# Visual working memory



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Visual working memory (VWM), the system of storing, manipulating, and utilizing, visual information is fundamental to many cognitive acts. Exploring the limitations of this system is essential to understand the characteristics of higher-order cognition, since at a basic level, VWM is the interface through which we interact with our environment. Given its important function, this system has become a very active area of research in the recent years. Here, we examine current models of VWM, along with the proposed reasons for what limits its capacity. This is followed by a short description of recent neural findings that have helped constrain models of VWM. In closing, we focus on work exploring individual differences in working memory capacity, and what these findings reveal about the intimate relationship between VWM and attention. © 2013 John Wiley & Sons, Ltd.

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# INTRODUCTION

ur ability to acquire, maintain, and use information from our environment relies on working memory, 1-3 a system that allows us to temporarily keep information 'in mind' while we manipulate or act upon it. Most theories of working memory propose that this system is limited in its storage capacity, and relies on separable verbal and visual storage subsystems. 4 The visual component, known as visual working memory (VWM), a supports the maintenance of a small amount of visual information over a short period of time. Considering the important role that VWM plays in both perception 5 and higher-level cognition, 6 understanding the limits of its processing has been the topic of sizable research efforts in the past several decades.

The most notable characteristic of working memory is its limited capacity. Both behavioral and neural studies have suggested that VWM capacity is limited to about three to four items. The first indications of this highly limited capacity were provided by Sperling's<sup>7</sup> classic experiments on iconic memory. In these studies, participants were shown brief displays of alphanumeric characters, and were instructed to immediately report as many items as they could remember. When asked to report all of the items in the display, Sperling found that participants

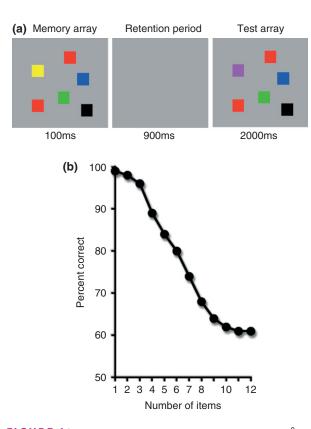
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could report only about four or five items on average. However, there are a few potential limitations of this estimate of VWM. First, participants were required to either vocalize or write down their responses, and this reporting process may have underestimated how many items were stored. Second, the memoranda were letters and numbers, which may have encouraged participants to use a verbal code to store the items, and thus performance may have also relied on verbal working memory mechanisms.

The work of Philips<sup>8</sup> overcame some of the limitations of the Sperling studies. Instead of whole or partial report, Philipps showed subjects two hard-toverbalize checkerboard patterns that were separated by a varying interstimulus interval and asked the subject to report whether the two checkerboards were the same or different. This change detection task revealed that performance was near perfect for very short intervals (e.g., <250 ms), then declined precipitously over the following several hundred milliseconds. He manipulated the complexity of the memoranda by increasing the number of cells in the checkerboard, and found that the more complex arrays showed more substantial declines in performance. While these results also reveal the capacity-limited nature of VWM, the use of complex arrays made it difficult to establish an easily quantifiable estimate of VWM capacity.

Using a similar approach, Luck and Vogel<sup>9</sup> used a variant of Phillips'<sup>8</sup> change detection paradigm<sup>10</sup>
Oregon, Eugene, OR, USA with displays that contained simple and highly

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**FIGURE 1** (a) Change detection task used by Luck and Vogel. Participants were shown a memory array for 100 ms, followed by a 900 ms retention period, and test array. The test array was either identical to the original memory array, or differed by one item. (b) Average accuracy as a function of set size. Performance was very high for set sizes 1–3, and began to systematically decrease as the set size increased beyond three items.

discriminable colored objects. In this procedure (see Figure 1), participants are briefly shown arrays of colored squares, which disappear for about 1 second (retention interval). Following the retention interval, a test array is presented that either perfectly matches the colors of the initial memory array on half of the trials, or contains one item that changed color on the other half of the trials. By systematically varying the set size of the memory array to contain from 1 to 12 items, Luck and Vogel, like Sperling, found capacity to be between three and four items. That is, participants were near perfect at detecting changes for arrays containing one, two, or three items, but then systematically declined in performance for larger array sizes. Importantly, this estimate was unaffected by a verbal memory load<sup>9,11</sup> indicating that verbal storage was not contributing to performance. Although there is continuing debate regarding the precise nature of these capacity limits (as will be discussed below), these experiments did demonstrate that the storage

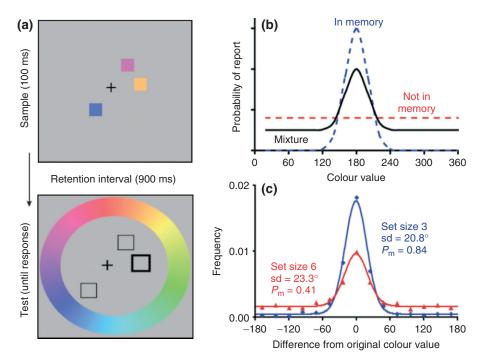
capacity of VWM is limited to a very small amount of visual information.

Given the importance of working memory for performing many cognitive tasks, there are numerous active research areas exploring a wide range of topics related to VWM. For the present review, however, our more feasible goal is to concentrate on three core issues within current work on VWM. First, we will discuss the ongoing debate regarding the nature of VWM capacity limits. Second, we focus on new research establishing neural measures of VWM capacity, and how these findings relate to models of VWM. Finally, we describe new findings that are highlighting the important relationship between VWM and selective attention, and what these two concepts reveal about individual differences in VWM capacity.

# CAPACITY LIMITS: NUMBER OR RESOLUTION?

There has been an ongoing debate over how to best characterize the limits of VWM. Luck and Vogel<sup>9</sup> interpreted their initial findings as evidence that capacity<sup>b</sup> is determined by a maximum number of items that individuals could store simultaneously. The view that a maximal number of items stored is what limits capacity is often termed the 'slot' or discrete resource model of VWM capacity. According to strong versions of this theory, the capacity of working memory is determined by the number of 'slots' available, and the resolution of the representations that occupy each slot is relatively stable.<sup>9,12</sup> In contrast, pure flexible resource models propose that VWM resources are distributed in a continuous manner, and may be flexibly shared between as few or many representations as necessary, with a tradeoff in the precision of representations. Consequently, the limiting factor for performance in these models is not how many items are stored, but rather how much resource is devoted to each representation. Thus, the reason that performance suffers as more items are stored is because each representation is allotted a smaller portion of a finite resource.<sup>13</sup>

To test whether the fidelity of representations changes as a function of the number of items stored, Wilken and Ma<sup>14</sup> applied a signal detection approach to a change detection task. According to their view, VWM representations are inherently noisy, and the greater the number of representations that must be maintained, the greater the amount of noise in the system. Following this logic, Wilken and Ma suggested that the loss of accuracy observed at higher set sizes is a consequence of the increase in the magnitude of noise, rather than a constant capacity limit. To test



**FIGURE 2** (a) Recall procedure used by Zhang and Luck.<sup>12</sup> Participants were shown a memory array, and following a 900 ms retention period, reported the color of a probed item by clicking on a color wheel. (b) Predicted results of Zhang and Luck's mixture model. The model combines a Gaussian distribution of responses for stored items (dashed blue line), with a uniform distribution of responses for items that were not stored (dashed red line). On average, performance will reflect responses to both stored and not stored items, resulting in a mixture of the two distributions (solid black line). (c) Results for set size 3 and 6; though the probability of reporting a color that was not stored increased with set size (reflected by difference between the tail ends of the distributions), the standard deviation of the distributions did not, indicating no change in resolution.

this hypothesis, they employed a continuous report procedure in which participants were given a memory array, much like the one used by Luck and Vogel, but were required to report the exact color of a cued item by adjusting a color wheel. The results of their experiments indicated that the accuracy of the participants' responses decreased as the number of memory items increased, indicating that the fidelity of VWM representations decreased as set size increased.

However, one potential problem with the Wilken and Ma findings is that they did not test the possibility of subjects storing a small number of fixedresolution representations, and randomly guessing when the tested item was not in memory. Using the same continuous report procedure, Zhang and Luck<sup>12</sup> used a mathematical technique to isolate participants' responses as either stored representations or random guesses. By analyzing the distribution of response errors, they were able to determine whether an item had been stored in VWM, and also the resolution of the stored representations. The results indicated that when the memory array contained one to three items, guessing rate was fairly low. However, as set size increased, so did the proportion of random guesses, suggesting that participants were indeed able to store no more than three items in VWM. Though the number of stored items did not vary by set size, the resolution of representations, as indexed by the standard deviation of responses, did. Zhang and Luck could account for this last finding by incorporating an averaging process to their model. According to this 'slots + averaging' theory, working memory is comprised of three discrete slots, and if the number of to-be-remembered items is below capacity, each slot can store an independent representation of each item. These independent copies can then be averaged together to yield more precise representations of memory items (Figure 2).

This leads us to an important assumption of the model: the precision of VWM representations can never exceed that of a single slot. The reason that precision is higher for fewer than three stored items is that multiple slots, each with an independent source of error, are averaged together to yield a more precise representation. When individuals are maintaining about three items, the precision of each representation will reflect the noise level of each slot, and thus, the standard deviation measure of precision should plateau when memory capacity is reached. This is exactly what Zhang and Luck observed.

However, others have suggested that this plateau in precision is an artificial phenomenon, resulting from individuals accidentally reporting the color feature of a non-target item.<sup>13</sup> Though more recent experiments have suggested that a likely reason for why a clear resolution cutoff may not always be found is because of substantial individual differences in working memory capacity. Importantly, Anderson et al.<sup>15</sup> demonstrated that when these individual differences are accounted for, the precision of VWM representations reaches a stable asymptote once an individuals' capacity has been reached.

Besides these two viewpoints, a third class of models propose that VWM capacity is limited both by a maximal number of items, as well as a limited amount of resolution resources that must be shared amongst the actively represented objects. For example, Alvarez and Cavanagh 16 found that capacity estimates are negatively related to stimulus complexity. In this set of experiments participants were shown items that could range from simple colored squares, to very complex objects such as Chinese characters, or shaded cubes. They operationalized the information load of each stimulus using a visual search paradigm, with search rate being used as a metric of information load. The results indicated that information load was inversely related to memory capacity for each class of items, such that individuals could remember about four or five simple squares, and approximately one complex shaded cube. Alvarez and Cavanagh interpreted these findings as evidence for a hybrid between the discrete- and flexible-resource models. Meaning that the amount of resource allocated to each representation will limit capacity, though there is also an upper bound to how many items may be represented, even when information load is very low. A potential caveat to these findings, however, is that as the complexity of the stimuli increased, so did the similarity between the memorandum and test. That is, for more complex items the perceptual difference between the item in memory and the changed item presented at test is much smaller than that for simple items. Awh et al.<sup>17</sup> showed that when this similarity confound is controlled for, memory capacity did not vary as a function of stimulus category. In these experiments, when the similarity between the memory and test array was high, such as when a Chinese character changes into a different Chinese character, individuals were pretty inaccurate at detecting that a change has occurred. However, when similarity between the two arrays decreased, such as when a Chinese character was changed into a colored cube, change detection performance increased, and memory capacity was again estimated to be about four items. These results suggest that the number of represented items does not decrease with object complexity, but rather that the resolution needed for an accurate judgment during a fine-grained comparison increases.<sup>18</sup>

Clearly there are limits to the amount of information that may be simultaneously represented in VWM. Unfortunately, there is still no definitive agreement in the literature on whether these capacity limits arise due to a fixed item-limit, or an exhausted continuous resource. Both general classes of models do a fairly good job of explaining the extant behavioral data. Consequently, we suggest that research on the neural bases of item limits may provide fruitful and informative new constraints on extant theories, yielding neurophysiologically plausible models of VWM processes.

# **NEURAL MEASURES OF VWM**

While long-term memory representations are sustained through relatively permanent changes at the synaptic level, VWM representations are maintained through the sustained firing of neurons. <sup>19</sup> This distinction between long-term memory and VWM is often difficult to determine using behavioral tasks because performance could depend on a range of processes that extend well beyond the 'online' maintenance demands on VWM. As a result, neural measures of VWM processing are critical to understanding the mechanisms involved in the active maintenance of information.

Over the past few decades, primate studies have been considerably successful in revealing which brain areas facilitate working memory. For example, single-unit recordings have shown that when monkeys perform a delayed-match-to-sample task, in which they have to maintain one representation in mind and match it to a subsequent test stimulus, neurons that initially fired to a to-be-remembered stimulus will continue to fire above their baseline firing rate throughout the retention period.<sup>20,21</sup> This phenomenon, referred to as delay activity, has been observed in a wide range of cortical areas, and is particularly prevalent in three key areas: the prefrontal cortex (PFC), the posterior parietal cortex, and inferior temporal cortex. 20,22,23 Importantly, the activity observed in each of these areas is often specific to the type of information that is currently being maintained. For example, some evidence suggests that delay activity in the posterior parietal cortex reflects the spatial location of encoded information,<sup>24–26</sup> while activity in the inferior temporal cortex is more important for representing the identity of representations.<sup>21,27</sup>

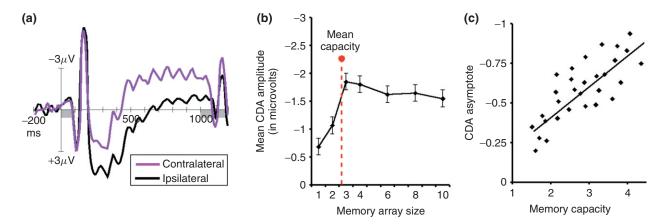
The prefrontal areas, however, seem to play a vital role in integrating the information associated with VWM representations, <sup>22</sup> likely through the intrinsic connectivity within the PFC. <sup>28</sup> Though the precise nature of interactions between posterior and prefrontal areas is far from being well understood, substantial evidence suggests that feedforward and feedback communication between these areas is vital for the maintenance of VWM representations. <sup>25,29</sup>

In addition to online maintenance, prefrontal regions have also been shown to be important for the retrieval of representations from long-term memory.<sup>30</sup> For example, Rainer et al.<sup>22</sup> showed that activity in the PFC toward the end of a retention period begins to reflect an anticipated stimulus (previously associated with the shown stimulus), rather than the initially presented stimulus. Experiments using human observers have yielded results that are remarkably similar to these findings. In a fMRI study, Ranganath et al.31 observed that activity in category-selective regions of the inferior temporal cortex begins to increase when participants performed either a working memory or delayed paired associates task. Furthermore, activity in the hippocampus and anterior prefrontal cortes was especially enhanced during the retrieval stage of the paired associates task. Overall, both experimental evidence, <sup>20,23,30,32–35</sup> and biophysical models of working memory<sup>36,37</sup> support the view that sensory information is mainly preserved in posterior regions, while the PFC exerts top-down control over these more posterior areas, possibly providing a mnemonic code for relevant representations or task rules. 38,39

Along with revealing the biological underpinnings of VWM processes, single-unit studies are beginning to provide information on why behavioral data can often support multiple models of working memory. Using a change detection task while simultaneously recording from the parietal and frontal cortex, Buschman et al. 40 obtained results consistent with a hybrid of both discrete- and flexible-resource models of working memory. In these experiments, monkeys were presented with visual displays of items that were either bilaterally or unilaterally distributed. When more items were presented on the same side as a subsequently tested item, performance began to decline, indicating that resources were shared among items presented in one visual hemifield. However, if more items were added to the side that was contralateral to the subsequent target item, performance was not affected, suggesting a discrete, slot-like capacity limit between the left and right hemifields. In all, the amount of information that the monkeys were able to maintain for each visual hemifield increased until

about two items, resulting in a capacity of about two for each hemifield, and a capacity limit of about three to four items in total across both hemispheres. Although human subjects do not appear to show the same performance deficits based on the lateralization of stimuli, 41,42 neuroimaging experiments have also provided support for aspects of both discreteand flexible-resource models of VWM. More specifically, the findings of Xu and Chun<sup>43,44</sup> suggest that neural activity in the inferior intra-parietal sulcus (IPS) reflects the number of items stored in memory, regardless of item complexity. After a four-item limit has been reached, activity in this area begins to plateau, indicating a fixed capacity on the number of items that may be represented. In contrast, activity in the superior IPS and lateral occipital complex fluctuated with the number and complexity of objects that individuals were able to hold in memory, suggesting a more flexible allocation of resources.

One weakness of neuroimaging experiments, however, is they have a limited temporal resolution, which makes it difficult to assess whether the observed activity reflects the active maintenance of VWM representations throughout the trial period, or some kind of retrieval process during the response phase. Though some experimenters have attempted to address this issue by increasing the retention interval during the scanning period, 43,45 recent findings suggest that with longer delays performance may begin to depend on contributions from long-term memory.<sup>46</sup> For this reason, electrophysiological measures of neural activity are especially well suited for assessing exactly how many representations individuals are actively maintaining in an 'online' state. For example, Vogel and Machizawa<sup>47</sup> found that event-related potentials (ERPs) time-locked to the onset of a bilateral display of items, show a negative wave over posterior electrode sites contralateral to the position of the remembered item (see Figure 3). This negativity, known as the contralateral delay activity (CDA), persisted throughout the retention interval until the test was presented. The amplitude of the CDA increased as a function of the number of to-be-remembered items, but reached an asymptote at approximately three items. Moreover, the point at which the CDA reached an asymptote was strongly related to each individual's working memory capacity, such that individuals with lower VWM capacity reached a plateau at lower set sizes than higher capacity individuals. These and follow-up experiments<sup>48</sup> have found that the CDA is unchanged by the number of locations monitored, task difficulty, or the size and spacing of memory items, indicating that the CDA is a pure measure of the number of



**FIGURE 3** | (a) The contralateral delay activity (CDA) as shown by Vogel and Machizawa. <sup>47</sup> In this task the contralateral negativity reflects the attended hemifield for a bilateral array of items. ERPs were time-locked to the onset of the memory array; posterior electrode sites ipsilateral and contralateral to the attended locations were averaged together. (b) Mean amplitude of the CDA as a function of memory array size. Note that amplitude plateaus at three items. (c) Correlation between an individual's memory capacity and their CDA asymptote.

items that individuals are able to actively maintain in VWM.

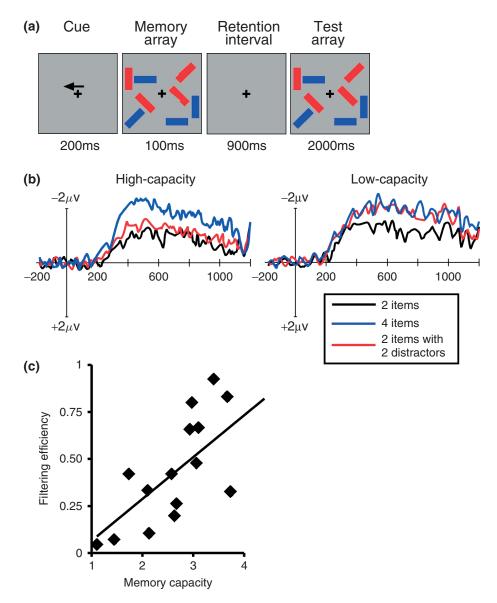
# INDIVIDUAL DIFFERENCES IN CAPACITY AND ATTENTION

Individuals show stable and systematic variability in VWM performance. These individual differences in VWM capacity are an important aspect of cognitive ability because they predict differences in intellectual ability, such as fluid intelligence and scholastic achievement. Accordingly, a significant question for a VWM researcher is why these individual differences exist in the first place, and how best to characterize the difference between a high- and low-capacity individual.

A dominant and intuitive model of individual differences in VWM is that high-capacity individuals simply have more 'slots' in memory than low-capacity individuals. However, growing evidence has begun to support an alternative explanation for these capacity differences. That is, rather than differing in terms of available storage space, high- and low- capacity individuals may instead differ primarily in their ability to use attention to control what is stored in working memory. In fact, a number of reports on verbal working memory have found that high and low WM capacity individuals differ in their performance on an anti-saccade task, a task thought to reflect executive attention ability. 49-51 In regards to VWM, this suggest that high-capacity individuals may be better at restricting the inputs to VWM to include only the most task-relevant items within the environment, whereas low-capacity individuals may be poorer at filtering out irrelevant items from being unnecessarily stored in VWM. 52-55

Further support for this controlled attention theory comes from reports showing that many of the cortical regions implicated in the formation and maintenance of VWM representations are also important for controlling the allocation of attention. <sup>56–60</sup> Indeed, some have argued that the limiting factor in short-term memory tasks is the scope of attention. <sup>61,62</sup> Given this tight coupling between attention and VWM, an important question concerns how the ability to control attention is related to memory capacity.

Both electrophysiological and neuroimaging studies have provided compelling demonstrations of individual differences in the ability to filter irrelevant information. In one such study, Vogel et al.<sup>55</sup> instructed participants to restrict which items they were to hold in memory by asking individuals to select and store only the red items in memory arrays that contained both red and blue items (see Figure 4). Using the CDA amplitude as a measure of filtering efficiency, Vogel et al. found that higher capacity individuals were much better at keeping irrelevant objects from being stored than low-capacity individuals. For example, when lowcapacity individuals were presented with displays that contained two red and two blue items, the amplitude of the CDA more closely resembled that of four relevant items presented on the screen; while for highcapacity individuals, CDA amplitude was more similar to that for two items, suggesting much more efficient filtering. Importantly, these results show that under many circumstances, low-capacity individuals actually hold more information in VWM than high-capacity



**FIGURE 4** (a) Filtering task used by Vogel et al.<sup>55</sup> Each trial began with an arrow cue indicating which side of the memory array was to be attended and compared to a test array. The memory array could contain two or four relevant items (e.g., two or four red items), or two relevant and two irrelevant items (e.g., two red and two blue, as shown). (b) CDA time-locked to the memory array, split between high- and low-capacity individuals. For high-capacity individuals, the amplitude of the CDA for displays containing distractors resembled that for displays containing only two relevant items, while for low-capacity individuals, activity was similar to that of four relevant items. (c) Correlation of filtering efficiency (as measured by the ability to exclude irrelevant items) and each individual's memory capacity.

individuals, but it is simply the wrong information for the task.

McNab and Klingberg found similar results in a recent neuroimaging experiment.<sup>54</sup> Here, individuals were given cues that indicated whether an upcoming memory array would contain irrelevant distractors or not. When filtering was required, activity in both the PFC and basal ganglia increased, and this increase in activity was positively related to individual VWM capacity. Furthermore, the researchers examined

activity in the posterior parietal cortex, an area that has been shown to be sensitive to the number of items stored in memory. When comparing the storage of displays that contained only target items, and displays of targets and distractors, similar to Vogel et al., the authors found that lower capacity individuals were more likely to store irrelevant distractor items.

A number of unresolved questions emerge from the above findings. One issue concerns why

low-capacity individuals fail at remembering displays without distracters. One possibility is that working memory tasks rely on the ability to maintain distinct representations throughout a retention period, and later compare the memorandum with a test array or item. If one concedes that VWM capacity is indeed limited, then it's possible that the items in a display that exceed an individuals' capacity are tantamount to being distractors. These extraneous items, which also compete for representational space, may hinder the ability select and compare only the relevant items to those in the test array; much in the same way that taskrule designated distractors can interfere with the ability to filter and selectively store only the task-relevant items. Though further work needs to explore this possibility, the present data suggest that the ability to filter irrelevant information is tightly related to the amount of relevant information that can be stored in VWM.

A second issue concerns why low-capacity individuals fail to filter out irrelevant information in the first place. Recent experiments by Fukuda and Vogel<sup>63</sup> have shown that differences in filtering abilities likely stem from how efficiently attention can be allocated to the task-relevant items, and disengaged from the irrelevant distractors. The authors explored this issue using an attention capture paradigm. In this task observers are told to attend to a particular target item, and are instructed to report on a certain property of this item. For example, individuals may be asked to report the location of the gap on a red-C target imbedded in a display of distractors. On a minority of trials, an irrelevant item that matches one of the defining features of the target, such as its color, will be flashed briefly somewhere around the periphery of the display. The results typically show that performance suffers the most when this irrelevant distractor matches the target by one of its defining properties (e.g., same color), and marginally influences performance if it does not. By using this task to investigate differences is attention allocation between high- and low-capacity individuals, Fukuda and Vogel demonstrated that lowcapacity individuals are much more likely to have their attention captured by the irrelevant flanking items. Subsequent electrophysiological experiments demonstrated that the irrelevant flankers also captured the attention of the high-capacity individuals.<sup>64</sup> However, these individuals were much faster at disengaging their attention from the irrelevant flankers and returning to the target item. The low-capacity individuals, on the other hand, were much more likely to be captured by irrelevant items, and have their attention linger at those locations. What this indicates is that both high- and low-capacity individuals were captured by irrelevant information. Though, the high-capacity

individuals were much quicker at disengaging their attention from irrelevant items, and reengaging their attention to the task-relevant items.

Overall, the results of both filtering and attention capture experiments suggest that individual

### BOX 1

#### FORGETTING FROM VWM

Though it is often noted that individuals can remember less items with longer retention intervals, the mechanisms underlying this occurrence remain relatively unknown. One noteworthy assessment by Zhang and Luck<sup>65</sup> found information can be held in VWM for at least 4 seconds, with little loss in either the number or precision of representations. While the probability of losing items did increase following this interval, the items maintained exhibited little change in either their strength or precision. Thus suggesting that a primary reason of why information is forgotten is due to an abrupt termination of representations, instead of a gradual decay over time.

A related question concerns how we fail to maintain the feature information of VWM representations. Recent findings by Fougnie and Alvarez<sup>66</sup> suggest that the features of objects fail independently of one another. Here, participants were shown colored oriented triangles, and following a delay, reported both the orientation and color of a probed triangle. The results showed that when individuals failed to represent either the color or orientation of the test item, they were not any more likely to lose the color or orientation of that particular item, suggesting that the features were lost independently. Subsequent experiments showed that this loss was contingent on the degree of overlap between feature dimensions. When participants stored height and width information, two dimensions that likely draw on common neural populations, the two features were lost together. However, though the loss of two non-overlapping feature dimensions argues against the view that perfectly integrated objects are the units of VWM, it is possible that the method of report may have encouraged a loose binding of representations. Although the nature of binding is still a highly debated topic, investigations on the mechanisms that integrate VWM representations together promise to be interesting area of research.

differences in VWM tasks likely reflect how effectively individuals can control their working memory storage, rather than consistent differences in the number of items stored. More specifically, individuals seem to differ in their ability to selectively attend to and fill memory with items that are task relevant, as opposed to salient distractors <sup>53,55</sup> (Box 1). A somewhat counterintuitive conclusion from these findings is that lower capacity individuals are storing more information than high-capacity individuals, though such information is irrelevant to the goal at hand (Box 2).

### BOX 2

## **UNITS OF VWM**

One central question in determining VWM capacity concerns whether representations are stored as integrated objects, <sup>9,11</sup> or whether they are stored as fragmented features. <sup>67,68</sup> Luck and Vogel explicitly tested this issue by requiring participants to remember either the color, the orientation, or both color and orientation of bar stimuli. If the number of features limit capacity, then individuals should have been about twice as accurate in the single feature conditions than in the dual feature condition. However, this was not what Luck and Vogel found. Instead, participants were just as accurate when remembering both the color and orientation of items, as when remembering either feature alone.

These conjunction results are also consistent with an independent feature store model of VWM capacity, in which each feature type (e.g., color, orientation, etc) has its own available capacity.<sup>69</sup> To test this alternative, Luck and Vogel ran a separate experiment in which the memory array was made up of dual-colored objects. If the two features compete for the same VWM resources, then accuracy should have been worse in the color-color conjunction condition than in the single color condition. Yet, participants were again just as accurate in the two color condition. Though this dual-color, pure object benefit has not been replicated by other labs, 67,68,70,71 we have yet to find complete cost, the independent feature model would predict. That is, the dual color conjunction cost is almost never equivalent to that of the same number of separately presented objects. Indeed, numerous recent behavioral and neurophysiological experiments have found at least some amount of object-based advantage for VWM representations even with two attributes from the same feature space. 71-73 Thus, while there may be a cost to representing multiple features within a single dimension, to our knowledge, there is currently little evidence showing that capacity is determined solely by the number of features with no object benefit. Indeed, while the independent feature store model appears to be fairly compelling, direct evidence supporting this model has never been reported. Specifically, if each feature dimension has its own separate capacity, one would expect greatly improved VWM performance for heterogeneous arrays of items containing different critical features (e.g., four colors, four oriented bars, four shapes, etc.). To our knowledge, no one has ever found such a separate feature benefit. So, which is it? Objects or features? To us, the current weight of evidence favors at least a 'weak' object benefit in which there is some, but not complete benefits of objecthood on VWM performance.

## **CONCLUSION**

Most work on VWM suggests that this multicomponent system is capacity limited. While there is considerable debate over the exact number or resolution limits, most researchers will agree that there are substantial constraints to the amount of information that may be retained in VWM. Here, we focused on the major theories of VWM, and the proposed factors that limit its processing. Though there are still many aspects of VWM models that are controversial, neural measures are laying the groundwork for agreement over physiologically plausible theories of VWM capacity. Neural components that provide 'online' measures of the amount of information that individuals are concurrently representing appear to be especially promising ways of measuring the limits of memory capacity. Components such as the CDA seem to be particularly powerful in this regard, since they can account for both overall estimates of VWM and individual differences in working memory capacity.

An important and often neglected aspect of VWM capacity is its relation to cognitive processing. Though this relationship has been thoroughly explored in the verbal domain, research on visual memory and intelligence has lagged behind. The few recent studies that have begun to explore this relationship have indicated that the intimate connection between working memory and attention seems to play a key role in this relationship. Distinguishing between where these two processes converge and diverge will be an important part of understanding

higher-order cognition, since, at a fundamental level, these capacity limitations mediate our ability to interact with the world.

## **NOTES**

"Here we use the term VWM to refer to the temporary retention of visual information that just perceived or retrieved from long-term memory. However, the term visual short-term memory would have been equally appropriate. These two terms are often used interchangeably, and often refer to the same memory process.

<sup>b</sup>In the present article, we define capacity as the amount of visual information that can be temporarily stored for use in a cognitive or sensory-guided task.

## **REFERENCES**

- 1. Baddeley A. Working memory. *Science* 1992, 255:556–559.
- 2. Baddeley AD. Working Memory, Thought, and Action. New York: Oxford University Press; 2007.
- 3. Baddeley AD, Hitch G. Working memory. In: Bower GH, ed. *The Psychology of Learning and Motivation:* Advances in Research and Theory. New York: Academic Press; 1974, 47–90.
- 4. Baddeley A. Working memory: looking back and looking forward. *Nat Rev: Neurosci* 2003, 4:829–839.
- Luck SJ. Visual short-term memory. In: Luck SJ, Hollingworth A, eds. Visual Memory. New York: Oxford University Press; 2008, 43–85.
- Fukuda K, Vogel E, Mayr U, Awh E. Quantity, not quality: The relationship between fluid intelligence and working memory capacity. *Psychon Bull Rev* 2010, 17:673–679.
- 7. Sperling G. The information available in brief visual presentations. *Psychol Monogr: Gen Appl* 1960, 74:1–29.
- 8. Phillips WA. On the distinction between sensory storage and short-term memory. *Percept Psychophys* 1974, 16283–290.
- Luck SJ, Vogel EK. The capacity of visual working memory for features and conjunctions. *Nature* 1997, 390:279–281.
- 10. Rensink RA. Change detection. *Annu Rev Psychol* 2002, 53:245–277.
- 11. Vogel EK, Woodman GF, Luck SJ. Storage of features, conjunctions, and objects in visual working memory. *J Exp Psychol: Hum Percept Perform* 2001, 2792–114...
- Zhang W, Luck SJ. Discrete fixed-resolution representations in visual working memory. *Nature* 2008, 453:233–235.
- 13. Bays PM, Catalao RFG, Husain M. The precision of visual working memory is set by allocation of a shared resource. *J Vis* 2009, 9:1–11.
- 14. Wilken P, Ma WJ. A detection theory account of change detection. *J Vis* 2004, 4:1120–1135.

- 15. Anderson DE, Vogel EK, Awh E. Precision in visual working memory reaches a stable plateau when individual item limits are exceeded. *J Neurosci* 2011, 31:1128–1138.
- 16. Alvarez GA, Cavanagh P. The capacity of visual short-term memory is set both by visual information load and by number of objects. *Psychol Sci* 2004, 15:106–111.
- 17. Awh E, Barton B, Vogel EK. Visual working memory represents a fixed number of items regardless of complexity. *Psychol Sci* 2007, 18:622–628.
- 18. Scolari M, Vogel EK, Awh E. Perceptual expertise enhances the resolution but not the number of representations in working memory. *Psychon Bull Rev* 2008, 15:215–222.
- 19. Johnson JS, Spencer JP, Luck SJ, Schöner G. A dynamic neural field model of visual working memory and change detection. *Psychol Sci* 2009, 20:568–577.
- 20. Miller EK, Erickson CA, Desimone R. Neural mechanisms of visual working memory in prefrontal cortex of the macaque. *J Neurosci* 1996, 16:5154–5167.
- 21. Miller EK, Li L, Desimone R. Activity of neurons in anterior inferior temporal cortex during a short-term memory task. *J Neurosci* 1993, 131460–1478. 4.
- 22. Rainer G, Rao SC, Miller EK. Prospective coding for objects in primate prefrontal cortex. *J Neurosci* 1999, 19:5493–5505.
- 23. Miller EK, Cohen JD. An integrative theory of prefrontal cortex function. Annu Rev Neurosci 2001, 24:167-202.
- 24. Chafee MV, Goldman-Rakic PS. Matching patterns of activity in primate prefrontal area 8a and parietal area 7ip neurons during a spatial working memory task. *J Neurophysiol* 1998, 79:2919–2940.
- 25. Crowe DA, Averbeck BB, Chafee MV. Rapid sequences of population activity patterns dynamically encode task-critical spatial information in parietal cortex. *J Neurosci* 2010, 30:11640–11653.
- 26. Inoue M, Mikami A, Ando I, Tsukada H. Functional Brain Mapping of the Macaque Related to Spatial Working Memory as Revealed by PET. *Cerebral Cortex* 2004, 14:106–119.

- 27. Fuster JM, Jervey JP. Neuronal firing in the inferotemporal cortex of the monkey in a visual memory task. *J Neurosci* 1982, 2:361–375.
- 28. Goldman-Rakic PS. Cellular basis of working memory. *Neuron* 1995, 14:477–485.
- 29. Chafee MV, Goldman-Rakic PS. Inactivation of parietal and prefrontal cortex reveals interdependence of neural activity during memory-guided Saccades. *J Neurophysiol* 2000, 83:1550–1566.
- 30. Rainer G, Asaad WF, Miller EK. Selective representation of relevant information by neurons in the primate prefrontal cortex. *Nature* 1998, 393:577–579.
- 31. Ranganath C, Cohen MX, Dam C, Esposito C. MD Inferior temporal, prefrontal, and hippocampal contributions to visual working memory maintenance and associative memory retrieval. *J Neurosci* 2004, 24:3917–3925.
- 32. Constantinidis C, Franowicz MN, Goldman-Rakic PS. The sensory nature of mnemonic representation in the primate prefrontal cortex. *Nat Neurosci* 2001, 4:311–316.
- 33. Cromer JA, Roy JE, Miller EK. Representation of multiple, independent categories in the primate prefrontal cortex. *Neuron* 2010, 66:796–807.
- 34. Desimone R. Neural mechanisms for visual memory and their role in attention. *Proc Natl Acad Sci USA* 1996, 93:13494–13499.
- 35. Funahashi S, Bruce CJ, Goldman-Rakic PS. Visuospatial coding in primate prefrontal neurons revealed by oculomotor paradigms. *J Neurophysiol* 1990, 63:814–831.
- Durstewitz D, Seamans and T. JK, Sejnowski J. Neurocomputational models of working memory. *Nat Neu*rosci 2000, 3:1184–1191.
- 37. Edin F, Klingberg T, Johansson P, McNab F, Tegner J, Compte A. Mechanisms for top-down control of working memory capacity. *Proc Natl Acad Sci USA* 2009, 106:6802–6807.
- 38. Curtis CE, D'Esposito M. Persistent activity in the prefrontal cortex during working memory. *Trends Cogn Sci* 2003, 7:415–423.
- 39. D'Esposito M. From cognitive to neural models of working memory. *Phil Trans Roy Soc B* 2007, 362:761–772.
- 40. Buschman TJ, Siegel M, Roy JE, Miller EK. Neural substrates of cognitive capacity limitations. *Proc Natl Acad Sci USA* 2011, 108:11252–11255.
- 41. Delvenne JF. The capacity of visual short-term memory within and between hemifields. *Cognition* 2005, 96:B79–B88.
- 42. Delvenne JF, Kaddour LA, Castronovo J. An electrophysiological measure of visual short-term memory capacity within and across hemifields. *Psychophysiology* 2011, 48:333–336.

- 43. Xu Y, Chun MM. Dissociable neural mechanisms supporting visual short-term memory for objects. *Nature* 2006, 440:91–95.
- 44. Xu Y, Chun MM. Selecting and perceiving multiple visual objects. *Trends Cogn Sci* 2009, 13:167–174.
- 45. Todd JJ, Marois R. Posterior parietal cortex activity predicts individual differences in visual short-term memory capacity. Cogn Affect Behav Neurosci 2005, 5:144–155.
- 46. Jeneson A, Wixted JT, Hopkins RO, Squire LR. Visual working memory capacity and the medial temporal lobe. *J Neurosci* 2012, 32:3584–3589.
- 47. Vogel EK, Machizawa MG. Neural activity predicts individual differences in visual working memory capacity. *Nature* 2004, 428:748–751.
- 48. Ikkai A, McCollough AM, Vogel EK. Contralateral delay activity provides a neural measure of the number of representations in visual working memory. *J Neurophysiol* 2010, 103:1963–1968.
- 49. Engle RW. Working memory capacity as executive attention. *Curr Dir Psychol Sci* 2002, 11:19–23.
- 50. Kane MJ, Bleckley ARA, Conway MK, Engle RW. A controlled-attention view of working memory capacity. *J Exp Psychol: General* 2001, 130:169–183.
- Bleckley MK, Durso FT, Crutchfield JM, Engle RW, Khanna MM. Individual differences in working memory capacity predict visual attention allocation. *Psychon Bull Rev* 2003, 10884–889.
- 52. Cusack R, Lehmann M, Veldsman M, Mitchell DJ. Encoding strategy and not visual working memory capacity correlates with intelligence. *Psychon Bull Rev* 2009, 16:641–647.
- 53. Linke AC, Vicente-Grabovetsky A, Mitchell DJ, Cusack R. Encoding strategy accounts for individual differences in change detection measures of VSTM. *Neuropsychologia* 2011, 49:1476–1486.
- 54. McNab F, Klingberg T. Prefrontal cortex and basal ganglia control access to working memory. *Nat Neurosci* 2008, 11:103–107.
- Vogel EK, McCollough AW, Machizawa MG. Neural measures reveal individual differences in controlling access to working memory. *Nature* 2005, 438:500–503.
- Awh E, Jonides J. Overlapping mechanisms of attention and spatial working memory. *Trends Cogn Sci* 2001, 5:119–126.
- 57. Awh E, Vogel and S. EK, Oh H. Interactions between attention and working memory. *Neuroscience* 2006, 139:201–208.
- 58. Chun MM, Golomb JD, Turk-Browne NB. A taxonomy of external and internal attention. *Annu Rev Psychol* 2011, 62:73–101.
- Duncan J. EPS Mid-Career Award 2004: brain mechanisms of attention. Q J Exp Psychol (Hove) 2006, 59:2–27.

 Yantis S, Serences JT. Cortical mechanisms of spacebased and object-based attentional control. *Curr Opin Neurobiol* 2003, 13:187–193.

- 61. Cowan N. The magical number 4 in short-term memory: a reconsideration of mental storage capacity. *Behav Brain Sci* 2001, 24:87–185.
- 62. Cowan N, Elliot EM, Saults JS, Morey CC, Mattox S, Hismjatullina A, Conway ARA. On the capacity of attention: its estimation and its role in working memory and cognitive aptitudes. Cogn Psychol 2005, 51:42–100.
- 63. Fukuda K, Vogel EK. Human variation in overriding attentional capture. *J Neurosci* 2009, 29:8726–8733.
- 64. Fukuda K, Vogel EK. Individual differences in recovery time from attentional capture. *Psychol Sci* 2011, 22:361–368.
- 65. Zhang W, Luck SJ. Sudden death and gradual decay in visual working memory. *Psychol Sci* 2009, 20:423–428.
- 66. Fougnie D, Alvarez GA. Object features fail independently in visual working memory: evidence for a probabilistic feature-store model. *J Vis* 2011, 11:1–12.

- 67. Olson IR, Jiang Y. Is visual short-term memory object based? Rejection of the "strong-object" hypothesis. *Percept Psychophys* 2002, 64:1055–1067.
- 68. Delvenne J, Bruyer R. Does visual short-term memory store bound features?. *Vis Cogn* 2004, 111–27.
- 69. Magnussen S, Greenlee MW, Thomas JP. Parallel processing in visual short-term memory. *J Exp Psychol: Hum Percept Perform* 1996, 22:202–212.
- 70. Wheeler ME, Treisman AM. Binding in short-term visual memory. *J Exp Psychol: General* 2002, 131:48-64.
- 71. Xu Y. Limitations of object-based feature encoding in visual short-term memory. *J Exp Psychol: Hum Percept Perform* 2002, 28:458–468.
- 72. Luria R, Vogel EK. Shape and color conjunction stimuli are represented as bound objects in visual working memory. *Neuropsychologia* 2011, 49:1632–1639.
- 73. Xu Y. Encoding color and shape from different parts of an object in visual short-term memory. *Percept Psychophys* 2002, 64:1260–1280.