

# Intercommunication Between Prefrontal and Posterior Brain Regions for Protecting Visual Working Memory From Distractor Interference

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## Abstract

Because visual working memory has a very restricted capacity, good filtering mechanisms are essential for its successful functioning. A neuronal signal emitted by the prefrontal cortex is considered to be an important contributor to filtering. Proof of the functional significance of this signal during normal cognitive functioning is, however, still missing. Furthermore, research has so far neglected that the prefrontal cortex must receive input from posterior brain areas that report the necessity to filter. From human electroencephalograms, we extracted several event-related components that reflect the different subprocesses of filtering. On the basis of their timing and a clear pattern of correlations, we reason that filtering might consist of a causal chain of events that involve prefrontal and posterior cortex regions: After distractors are detected in posterior regions, a prefrontal mechanism is activated, which in turn prevents subsequent unnecessary parietal storage of distractor information.

## Keywords

prefrontal cortex, cognitive control, fronto-parietal network, electroencephalography, delay activity, visual memory, electrophysiology, neural networks, visual attention, evoked potentials

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Visual working memory (VWM) has a very restricted capacity (Cowan, 2001; Luck & Vogel, 1997). To reserve this precious storage space for only the most important information, filtering mechanisms that regulate access to VWM are vital. Well-functioning filtering mechanisms should prevent the unnecessary storage of all information that is irrelevant for a person's current task. Previous research using VWM tasks has identified activity in parietal brain regions during the delay between the presentation of a memory array and the subsequent test array (the *retention interval*). This activity is typically employed as a neuronal marker of information maintenance in VWM (Todd & Marois, 2004; Vogel & Machizawa, 2004). Because this delay activity scales with the number of objects maintained (Todd & Marois, 2004; Vogel & Machizawa, 2004), it also can be exploited as an index of whether irrelevant objects are unnecessarily stored in VWM or are successfully filtered out (Arend & Zimmer, 2012; Vogel, McCollough, & Machizawa, 2005).

In line with the central role of filtering in VWM functioning, estimates of filtering ability derived from this delay activity are strong predictors of individuals' VWM capacity (Awh & Vogel, 2008; Fukuda & Vogel, 2009; McNab & Klingberg, 2008; Vogel et al., 2005). The importance of filtering mechanisms for higher cognitive functioning, such as VWM, is well established. How exactly these filtering mechanisms operate is, in contrast, less well known. In the present study, we elucidated the chain of cognitive and neuronal processes that contribute to efficient filtering in VWM. In particular, we found neurophysiological correlates of (a) initial object processing and distractor detection, (b) initiation of filtering, and (c) exclusion of distractors from VWM. Our

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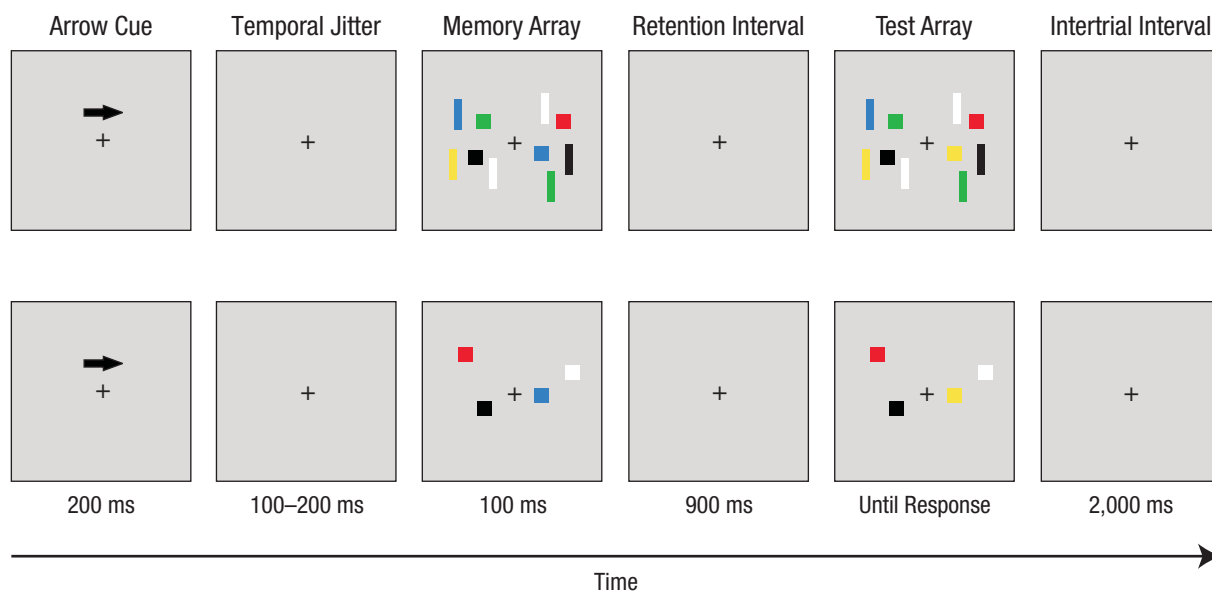
results indicate that these processes are causally related during normal cognitive functioning.

To reach these conclusions, we made electroencephalogram (EEG) recordings while participants performed a VWM task in which we manipulated filtering demands (Fig. 1). Specifically, we employed a type of change-detection task as designed by Vogel and colleagues (Fukuda & Vogel, 2009; Vogel et al., 2005). The memory array contained either both targets and distractors (*distractors-present trials*; trials with filtering demands) or only targets (*distractors-absent trials*; trials without filtering demands); both conditions were randomly intermixed, and participants did not know in advance whether the memory array would contain distractors. Participants' task was to selectively maintain the targets over a short retention period in order to decide whether one target in the ensuing test array had changed color. Consequently, they had to control which objects to store and which objects to keep out of VWM.

In addition to parietal brain areas, prefrontal areas are heavily involved in VWM functioning as shown by lesion studies (Baier et al., 2010; Voytek & Knight, 2010). Therefore, many experts in the field advocate frontoparietal-network models of working memory maintenance (Salazar, Dotson, Bressler, & Gray, 2012; Zimmer, 2008). In particular, because the prefrontal cortex provides cognitive control processes (Miller & Cohen, 2001),

it appears plausible that frontal areas exert control over deciding which information is stored in parietal areas (Curtis & D'Esposito, 2003; Postle, 2006). That is, the neuronal source for the initiation of filtering should be located in prefrontal regions. A bias signal might be emitted there that prioritizes relevant over irrelevant information for access to VWM (see Vogel et al., 2005). Indeed, when distractors are shown during retention, working-memory-related delay activity in posterior areas is influenced by transcranial magnetic stimulation of dorsolateral prefrontal areas (Feredoes, Heinen, Weiskopf, Ruff, & Driver, 2011). Furthermore, functional MRI (fMRI) studies have shown increases in prefrontal activation with filtering demands during normal cognitive function (McNab & Klingberg, 2008, showed such activity in the middle frontal gyrus, and Zanto, Rubens, Thangavel, & Gazzaley, 2011, showed it in the inferior frontal junction).

This prefrontal activity was predictive of VWM capacity, whereas a correlation with filtering success has not yet been found (McNab & Klingberg, 2008). For establishing the functional significance of this signal for filtering, however, this latter correlation must be shown. Additionally, if this prefrontal signal has a causal role in filtering, it must emerge before the filtering success can be measured in parietal delay activity. In contrast to most other neuroscientific techniques, the EEG has the temporal resolution necessary to determine the temporal order



**Fig. 1.** Example trial from a distractors-present condition (upper row) and the respective distractors-absent condition (lower row). Trials began with a central fixation cross below an arrow pointing either right (as shown here) or left to indicate which side of the ensuing memory array had to be maintained. The arrow then disappeared and, after a blank interval, the memory array briefly appeared. Targets were squares, and distractors were rectangles. After a blank retention interval, the test array appeared. Participants had to indicate whether any of the targets had changed color between the memory array and the test array (in these examples, a participant would have to remember the two targets on the right side of the display in order to detect the change of the lower square from blue to yellow).

of events that leads to successful filtering in VWM. Therefore, one major goal of the present study was to extract from human EEGs a prefrontal signal that is sensitive to filtering demands, precedes parietal delay activity, and predicts filtering success.

But also this prefrontal signal must have its precursors: In natural situations, observers are confronted with visual scenes that sometimes contain irrelevant objects in addition to the currently relevant objects. They consequently cannot predict in advance whether distractors are present in a new scene and, if distractors are present, must somehow manage to focus on the relevant objects. To mimic these situations in the present VWM task, we randomly intermixed distractors-absent trials with distractors-present trials. Whereas previous research has focused on the involvement of prefrontal areas in the selective processing of information, one crucial question has been largely neglected: How do prefrontal areas become aware of distractors? Notably, visual information is processed in posterior, retinotopic areas in the striate and extrastriate cortex (Tong, 2003); the prefrontal cortex itself is completely blind. The initial processing of visually perceived objects and the detection of distractors should, consequently, take place in posterior regions. For measuring this potentially short-lived process, we again relied on the high temporal resolution of the EEG.

In sum, filtering contains the following chain of processes. First, posterior brain regions must perform a preliminary scanning of all objects to determine whether any distractors are present in a given trial. Only after distractors have been detected can an informative prefrontal bias signal be emitted to trigger the filtering process. Furthermore, if this bias signal is of functional significance for successful filtering, it must precede VWM storage—as reflected by the parietal delay activity—and predict the success of filtering. If filtering is imperfect, delay activity is influenced by distractors, which indicates that part of the distractor information is unnecessarily stored. This bouncing back and forth of information on distractors between posterior and prefrontal regions might prevent unnecessary crowding of VWM. The present study revealed electrophysiological correlates of all three cognitive processes—detection of distractors, preparation of filtering, and unnecessary storage—and provided evidence that these form a causal chain of events that constitute filtering in VWM.

## Method

### *Design and procedure*

Participants (40 university students) performed a lateralized change-detection task with colored squares (targets) and colored rectangles (distractors) as displayed in Figure 1. At

the start of each trial, an arrow indicated whether the left or right side of the ensuing memory array was relevant and consequently had to be remembered. A memory array consisting of two groups of objects (one on the left and one on the right of the display) was then presented. Arrays contained either targets only or targets and distractors, but the same number of each type of object always appeared on each side of the display. Stimuli were colored (red, blue, green, yellow, black, white, and purple), and each color appeared only once per trial on each side of the display. Following the memory array, there was a 900-ms retention interval, and then a test array appeared. Participants pressed a key (using their left or right index finger; counterbalanced) to indicate whether a color had changed between the memory array and the test array.

We ran four distractors-absent conditions (two to five targets; 2T, 3T, 4T, and 5T) and three distractors-present conditions (two targets and two distractors, two targets and three distractors, and three targets and two distractors; 2T2D, 2T3D, and 3T2D, respectively). Participants were instructed that the best method to encode the targets was to fixate on the central cross and to covertly move their attention to the side indicated by the arrow. In 50% of the trials, one of the targets on the relevant side changed color from memory to test array; in the other half of the trials, all colors remained the same. Independent variables (set size, relevant side of the display, change or no change in color) were varied within participants and randomized over all trials (100 trials per set size, 700 trials in total). Additional details on stimuli and participants are given in the Supplemental Material available online.

### *Extraction of event-related-potential (ERP) components and statistical analysis*

ERPs were extracted by averaging stimulus-locked signals from  $-200$  to  $1,000$  ms relative to the onset of the memory array. Because of the structure of the visual system, laterally perceived stimuli are initially represented in the contralateral hemisphere. The contralateral hemisphere then holds the working memory representation of the objects on the relevant side (Arend & Zimmer, 2011). Therefore, we extracted contralateral posterior ERPs by averaging activity over right electrodes when the relevant stimuli were presented on the left side and vice versa for the right side of the display. As this logic does not apply to frontal electrode sites, where we do not assume representations of visually perceived stimuli to occur, we averaged across left and right frontal recording sites to extract the prefrontal bias signal that should reflect the initiation of filtering processes. Because all these calculations

involved two corresponding electrodes from both hemispheres (e.g., PO3 and PO4), we refer to the respective electrode site by the name of both electrodes involved (e.g., PO3/PO4). Additional information regarding EEG recording and preprocessing can be found in the Supplemental Material.

Time intervals and regions of interest were identified using the method of Maris and Oostenveld (2007), as detailed in the Supplemental Material. In a nutshell, we determined spatiotemporal clusters of contiguous time points and electrodes that showed a prespecified effect of interest and performed nonparametric tests via a Monte Carlo procedure to determine each cluster's significance. Within-subjects analyses of variance and  $t$  tests were then conducted on the mean activity in each cluster. We employed the Greenhouse-Geisser correction on analyses of variance and confidence intervals to correct for violations of the sphericity assumption. Following McNab and Klingberg (2008), correlations were tested one-tailed with the one-sided hypothesis that during the chain of filtering processes, efficient preceding processes lead to efficient subsequent processes.

Our analyses of ERP components focused on two contrasts: (a) effects of the number of objects and (b) effects of distractor presence. The main effect of the number of objects was calculated with distractors-absent trials only (2T, 3T, 4T, 5T) in order to dissociate it from effects of distractor presence. The distractor-presence contrast was defined as mean activity from the 4T and 5T conditions minus mean activity from all three distractors-present conditions. We employed the 4T and 5T conditions as a baseline for the distractor-presence contrast because four or five objects were also shown in the distractors-present conditions. This approach, therefore, controlled for any effect of the number of objects shown; all activity in the distractors-present conditions that emerged in addition to activity in the 4T and 5T conditions must be due to the processing of distractor information.

We additionally determined individual peaks of the components that are taken to reflect the detection of distractors and the initiation of filtering via peak detection on the distractor-detection contrast in the respective region of interest. Because we wanted to test whether the timing of both components differed, we searched for the local peaks of both components in their combined time windows (201–289 ms).

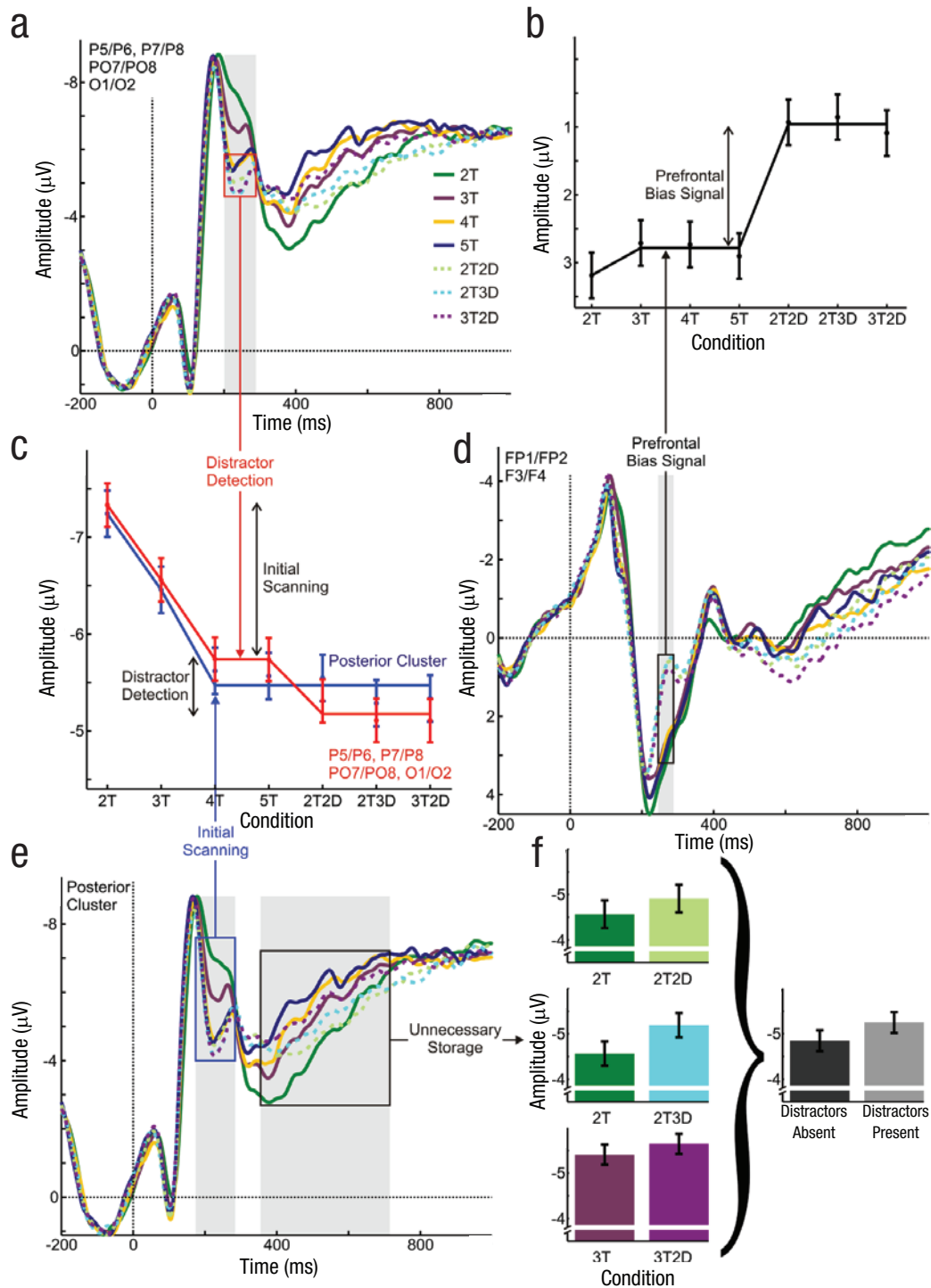
## Results

### ***Parietal delay activity: unnecessary storage***

We first identified parietal delay activity as an effect of the number of objects. As expected, this effect was evident over posterior electrode sites,  $F(3, 117) = 29.42$ ,

$p < .001$ ,  $\eta_p^2 = .43$ . This cluster encompassed all posterior electrodes and lasted from 290 to 715 ms after memory-array onset. Note that when delay activity starts, filtering processes do not necessarily already have an effect. An unbiased measure of filtering success should, however, take only those time intervals into account in which filtering is effective. At the beginning of the delay-activity interval, ERPs for distractors-present conditions did indeed not differ significantly from ERPs for the highest set size (5T; see Fig. 2e),  $t(39) = 1.42$ ,  $p = .16$ ; this indicates that, at that time, all distractor information was still processed. We identified the time point at which filtering becomes effective by searching for a subcluster within the delay activity in which the amplitude for distractors-present ERPs was smaller than the amplitude for ERPs for the highest set size. This cluster was identical to the delay-activity cluster but started later, at 355 ms. We extracted activity from this latter cluster to analyze individual differences in filtering ability.

To do this, we calculated the amount of *unnecessary storage*, which we defined as the difference in delay activity between distractors-present conditions and the respective distractors-absent conditions (Fukuda & Vogel, 2009; McNab & Klingberg, 2008). Take, for example, a distractors-present trial with two targets and three distractors (2T3D). An efficient filterer would store only the two targets in VWM and filter out the three distractors. Consequently, parietal delay activity in this condition would be equivalent to the respective distractors-absent condition with two targets only (2T). An inefficient filterer, in contrast, would also store some distractor information, and delay activity would therefore be higher in the 2T3D condition than in the 2T condition. This additional amount of delay activity reflects the amount of unnecessarily stored distractor information and can be isolated by subtracting activity in the 2T condition from that in the 2T3D condition. In addition to the 2T3D condition, we measured filtering ability in the two other distractors-present conditions, 2T2D and 3T2D. The index for unnecessary storage employed as a measure for filtering ability was thus the average of the three differences 2T2D minus 2T, 2T3D minus 2T, and 3T2D minus 3T. In Fig. 2e, the effect of unnecessary storage becomes evident by comparing delay activity in the 2T and 2T2D conditions, in the 2T and 2T3D conditions, and in the 3T and 3T2D conditions. In Fig. 2f, unnecessary storage is illustrated by comparing each distractors-present condition with the relevant distractors-absent condition. The mean effect of unnecessary storage is also illustrated as the average over all distractors-present conditions and the average of the relevant distractors-absent conditions,  $t(39) = 2.51$ ,  $p = .016$ . As in previous studies (Fukuda & Vogel, 2009; McNab & Klingberg, 2008; Vogel et al., 2005), unnecessary storage was correlated with VWM capacity,  $r = -.30$ ,  $p = .030$  (Fig. 3c).



**Fig. 2.** Event-related-potential (ERP) results. ERP waveforms are shown for (a) the distractor-detection component, (d) the frontal bias signal, and (e) the initial-scanning component and delay activity (reflecting unnecessary storage) in all conditions, separately for relevant electrode clusters (the cluster in (e) contains the full set of recorded posterior electrodes). Analyzed time windows are indicated by gray shading. Mean amplitudes in the respective spatial clusters and time windows are shown for all conditions for (b) the prefrontal bias signal and (c) the initial-scanning component and distractor detection. Relevant effects are emphasized by double-headed arrows. Adjacent data points that are connected by a horizontal line do not significantly differ from each other (all  $p$ s  $> .19$ , except for the difference between the 2T2D and 2T3D conditions in the initial-scanning,  $p = .07$ , and the distractor-detection,  $p = .12$ , cluster); data points connected by a sloped line differ significantly ( $p = .049$  for the difference between the 2T and 3T conditions in the prefrontal bias signal and  $p$ s  $< .001$  for all other contrasts). The graphs in (f) display mean delay-activity amplitudes for each distractors-present condition and its respective distractors-absent condition, separately for each unnecessary-storage comparison (colored bars) and averaged across all three comparisons (gray bars). In all graphs, condition names indicate the number of targets (T) and distractors (D) that appeared on each side of the display. Error bars display 95% confidence intervals based on the respective main effect from within-subjects analyses of variance. See the text for details of the indicated chain of processes involved in filtering (detection of distractors, elicitation of the prefrontal bias signal, and unnecessary storage).  $N = 40$ .



### **Prefrontal bias signal: initiation of filtering**

Unnecessary-storage effects in the parietal delay activity reflect the result of more or less successful filtering. The process that initiates this filtering must, of course, take place earlier in time. We expected a prefrontal bias signal to reflect this process. In particular, the presence of distractors should elicit additional activation over frontal electrode sites, the strength of which should be correlated with the amount of unnecessary storage. This was the case in a cluster that contained electrodes FP1/FP2 and F3/F4 and lasted from 245 ms to 288 ms (Figs. 2a and 2b).

There was a strong effect of distractor presence on mean activity in this cluster,  $t(39) = 10.00$ ,  $p < .001$ ,  $d_z = 1.58$  (Fig. 2d). To determine the strength of each individual's prefrontal bias signal, we extracted activity 10 ms around the peak of the distractor-presence contrast. Like the filtering-related prefrontal fMRI signal reported by McNab and Klingberg (2008), the strength of this prefrontal bias signal was strongly predictive of VWM capacity,  $r = .51$ ,  $p < .001$  (Fig. 3b). Hence, this fMRI signal and our EEG signal very likely reflect the same neuronal mechanism.

Expanding on the research of McNab and Klingberg (2008), our results showed that the strength of our bias signal also predicted the amount of unnecessary storage: The stronger the prefrontal bias signal was, the less unnecessary distractor information was stored (as indicated by the pattern of parietal delay activity),  $r = -.42$ ,  $p = .003$  (Fig. 3e). This correlation represents an up-to-now missing piece of evidence for the assumption that the prefrontal bias signal is of functional significance for preventing unnecessary storage of distractor information in VWM (see Awh & Vogel, 2008; McNab & Klingberg, 2008; Vogel et al., 2005).

### **Posterior detection component: presence of distractors**

The prefrontal bias signal can be elicited only after distractors are detected on a given trial. As mentioned in the introduction, to detect distractors, first, a preliminary scanning of the visual scene is necessary. We searched ERPs for two effects. The preliminary scanning of objects should result in an effect of the number of objects shown. The detection of distractors should result in an effect of distractor presence. The first effect emerged in a cluster that encompassed all posterior electrodes in the interval from 174 to 284 ms (i.e., before the delay activity),  $F(3, 117) = 42.62$ ,  $p < .001$ ,  $\eta_p^2 = .52$ . Here, amplitude increased from two to three targets,  $t(39) = 5.11$ ,  $p < .001$ ,  $d_z = 0.81$ , and from three to four targets,  $t(39) = 4.97$ ,  $p < .001$ ,  $d_z = 0.79$ , and leveled off from four to five targets,  $t(39) = 0.34$ ,

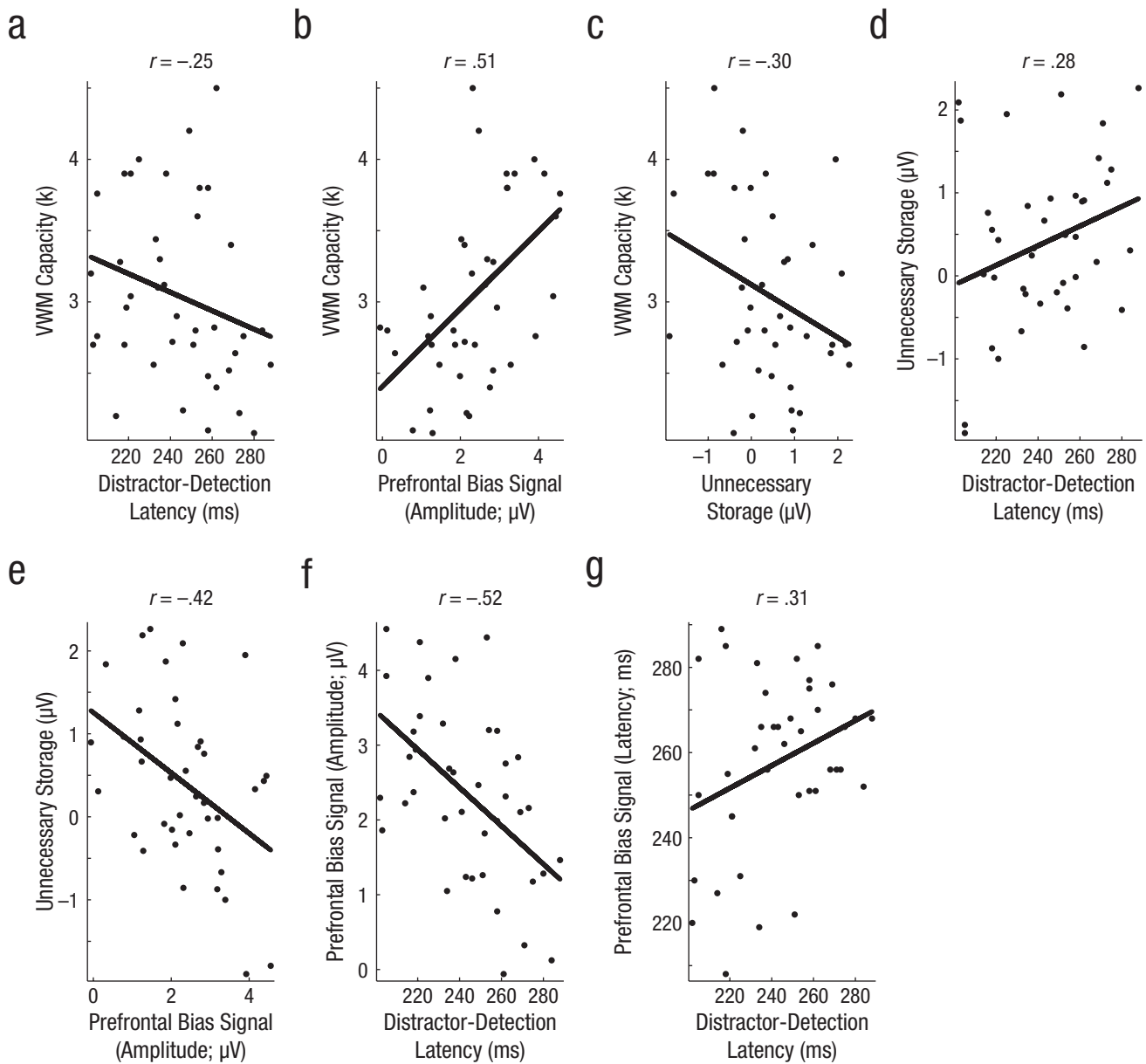
$p = .74$ ; these results indicate that up to four objects are initially processed.

Distractor presence had only a small (nonsignificant) effect on this cluster,  $t(39) = 1.87$ ,  $p = .07$  (Fig. 2c, blue line). The genuine cluster for the effect of distractor presence contained only electrodes P7/P8, P5/P6, PO7/PO8, and O1/O2 and lasted from 201 ms to 289 ms. In addition to the effect of the number of objects,  $F(3, 117) = 50.00$ ,  $p < .001$ ,  $\eta_p^2 = .56$ , distractor presence led to a significant increase in amplitude,  $t(39) = 5.14$ ,  $p < .001$ ,  $d_z = 0.81$  (Fig. 2c, red line). Obviously, the initial-scanning cluster (Fig. 2e) contains two overlapping components, one component that reflects the initial scanning of up to four objects (with a broad spatial distribution encompassing all posterior electrodes) and an additional component that reflects the detection of distractors (which is spatially much more confined). In line with a causal role for later filtering processes, the distractor-detection component clearly peaked before the prefrontal bias signal (228 ms vs. 243 ms),  $t(39) = 3.51$ ,  $p = .001$ ,  $d_z = 0.56$ . In fact, the earlier this component peaked, the stronger the prefrontal bias signal's amplitude was,  $r = -.52$ ,  $p < .001$  (Fig. 3f), and the earlier the prefrontal bias signal peaked,  $r = .31$ ,  $p = .024$  (Fig. 3g). In contrast to this speed of distractor detection, the strength of the distractor-detection component (mean amplitude 10 ms around peak) did not predict the strength,  $r = .06$ ,  $p = .74$ , nor the latency,  $r = -.14$ ,  $p = .39$ , of the prefrontal bias signal. Apparently, at this early point in time, it matters how quickly distractors are detected and how quickly processes that prevent their unnecessary storage can, consequently, be initiated. Also, the speed of distractor detection predicted unnecessary storage,  $r = .28$ ,  $p = .04$ , and working memory capacity,  $r = -.25$ ,  $p = .06$  (Figs. 3d and 3a, respectively).

## **Discussion**

In the present study, we examined the chain of processes that allow prioritized processing of relevant over irrelevant objects in VWM. In particular, filtering in a VWM task should involve a fronto-parietal network where visual processing of a scene and the storage of relevant visual information is located in posterior areas, and the necessary control functions that induce filtering of irrelevant objects are provided by prefrontal areas. The present article is the first to report indications that these three cognitive processes form a causal chain of events that leads to successful filtering in VWM: The detection of distractors in posterior brain regions triggers a prefrontal bias signal that reduces the amount of unnecessary storage in maintenance-related parietal delay activity.

When participants are confronted with a new visual scene, they obviously first have to process all objects to a



**Fig. 3.** Scatter plots (with best-fitting regression lines) showing correlations between key measures ( $N = 40$ ). Visual working memory (VWM) capacity is shown as a function of (a) distractor-detection latency, (b) the amplitude of the prefrontal bias signal, and (c) unnecessary storage. Unnecessary storage is shown as a function of (d) distractor-detection latency and (e) the amplitude of the prefrontal bias signal. The (f) amplitude and (g) latency of the prefrontal bias signal is shown as a function of distractor-detection latency. Unnecessary storage refers to the increase in delay-activity amplitude indicating that distractor information has been stored. Scatter plots with descending lines indicate negative relationships (e.g., a stronger prefrontal bias signal leads to less unnecessary storage), whereas ascending lines indicate positive relationships (e.g., a stronger prefrontal bias signal leads to higher VWM capacity).

certain degree to determine whether any distractors are present. We found that the speed of this distractor detection predicts unnecessary storage and VWM capacity. These results are in line with Fukuda and Vogel's (2009) findings that the more susceptible a participant is to distraction at the beginning of a trial, the more information

is unnecessarily stored and the lower his or her VWM capacity is. Furthermore, Fukuda and Vogel (2011) showed that participants initially process all objects in a visual array and that participants with a higher VWM capacity more quickly disengage attention from irrelevant distractors. Apparently, the efficiency of discriminating

targets from distractors at this early point in visual processing already is of high functional significance for efficient VWM functioning.

The next step after the detection of distractors is the initiation of filtering. Such cognitive control processes are considered to be performed by the prefrontal cortex (McNab & Klingberg, 2008; Miller & Cohen, 2001; Vogel et al., 2005) and are probably reflected by the reported prefrontal bias signal. The earlier distractor presence is detected, the more vigor can be put into their suppression and the earlier this suppression can be initiated. These relationships are reflected by the observed correlations between the latency of the posterior distractor-detection component and the strength and latency of the prefrontal bias signal. A strong prefrontal bias signal, in turn, leads to strongly reduced unnecessary storage, as became evident in the parietal delay activity we observed here.

Awh and Vogel (2008) compared VWM capacity with the restricted space in an exclusive nightclub and filtering mechanisms with the bouncer that regulates access to this nightclub. In keeping with this analogy, our posterior distractor-detection component might reflect the eyes and the prefrontal bias signal the hands of the bouncer: Only when his eyes detect unwanted guests will his hands close the club doors. The faster and the more firmly he locks the doors, the less unwanted guests will slip in. If interindividual differences in VWM capacity are not determined by the size of the nightclub but by the efficiency of the bouncer (see Awh & Vogel, 2008; Awh, Vogel, & Oh, 2006), the bouncer's eyes and hands are vital, which explains why the functioning of both processes is correlated with VWM capacity in the present data set.

Future work could extend this model to include even earlier processes in the chain of filtering: How does the bouncer know which guests are allowed to enter the club on a given night? Recent research indicates that oscillatory synchronizations in the prefrontal cortex represent such task rules (Buschman, Denovellis, Diogo, Bullock, & Miller, 2012; see also Engel, 2012) and that these rules influence activity in working-memory-related areas via long-range synchronization (Bonnefond & Jensen, 2012; Zanto et al., 2011, see also Jensen & Bonnefond, 2013). This synchronous activity might be the neuronal representation of the bouncer's guest list.

VWM is provided by a neuronal network spanning prefrontal and parietal areas (e.g., Salazar et al., 2012; Zimmer, 2008). Concerning the respective roles of these areas, it has been speculated that prefrontal areas, which are known to be the neuronal base of cognitive control processes (Miller & Cohen, 2001), influence which information is stored in parietal areas (Curtis & D'Esposito, 2003; Postle, 2006). Specifically, prefrontal areas may emit a bias signal that triggers the selective processing of only relevant information (Vogel et al., 2005). Using fMRI, McNab and Klingberg (2008) have identified a prefrontal

signal that could potentially fulfill this role. As this signal and the prefrontal ERP component we observed here share many characteristics, these signals are very likely emitted by the same neuronal source. Unfortunately, fMRI measurement of this neuronal activation in McNab and Klingberg was apparently not sensitive enough on a single-subject level to detect a correlation with unnecessary storage as measured in parietal delay activity. Such a correlation must, however, exist if the prefrontal bias signal plays a causal role for filtering in VWM.

Unnecessary storage in the McNab and Klingberg (2008) study was correlated only with filtering-related activity in the globus pallidus. Therefore, Awh and Vogel's (2008) filtering model places the neuronal locus for the nightclub bouncer into this subcortical structure within the basal ganglia. Nevertheless, they speculated that the bouncer influences VWM via the prefrontal cortex. In line with this model, filtering is disturbed in stroke patients with lesioned basal ganglia (Baier et al., 2010). Furthermore, anatomical and physiological studies have shown that the basal ganglia receive input from all over the cerebral cortex (Alexander, DeLong, & Strick, 1986; Miller & Cohen, 2001), a characteristic that makes them suited to act as a gatekeeper. Problematically, however, the basal ganglia's major output goes (via the thalamus) to the frontal and motor cortices and not toward parietal working-memory-related areas (Alexander et al., 1986; Miller & Cohen, 2001). McNab and Klingberg's (2008) source of filtering-related activity in the globus pallidus therefore more likely is a relay station that only transmits information on filtering affordances (or general VWM affordances; Voytek & Knight, 2010) to prefrontal areas. Because the prefrontal cortex is closely interconnected with virtually all cortical sensory areas (Miller & Cohen, 2001), information on distractors can be bounced back from the prefrontal cortex to parietal brain areas to prevent unnecessary storage in VWM. The results reported here therefore constitute the missing piece of evidence in Awh and Vogel's (2008) model that allows for a functional role of the prefrontal cortex for the crucial higher cognitive control function of filtering in VWM.

### Author Contributions

A. M. Liesefeld and H. R. Liesefeld contributed equally to this work. A. M. Liesefeld and H. D. Zimmer designed the study. A. M. Liesefeld supervised the data collection. A. M. Liesefeld and H. R. Liesefeld analyzed and interpreted the data and wrote the manuscript. H. D. Zimmer gave conceptual advice and edited the manuscript. All authors approved the final version of the manuscript for submission.

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now at Department Psychologie, Ludwig-Maximilians-Universität Munich.

### Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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### Supplemental Material

Additional supporting information may be found at <http://pss.sagepub.com/content/by/supplemental-data>

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