & Seth, 2011), they observed communication from PFC to VIP in lower frequency bands (including theta) and VIP-to-PFC communication in the beta band during the memory delay. This result was also supported by an analysis of cross-regional spike-field locking. Follow-up analyses indicated that the bottom-up communication (VIP to PFC) in the beta band carried information on the most recent input (target and distractors) and was inconsequential for behavioural performance, whereas top-down communication (PFC to VIP) differentiated between targets and distractors and predicted performance. In line with the idea of alpha as a blocking signal (Sauseng et al., 2009), distractor information was strongest in the alpha band. That target and distractor information were coded in different phases of parietal theta oscillations indicated a further potential filtering mechanism: phase-dependent coding might keep the representations of targets and distractors separate. Knowing which stimuli were the targets and which the distractors enables the observer to ignore distractor information even though it is still represented. That is, rather than distractor suppression or target enhancement, filtering could also be implemented (in part) by well-ordered coding.

Relationship between filtering ability and VWM capacity

Unnecessary storage of distractors as measured with the CDA and fMRI correlates with VWM capacity measured from displays without distractors (Fukuda & Vogel, 2009; Liesefeld et al., 2014; McNab & Klingberg, 2008; Vogel et al., 2005). Lateralised alpha activity (the above-introduced potential index of distractor blocking) predicts individual VWM capacity, too (Sauseng et al., 2009). In their night-club-bouncer metaphor, Awh and Vogel (2008) suggested that, potentially, VWM capacity per se does not vary between individuals. Instead, everybody's nightclub has exactly the same size, and variability in the efficiency of the bouncer (i.e., filtering ability) results in more or less efficient use of this space. The ratio of relevant to irrelevant information gaining access to the limited space might determine the observed interindividual differences in measured VWM capacity.

However, there is reason to question whether filtering ability can even theoretically be the cause of high VWM capacity (Oberauer, 2019): often, capacity is measured in VWM displays that do not contain any distractors, the explicit goal being to obtain independent measures of VWM capacity and distractor handling; nevertheless, a correlation between the two measures is typically observed. Logically, filtering would not be required when there are no distractors; the bouncer could simply let all guests in, so that the bouncer's ability to select only wanted guests is irrelevant for performance on these tasks. If this was true, whatever is measured in VWM tasks without distractors could not be influenced by the ability to filter out distractors. Consequently, it appears, filtering ability cannot be the reason for the correlation between capacity measured in tasks without distractors and filtering ability measured in tasks with distractors.

The up-weighting component of the biased-competition explanation of distractor handling suggested here provides a possible way out of this theoretical predicament, while allowing (some component of) filtering ability to be maintained as the cause for VWM capacity: as detailed above, the ability to increase target priority would serve to give targets a competitive advantage over distractors in tasks designed to measure filtering ability. Increasing target priority might be necessary when distractors are absent as well as when distractors are present. Potentially, initial target saliency is not sufficient for encoding, but an additional boost is needed to pass some encoding threshold. We have used the metaphor of a moderately attractive night club that guests visit only if they are persuaded. Thus, filtering ability would in part be the ability of getting wanted but somewhat hesitant guests in, rather than the ability of keeping enthusiastic but unwanted guests out (as illustrated in Figure 2). It might be interindividual variation in this specific cognitive mechanism that drives the correlation between filtering ability and VWM capacity.

Conclusions

The present review highlights that VWM filtering is a central cognitive function of crucial importance for general VWM performance. It is likely causally involved in the selection of relevant information from the recent and distant past as well as the present moment. We extend the traditional view of filtering ability as distractor suppression by introducing the theoretical possibility of VWM filtering by target enhancement and discuss the potential complementary roles of suppression and enhancement. Both filtering mechanisms can be modelled as modulations of activations on a pre-attentive priority map that controls the allocation of processing resources (biased competition). Two key empirical observations had triggered, and can be explained by, the idea of filtering as target enhancement: (i) prefrontal brain areas are involved in upholding of VWM content as well as filtering and (ii) filtering ability correlates with VWM capacity measured in tasks without distractors.

Furthermore, we argue that neural implementations of filtering ability do not reside in individual brain areas, but they likely emerge from the interaction of brain mechanisms with PFC taking a lead role.

Outlook

In line with a partial overlap in selection mechanisms in situations with and without distractors (see section Relationship between Filtering Ability and VWM Capacity), even the higher estimates of the correlation between filtering ability and VWM capacity leave much variance unexplained, so that there is room for unique as well as shared influences. The drawing-in part of filtering ability might correlate with VWM capacity, while the keeping-out part does not. Of note in this context, in a latent variable analysis on a large test battery covering various cognitive functions, Unsworth et al. (2014) found that capacity, attentional control, and secondary (long-term) memory were all uniquely related to VWM performance. Thus, filtering ability (attentional control) might be one among several reasons for individual differences in VWM capacity. This brings us back to the induced lateralised alpha reported by Sauseng et al. (2009): the authors found that VWM capacity was not only predicted by the increase in alpha with the numbers of distractors, but also by the increase in theta-gamma coupling over cortical sites processing targets. Potentially, one reflects the up-weighting of the targets and the other the down-weighting of distractors (Riddle et al., 2020; Sauseng & Liesefeld, 2020; see section Concurrent Target Enhancement and Distractor Suppression). Relatedly, recall that Fukuda et al. (2015) found delay activity and alpha to predict unique portions of variance in VMW capacity in a task without distractors. Consequently, asking whether variation in filtering ability causes variation in VWM capacity might not be quite the right question. Instead, future research should focus on the more nuanced question of which part of filtering ability influences which part of VWM capacity and disentangle electrophysiological markers of the various processes and their interactions.

We believe that the priority-map concept provides a useful theoretical framework to understand VWM distractor handling. However, much of our theorising is as yet highly speculative and requires dedicated empirical testing. Many interesting predictions follow from applying various priority-map mechanisms that were discovered using the visual-search paradigm to VWM research. For example, the priority map is thought to be influenced by saliency, goals, and experience (Awh, Belopolsky, & Theeuwes, 2012; Liesefeld et al., 2018; Wolfe & Horowitz, 2017). While these types of influence have been explored also for VWM (e.g., Constant & Liesefeld, 2019; Emrich, Lockhart, & Al-Aidroos, 2017; Umemoto, Scolari, Vogel, & Awh, 2010), many details remain to be filled in (e.g., regarding the consumption of cognitive resources by individual processes and the conditions influencing the efficiency of the various processes). A particularly hot topic with regard to distractor handling is the effect of statistical regularities in the spatial position of distractors (one form of prior experience): If distractors are presented often at a particular location or region in space, they cause less interference at that location compared to other locations, which is interpreted as a suppression of the respective location(s) at the priority map (e.g., Chelazzi et al., 2019; Failing, Feldmann-Wüstefeld, Wang, Olivers, & Theeuwes, 2019; Ferrante et al., 2018; Goschy et al., 2014; Sauter et al., 2018, 2019; van Moorselaar & Slagter, 2020; Wang & Theeuwes, 2018). It would be highly interesting to see whether this and other priority-based distractor handling mechanisms also apply to VWM encoding.

Notes

1. The present review focuses on the ability to disregard irrelevant information during encoding into VWM. There is also work on shielding already encoded VWM content from distraction occurring during the retention period of the task (e.g., Bonnefond & Jensen, 2012; Feredoes, Heinen, Weiskopf, Ruff, & Driver, 2011). We draw upon this work here only if respective studies on filtering during encoding are lacking. Owing to the present focus, we use the word *filtering ability* to refer to the ability to selectively encode task-relevant information while disregarding concurrently presented, irrelevant information (distraction).
2. Discrimination between targets and distractors can likely only be achieved by pro-active (i.e., before memory-display onset) tuning of posterior areas according to (frontally communicated) task goals. In a task where distractor presence is unpredictable (as in the Liesefeld et al., 2014, study), this tuning would occur on distractor-absent as well as distractor-present trials and does therefore not produce an effect of distractor presence.

Purpose-designed studies are needed to examine this pro-active part of distractor handling (see Vissers, van Driel, & Slagter, 2016, for some indication that such a preparatory mechanism might be reflected in lateralised alpha).

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