Re-evaluating the Relationships Among Filtering Activity, Unnecessary Storage, and Visual Working Memory Capacity

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Acknowledgements

Abstract

The amount of task-irrelevant information encoded in visual working memory (VWM), referred to as *unnecessary* storage, has been proposed as a potential mechanism underlying individual differences in VWM capacity. In addition, a number of studies have provided evidence for additional activity that initiates the filtering process originating in frontal cortex and the basal ganglia, and is therefore a crucial step in the link between unnecessary storage and VWM capacity. Here, we re-examine data from two prominent studies that identified unnecessary storage activity as a predictor of VWM capacity by directly testing the implied path model linking filtering-related activity, unnecessary storage, and VWM capacity. Across both studies, we found that unnecessary storage was not a significant predictor of individual differences in VWM capacity once activity associated with filtering was accounted for; instead, activity associated with filtering better explained variation in VWM capacity. These findings suggest that unnecessary storage is not a limiting factor in VWM performance, whereas neural activity associated with filtering may play a more central role in determining VWM performance that goes beyond preventing unnecessary storage.

Re-evaluating the Relationships Among Filtering Activity, Unnecessary Storage, and Visual Working Memory Capacity

Over the past few decades, there has been enormous interest in understanding the nature of visual working memory (VWM), which enables the on-line maintenance of a limited amount of visual information over short periods of time. In particular, a number of studies have focused on understanding the origins of *individual differences* in VWM capacity (Luck & Vogel, 2013). That is, VWM has a limited bandwidth, and as such, the number of items (capacity) and/or the fidelity of information stored in VWM appear to be severely limited, with significant individual differences in this ability.

Although the precise origins of individual differences in VWM capacity remains unclear, one mechanism that has been proposed to account for these differences is the ability to efficiently allocate limited capacity resources through the filtering of unnecessary (distractor) information, thereby minimizing the unnecessary storage of task-irrelevant information (Awh & Vogel, 2008; Luck & Vogel, 2013). Specifically, if VWM is characterized as having a limited number of storage "slots," then any item that is encoded into VWM will occupy one of these storage units. According to this model, the more control you have over which information gains access to VWM, the less likely you are to encode task-irrelevant information that will occupy these limited storage slots thereby freeing up these resources for the task-relevant items. This efficient allocation of capacity-limited resources has been linked to VWM capacity, as shown by a positive correlation between measures of filtering efficiency and VWM capacity (Vogel, Mccollough, & Machizawa, 2005). From this perspective, filtering efficiency can be indexed by the amount of unnecessary activity – that is, the amount of additional maintenance-related activity in the presence distractors compared to conditions without distractors. Those individuals

who demonstrate less unnecessary storage also tend to have higher VWM capacity, suggesting that the control over what information is encoded into VWM may be an important determinant of individual differences in VWM capacity.

This account emphasizing filtering ability as a primary predictor of individual differences in VWM capacity has been extremely influential (Luck & Vogel, 2013). However, despite the emphasis that has been placed on the role of unnecessary storage, its exact contribution to individual differences remains somewhat unclear. Here, based on a reanalysis of two studies examining neural activity associated with filtering preparedness or initiation, as well as unnecessary storage (Liesefeld, Liesefeld, & Zimmer, 2014; McNab & Klingberg, 2008), we re-examine the evidence in support of unnecessary storage as a predictor of VWM capacity by testing the implied path model linking activity associated with filtering, unnecessary storage, and VWM capacity. Our findings reveal that unnecessary storage is a poor predictor of individual differences in VWM capacity when examined alongside activity driving the filtering process. Instead, activity associated with attentional control (i.e., the activity that initiates the filtering of irrelevant distractors) uniquely predicts VWM capacity independent of unnecessary storage.

The Bouncer in the Brain

The relationship between filtering ability and VWM capacity was first identified in a study by Vogel and colleagues (Vogel et al., 2005), who demonstrated that low-capacity individuals (as opposed to high-capacity individuals) were more affected by task-irrelevant distractors presented during encoding, and that these low-capacity subjects also exhibited greater contralateral delay activity (CDA) in the presence of distractors. From an information processing perspective, the objective for the observer should be to efficiently allocate limited VWM resources by preventing irrelevant information from being unnecessarily represented in VWM.

Given that the CDA is an event-related potential (ERP) associated with VWM maintenance (McCollough, Machizawa, & Vogel, 2007), these low-capacity subjects appear to have encoded more task-irrelevant distractors than did high-capacity subjects. That is, greater neural measures of VWM maintenance in the presence of task-irrelevant distractors (namely, unnecessary storage) is indicative of a "leaky filter" in these low-capacity subjects.

Such negative correlations between unnecessary storage and VWM capacity has led to the suggestion that individual differences in the ability to effectively allocate capacity-limited resources through the filtering of irrelevant information may be a determining source of variation in overall VWM capacity. Awh and Vogel (2008) compared this ability to a bouncer at a nightclub. According to this view, individuals with higher (vs. lower) capacity have bouncers that are better able to keep unwanted patrons (i.e., task-irrelevant information) from entering the nightclub. By keeping unwanted patrons out, the nightclub is less likely to be overloaded and overworked by unwanted guests (i.e., irrelevant information). In other words, better performance could be attributed to a better bouncer, rather than to a larger nightclub *per se*.

Importantly, although these findings suggest that attentional selection mechanisms, rather than storage capacity, may determine VWM capacity (Luck & Vogel, 2013), this notion has largely been inferred based on the association between unnecessary storage and VWM capacity. That is, the role of the "bouncer" (the attentional selection mechanism) has been observed primarily through its role in preventing irrelevant information from occupying capacity-limited resources. It is clear how this sort of filtering mechanism would lead to better VWM performance in the presence of distractors: By preventing the selection and encoding of task-irrelevant distractors, more resources can be allocated to the task relevant information. Less clear, however, is how this selection mechanism (namely the mechanism used to prevent

unnecessary storage) could affect VWM capacity in the absence of distractors. That is, how does a mechanism that prevents the storage of irrelevant distractors determine VWM capacity when no distractors are present?

One possibility is that the activity associated with the selection and filtering of information, rather than unnecessary storage *per se,* is a more central factor determining VWM capacity. In other words, unnecessary storage may correlate with individual differences in VWM capacity not because the allocation of capacity limited resources is what drives VWM performance, but rather because unnecessary storage reflects other processes that drive selection and encoding more general (i.e., attentional selection mechanisms). One way to test this possibility is determine whether the misallocation of resources (as measured by unnecessary storage) still predicts VWM capacity once neural activity associated with the filtering process is accounted for. That is, if we can more directly measure the attentional selection mechanisms driving filtering, does this activity explain both unnecessary storage, as well as individual differences in VWM capacity? Here, we address this question by re-analyzing data from two studies that examined associations among individual differences in filtering-related activity, unnecessary storage, and VWM capacity.

Study 1: Reanalysis of McNab and Klingberg (2008)

In the first study, we re-examined the results of an influential fMRI study by McNab and Klingberg (2008) examining correlations between the neural measures of filtering set activity, the neural measure of unnecessary storage activity, and VWM capacity. For full methods including fMRI scanning parameters, see McNab and Klingberg (2008).

Summary of the Original Study

In the original study by McNab and Klingberg (2008), 25 participants performed a working memory task while undergoing fMRI. Participants were presented with a variable number of red and yellow circles to remember, presented for one second. Prior to the presentation of the memory sample, participants were presented a display (for between three to five seconds) instructing them either to remember all of the items (no distraction) or only the red items (the "distraction" condition). Thus, participants were instructed to hold in memory either three red circles while ignoring two yellow circles (the "distraction" condition), or to remember three or five items, including in some cases the yellow circles. After a delay of two to four seconds, participants had to indicate whether a probe item was presented in the location of one of the target items.

fMRI BOLD signals were modeled using a canonical hemodynamic response ,and examined for two types of activity. *Filtering set activity* was defined by contrasting activity observed during the instruction cue in the distraction compared to the no distraction trials. That is, separate regressors were used for each of the instruction conditions, for the sample presentation (with a covariate for the number of items presented during the sample), and regressors for both the maintenance and storage phases. Thus, this activity was thought to reflect the preparation to filter out distractors, and was observed in bilateral regions of prefrontal cortex (middle frontal gyrus) and the left basal ganglia (with peaks in the putamen and global pallidus). *Unnecessary storage activity* was defined as the amount of activity in load-sensitive regions of parietal and occipital cortices in the presence of distractors compared to when no distractors were present. In this case, separate regressors were used for each of the instruction displays, and for each of the distraction and no-distraction conditions, as well as the response period. Specifically, the authors isolated the regions of parietal and occipital cortex by comparing delay-period

activity in load 5 and load 3 trials in the no distraction condition. Unnecessary storage activity

was then calculated by comparing the load 3 no distraction conditions to the load 3 distraction

conditions (which included two yellow distractors). Thus, any increase in activity in these areas

in the presence of the distractors was thought to reflect the number of task-irrelevant distractors

stored in VWM compared to when no distractors were present.

Importantly, VWM capacity was measured using a variant of the no-distraction task out

side of the scanner, and calculated using the Pashler-Cowan formula (Cowan, 2001) following

the presentation of the stimuli.

Of interest here were the observed relationships between neural measures associated with

filtering set activity and unnecessary storage, and the behavioural measure of VWM capacity.

The authors observed that filtering set activity in the PFC and basal ganglia was positively

correlated with VWM capacity, and filtering set activity in the globus pallidus region of the basal

ganglia (but not activity in the PFC) was negatively correlated with unnecessary storage. Further,

unnecessary storage was negatively correlated with VWM capacity. According to the study

authors, the patterns of correlations were "consistent with the hypothesis that unnecessary

storage accounts for the correlation between filtering set activity and working memory capacity"

(McNab & Klingberg, 2008, p. 105). This account thus positions unnecessary storage as the

intervening mechanism between filtering set activity and VWM capacity (i.e., filtering set

activity → unnecessary storage → VWM capacity).

This explanation has important conceptual and empirical implications for understanding

individual differences in VWM capacity. Conceptually, the filtering mechanism determines the

efficiency of VWM through preventing irrelevant information from occupying capacity-limited

resources (i.e., unnecessary storage). Empirically, the model proposed by McNab and Klingberg

(2008) implies that preparatory filtering activity has no unique or direct impact on VWM

capacity independent of unnecessary storage. Rather, the effect of filtering set activity should be

fully explained by unnecessary storage such that unnecessary storage would predict VWM

independent of filtering set activity, but filtering would not predict VWM capacity independent

of unnecessary storage. However, this assumption was not tested directly in the original study.

For the present reanalysis, we evaluated the path model implied by the proposed mechanism, as

well as a modified model in which both filtering set activity and unnecessary storage predicted

VWM capacity.

Reanalysis

We first evaluated a path model using AMOS software in which filtering set activity in

the globus pallidus region of the basal ganglia predicted unnecessary storage activity, and

unnecessary storage activity predicted VWM capacity. Results are shown in Figure 1A. Note that

the standardized path coefficients shown in this figure are identical to the observed pairwise

correlations between adjacent variables because each path in the model represents a regression of

one criterion variable on one predictor. Critically, this model provided poor fit to the data ($\chi^2 =$

5.54, $df = 1$, $p = .02$; CFI = .68; RMSEA = .44, p for close fit = .02) owing to a large residual

association between filtering set activity and VWM capacity not accounted for by the model as

specified. Thus, a modified model was tested in which an additional direct path from filtering set

activity to VWM capacity was included. Because this model was just-identified (i.e., $df = 0$), it

necessarily provided perfect model fit. More importantly, results from this model (see Figure 1B)

indicated that filtering set activity had a unique direct effect on VWM capacity ($p = .01$),

whereas the direct predictive effect of unnecessary storage was non-significant ($p = .31$).

Critically, this model explained nearly twice the variance in VWM capacity ($R^2 = .35$) than the
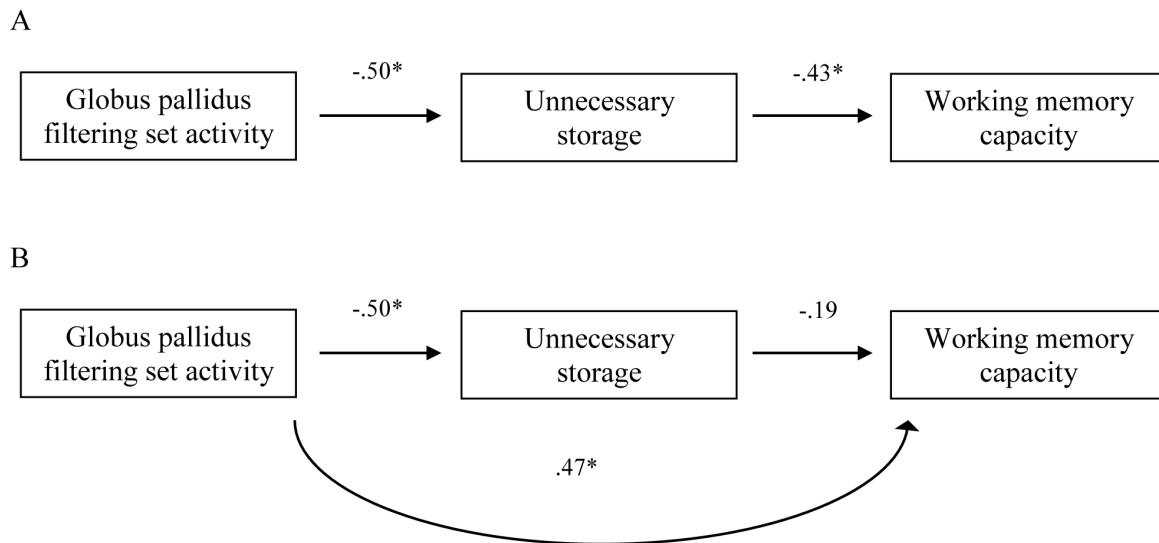
original model ($R^2 = .18$).

A

B

Figure 1 - *Results from the reanalysis of the findings presented by McNab and Klingberg (2008)*. Panel A shows results from the causal model proposed by the study authors. Panel B shows results from the modified model. Standardized path coefficients are shown. * *p* < .05.

These results indicate that unnecessary storage *did not* account for the association between

filtering set activity and VWM capacity. Further, unnecessary storage activity was not a unique

predictor of VWM capacity independent of filtering set activity. However, filtering set activity

was a unique predictor independent of unnecessary storage. Thus, rather than revealing a neural

mechanism whereby filtering activity is linked with VWM capacity via the amount of

unnecessary storage, the revised findings suggest that the neural activity underlying filtering

ability has a direct predictive effect on both unnecessary storage and VWM capacity. Moreover,

contrary to the conclusions of McNab and Klingberg (2008), unnecessary storage had no unique

predictive effect on VWM capacity.

Study 2: Reanalysis of Liesefeld et al. (2014)

A recent study by Liesefeld et al. (2014) provides additional insight into the puzzle concerning the successful operation of filtering mechanisms in VWM, through examining correlations among electrophysiological measures of three filtering-related processes (distractor detection, filtering initiation, unnecessary storage) and VWM capacity. For a detailed description of methods, see Liesefeld et al., (2014).

Summary of Original Study

In the original study by Liesefeld et al., 40 participants performed a lateralized change-detection task while EEG was recorded. Each trial began with an arrow cue, lasting for 200 ms, that cued one side of the display to be attended. Following the cue, colored squares and rectangles were presented for 100 ms, following a 100 – 200 ms fixation. On some trials, only targets (e.g., squares) were presented, whereas on other trials both targets and distractors (e.g., rectangles) were presented. Participants were instructed to remember the colors of the squares (targets) while ignoring the rectangles (distractors). The number of targets and distractors varied (two to five targets only, or two targets with two or three distractors, and three targets with two distractors). Thus, by varying independently the number of targets and distractors, the authors were able to isolate independently the effects of (1) the total number of items, (2) the number of targets, and (3) the number of distractors. After a 900 ms delay, participants had to detect the presence or absence of a change in the target (square) items on the cued side of the display.

Similar to McNab and Klingberg (2008), the analysis by Liesefeld et al. focused on two main contrasts. The *distractor-presence* contrast compared trials with four or five targets only to those trials with distractors. Thus, this comparison could isolate the effect of distractors on electrophysiological components while controlling for the total number of items. This analysis isolated two separate components. The earliest component was the *distractor detection*

component, which was observed in posterior electrodes, and showed larger peak amplitude in the

presence of distractors. This component occurred over contralateral (attended) channels about

228 ms after the onset of the sample display, and showed larger amplitudes for trials with

distractors than those trials with only targets, suggesting a role in the initial detection of

distractors in the display. Following the distractor detection component was a component that

occurred over frontal electrode sites, and which was affected primarily by the presence or

absence of distractors from the sample array. The authors hypothesized that this second

component – a "prefrontal bias signal" – reflected the initiation of filtering processes once the

distractors were identified by the posterior distractor detection processes.

The second analysis by Liesefeld et al. focused on isolating the effects of *unnecessary*

storage. This was achieved by isolating the parietal components that increased as a function of

the number of objects, and was sustained throughout the delay. This analysis revealed a slow-

wave component that occurred over posterior electrode sites and was affected by the number of

targets as well as distractors, and is similar to the CDA. Slow-wave parietal activity was then

compared between target-only trials and distractor-present trials with the same number of targets.

Thus, this unnecessary storage activity is thought to reflect the additional number of task-

irrelevant distractors stored in VWM.

Liesefeld et al. found that distractor detection latency was negatively correlated with

prefrontal bias signal and VWM capacity, and positively correlated with unnecessary storage.

Prefrontal bias signal strength was negatively correlated with unnecessary storage, and positively

correlated with VWM capacity. Further, unnecessary storage was negatively correlated with

VWM capacity. Thus, the authors proposed a three-stage model of efficient filtering, whereby

faster detection of distractors (as indicated by posterior EEG components) leads to a stronger

bias signal from the prefrontal cortex triggering the filtering process (observed as a frontal ERP that preceded the onset of unnecessary storage activity), which then enables greater exclusion of distractors from VWM and thus less unnecessary storage (as assessed by parietal delay activity similar to the CDA). Together, these three processes are thought to form a "causal chain of events that constitute filtering in VWM" (Liesefeld et al., 2014, p. 327) wherein more successful filtering is indicated by less unnecessary storage. With respect to the bouncer analogy, Liesefeld et al. liken distractor detection to the bouncer's eyes and filter initiation to the bouncer's hands; in their model, the bouncer must first identify the unwanted guests before preventing them from entering the club.

Although these individual pairwise associations, as well as the observed temporal order of the electrophysiological components, are consistent with their proposed model, the authors did not test the path model implied by their causal chain, nor did they evaluate these processes as simultaneous predictors of VWM capacity. Consequently, it remains unclear whether the impact of distractor detection on unnecessary storage is fully explained by prefrontal bias strength, as suggested by the causal chain model. Further, although the authors proposed that "both the bouncer's eyes and hands are vital" (p. 332) to determining individual differences in VWM capacity, it is unclear whether any or all three of the processes comprising efficient filtering uniquely (i.e., when examined as simultaneous predictors) predict VWM capacity.
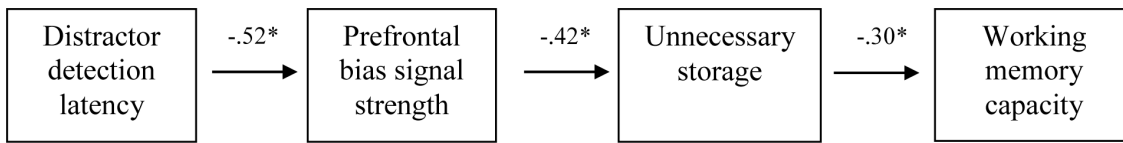
Reanalysis

To address this issue, we used the correlations provided in Liesefeld et al. (2014) to test the proposed causal chain among the three filtering-related processes (i.e., distractor detection, filtering initiation, unnecessary storage) and an additional link from unnecessary storage to VWM capacity (consistent with Awh & Vogel, 2008; McNab & Klingberg, 2008). Results are

shown in Figure 2A. This model provided poor fit (model $\chi^2 = 8.83$, $df = 3$, $p = .03$, CFI = .78,

RMSEA = .22, p for close fit = .05) owing to a large residual association between prefrontal bias

signal strength and VWM capacity not accounted for by the model as specified. Thus, a modified

model was tested in which an additional direct path from prefrontal bias to VWM capacity was

included. This modified model provided excellent model fit (model $\chi^2 = 0.28$, $df = 2$, $p = .687$,

CFI > .99, RMSEA < .01, p for close fit = .88). Further, the remaining residual associations

(between distractor detection latency and unnecessary storage, and between distractor detection

and VWM capacity) were small and non-significant. As shown in Figure 2B, prefrontal bias

strength was a unique predictor of VWM capacity ($p = .002$), whereas the predictive effect of

unnecessary storage was non-significant ($p = .49$). Note that results were consistent when the two

remaining predictive paths (from distraction detection to unnecessary storage and to VWM

capacity) were added to the model ($df = 0$); see Figure 2C for these results. Critically, the model

identifying filtering activity as a direct predictor of VWM capacity explained three times as

much variance in individual differences of VWM capacity ($R^2 = .27$) as did the original model

attributing that variance to unnecessary storage ($R^2 = .09$).
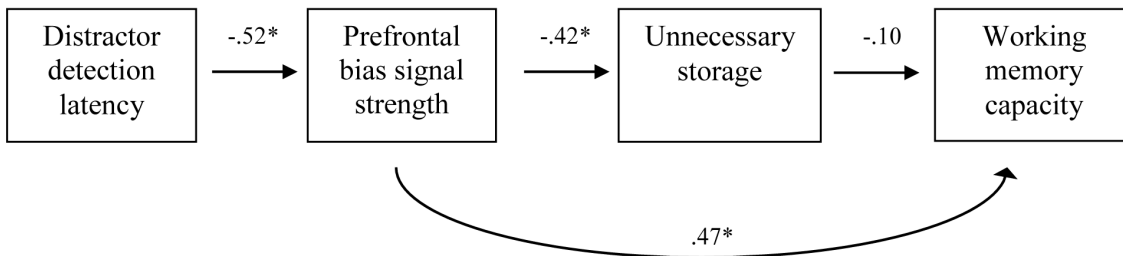
 Consistent with Liesefeld et al.s' proposed causal chain comprising three filtering-related

processes, the path model results indicate that distractor detection directly predicted prefrontal

bias signal strength, prefrontal signal strength directly predicted unnecessary storage, and this

latter path fully accounted for the link between distraction detection and unnecessary storage.

With respect to predicting VWM capacity, however, results also indicate that unnecessary

storage *did not* account for the association between the initiation of filtering activity (as reflected

by prefrontal bias strength) and VWM capacity. Further, unnecessary storage activity and

distractor detection *were not* unique predictors of VWM capacity independent of filtering

initiation. The revised findings thus suggest that of the three filtering-related processes, *only* prefrontal bias strength was a unique predictor of VWM capacity – not the processes occurring prior to (distraction detection) or subsequent to (unnecessary storage) it in the causal chain.
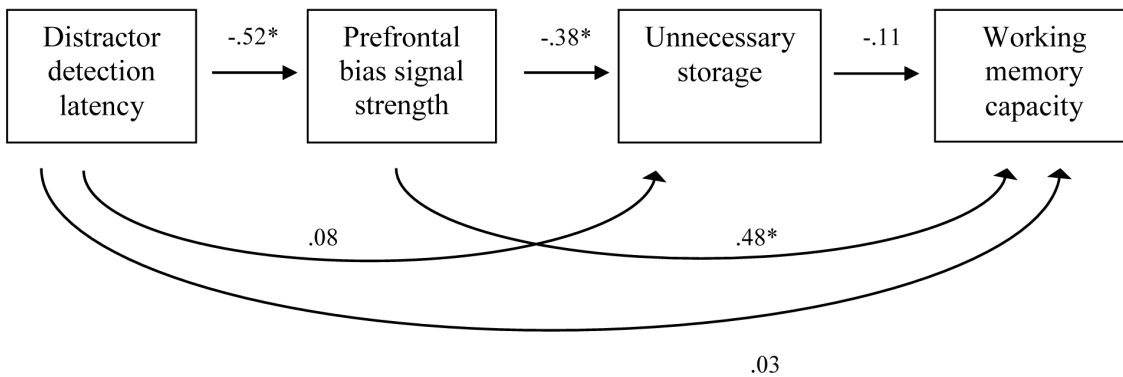
A

| Distractor detection latency | → -.52* → | Prefrontal bias signal strength | → -.42* → | Unnecessary storage | → -.30* → | Working memory capacity |

B

| Distractor detection latency | → -.52* → | Prefrontal bias signal strength | → -.42* → | Unnecessary storage | → -.10 → | Working memory capacity |

.47*

C

| Distractor detection latency | → -.52* → | Prefrontal bias signal strength | → -.38* → | Unnecessary storage | → -.11 → | Working memory capacity |

.08   .48*

.03

Figure 2 - *Results from the reanalysis of the findings presented by Liesefeld, Liesefeld, and Zimmer (2014).* **Panel A shows results from the first path model tested. Panel B shows results from the modified model. Path C shows results from a model incorporating all predictive effects. Standardized path coefficients are shown. * *p* < .05.**

That is, how effectively targets and distractors are selected is particularly important to VWM capacity, rather than how quickly the distractors are identified. In this regard the present findings suggest a modification to the proposal from Liesefeld et al. (2014) that both the

bouncer's eyes and hands are vital to determining individual differences in VWM capacity: Although distractor detection is important for the filtering process (as revealed by the significant link between distraction detection and filtering initiation), distractor detection is not directly or uniquely relevant to determining individual differences in VWM capacity (as revealed by the non-significant link between distractor detection latency and VWM capacity, independent of filtering activity).

General Discussion: Does the Bouncer Need a Raise?

Together, the reanalyses from both studies converge on the conclusion that the amount of unwanted information in VWM (as reflected by unnecessary storage) is *not* the primary determinant of VWM capacity. Rather, when tested alongside neural indicators of filtering preparedness or engagement (occurring temporally prior to the onset of the unnecessary storage activity), it is this activity that is uniquely predictive of VWM capacity. Further, the revised models in which activity associated with filtering directly predicts VWM capacity explained roughly two to three times as much variance in individual differences in VWM capacity as did the original models in which the link between filtering activity and VWM capacity was assumed to be indirect, via unnecessary storage. Accordingly, the present findings help to elucidate the mechanisms underlying individual differences in VWM capacity by ruling out particular stages and types of processing (i.e., unnecessary storage and distraction detection) as unique and direct predictors of VWM capacity, while also identifying filtering-related activity (i.e., filtering preparedness and initiation) as the primary predictor of VWM capacity in these studies.

How could filtering-related activity impact VWM capacity if not through unnecessary storage? The conceptual framework for how unnecessary storage relates to VWM capacity is somewhat murky. Unnecessary storage activity in both fMRI (McNab & Klingberg, 2008) and

ERPs (Vogel et al., 2005) is identified by comparing activity when low numbers of both targets and distractors are present to when only low numbers of distractors are present. The additional "storage" related activity in the presence of distractors indicates a poor selection mechanism, and it is this additional activity that is predictive of VWM capacity. Thus, the conceptual model of unnecessary storage impacting VWM capacity was conceived largely within a framework in which VWM contains a limited number of storage slots; according to this framework, processing of irrelevant (i.e., distractor) information is critical to predicting VWM performance insomuch as unwanted information occupies these limited storage units and restricts the amount of target information that can be stored. However, although it is clear why storing irrelevant distractors should reduce the number of available slots for storing targets, it is unclear how this mechanism applies when only target information is present. That is, if capacity is measured by how many targets can be stored when no distractors are present, how does unnecessary storage impact capacity when no distractors are present? It would appear, therefore, that identifying a mechanism through which target (in addition to distractor) information is processed may have more explanatory power, even within the context of a limited number of storage slots.

Moreover, there is recent debate in the field as to whether, in fact, VWM capacity is limited by the number of storage slots alone, thus potentially calling into question the framework by which unnecessary storage limits VWM performance in a capacity limited system. Namely, resource models conceptualize working memory as a limited pool of resources that must be allocated across all (task-relevant) items – as the proportion of resources allocated to each item decreases, the precision or fidelity of those representations decrease (Bays, Catalao, & Husain, 2009; Bays & Husain, 2008; Huang, 2010; van den Berg, Shin, Chou, George, & Ma, 2012). Importantly, the precision of the maintained representations can vary between items (Fougnie,

Suchow, & Alvarez, 2012), trials (van den Berg et al., 2012), by the allocation of attention

(Gorgoraptis, Catalao, Bays, & Husain, 2011), and may be under cognitive control (Machizawa,

Goh, & Driver, 2012), such that precision and the number of items maintained can be traded off

against each other (Roggeman, Klingberg, Feenstra, Compte, & Almeida, 2014). Consequently,

although the processing of irrelevant information would reduce the amount of resources allocated

to task-relevant information, preparatory activity that is associated with filtering may also be

related to VWM performance through the efficient processing of *relevant* (target) information

(e.g., by selectively enhancing the precision of target items through the allocation of resources).

For example, one study identified activity in the inferior frontal sulcus that correlates with a

trade-off between the number and fidelity of the stored target items (Roggeman et al., 2014).

Interestingly, changes in the precision of representations maintained in VWM may occur in

sensory cortex rather than in the storage-related activity associated with the intraparietal sulcus

(IPS) (Emrich, Riggall, Larocque, & Postle, 2013), thereby potentially calling into question the

role of delay-period parietal activity in VWM maintenance and representation. Results from the

reanalyses presented in the present work do not speak to the slots-versus-resources debate, and it

is possible that changes in VWM precision via top-down attentional control signals can be

accomodated within a slots + resource model (van den Berg et al., 2012; Zhang & Luck, 2008).

Nevertheless, the present results do suggest that understanding precisely how target information

is encoded into VWM may be more critical to determining individual differences in VWM than

is the unnecessary storage of irrelevant information.

The proposal that filtering preparedness or initiation activity may be related to the

processing of targets as well as distractors is also consistent with the hypothesized role of

filtering activity as indicative of top-down control over the flow of information into VWM (Awh

& Vogel, 2008; Gazzaley & Nobre, 2012; McNab & Klingberg, 2008). From this perspective,

filtering activity could reflect general top-down (executive) attentional control mechanisms that

are also involved in the selection and encoding of information in VWM. Individual differences in

such top-down attentional processes may be responsible for the coordination of filtering and

unnecessary storage, as reflected in the association between these two processes, and for their

links with VWM capacity. Such an account is consistent with findings indicating that VWM

capacity is correlated with the ability to recover from the attentional capture by task-irrelevant

distractors (Fukuda & Vogel, 2009). Thus, the top-down attentional processes that drive efficient

filtering may be the same processes that drive the efficient selection and encoding of

information, and it is this more general top-down attentional mechanism that underpins

individual differences in VWM capacity. In this sense, "filtering set activity" and the "prefrontal

bias signal" may not reflect activity specific to filtering, but rather activity related to a broader

top-down mechanism that is involved with the processing of both relevant and irrelevant

information.

Interestingly, recent evidence may provide some insight into the precise mechanisms that

may mediate the top-down processing of targets in VWM. Feredoes and colleagues (Feredoes,

Heinen, Weiskopf, Ruff, & Driver, 2011) examined the role of the dorsolateral prefrontal cortex

(DLPFC) in processing targets and distractors. Participants were instructed to maintain images of

faces or houses, and on some of the trials images from the other category could be presented as

distractors during the delay. Critically, when the DLPFC was stimulated with transcranial

magnetic stimulation (TMS) during the delay period, an increase in activity was observed in the

areas of visual cortex involved in processing the target stimuli (e.g., the fusiform face area).

Thus, the DLPFC may serve as the source of a top-down signal that is involved in the enhancement of target stimuli.

In many ways, our observation that filtering-related activity predicts VWM capacity independent of unnecessary storage activity is subject to the same limitations as the model it disconfirms. Whereas the original model stated that the unnecessary storage of task-irrelevant distractors predicts VWM capacity – even when capacity is measured in the absence of distractors – the revised model suggests that filtering-related activity predicts VWM capacity *even in the absence of filtering*. That is, the filtering-related activity in the two studies re-examined in the present work was operationalized as activity present during active filtering and absent when filtering is not required. Thus, it is unclear how this activity (and the process(es) reflected by it) might affect VWM capacity when filtering is not required. Consequently, it will be critical for future studies to determine how to identify filtering-related activity in the absence of distractors, or how to better operationalize the activity observed during filtering. A potential candidate for such activity may be provided by a study that found a positive correlation between VWM capacity (which was measured both by behavioral performance and by the amount of BOLD signal observed in the IPS) and activity in the DLPFC (Edin et al., 2009). The authors of this study suggested that VWM capacity was partly determined by top-down control driven by activity originating in the DLPFC, even when distractors were not present. In other words, consistent with the analysis reported here, findings from Edin et al. suggest that individual differences in VWM performance may be explained by top-down signals driving target processing, rather than by unnecessary storage. Importantly, the top-down activity reported by Edin et al. was modulated by working memory load, suggesting that top-down signals from DLPFC are tied to variations in the amount of attentional control required. Thus, one possible

reason why tasks that require filtering elicit a strong top-down control signal is because filtering requires greater attentional control. However, further research is required to fully establish the links between DLPFC activity, VWM capacity, and filtering.

It is important to stress that although the models tested here provide strong evidence against the unique role of unnecessary storage in predicting VWM capacity, we acknowledge that the revised model, too, may be incomplete or incorrect, as may be revealed in future studies based on additional experimental evidence. For example, future studies may identify more sensitive or valid measures of the key underlying cognitive processes under consideration in the present work; in such cases, further examination of the models examined here would be valuable. In addition, there are limitations to the path analytic approach we employed. For example, we do not know the reliabilities of the various measures, nor have we tested possible non-linear effects, both of which could affect the outcome of these analyses. Furthermore, the modest sample sizes of both studies we re-examined likely attenuated the statistical power to detect as statistically significant relatively small predictive effects.[1] Moreover, it is possible that activity that has previously been identified as reflecting "unnecessary storage" or "filtering initiation" reflect as-of-yet undefined processes or cognitive mechanisms. Finally, further studies are required to determine more precisely the relationship between top-down signals (e.g., DLPFC activity), the processing of targets and distractors, and unnecessary storage; indeed, the results presented here highlight the importance of fully testing the different possible models moving forward, ideally through directly evaluating competing models.

Conclusion

Findings from our reanalyses indicate that Awh and Vogel (2008) were correct in emphasizing the importance of a good bouncer (i.e., a strong filtering mechanism) to determining

the success of the VWM nightclub. And yet the value of the activity associated with the initial

stages in filtering is not limited to or explained by the relationship between unnecessary storage

and VWM capacity. Rather, activity associated with filtering preparedness or initiation appears

to play a more central role in predicting individual differences in VWM capacity than has been

previously recognized. The precise nature of this activity (e.g., as an determinant of efficient

selection and encoding of relevant information, or as an indicator of a more general top-down

attentional control process) has yet to be clarified. To this end, our work provides novel

conceptual and empirical insights concerning the roles of filtering-related activity and

unnecessary storage in understanding individual differences in VWM capacity.

Notes

[1] To evaluate the robustness of our findings, we re-estimated the parameters in each model (path coefficients, *p* values) using a bootstrapping approach and based on bias-corrected estimates from 1000 resamples. Results were consistent with those presented in the main text. These bootstrapping results indicate that our findings are not overly biased by the relatively small sample sizes of the studies we re-analyzed. However, the statistical power to detect relatively smaller predictive effects was limited by the sample sizes; for example, a sample size of approximately 100 participants would be needed to find the path from unnecessary storage to working memory capacity shown in Figure 1B to be statistically significant.

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