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Individual Differences in Visual Working Memory Capacity: Contributions of Attentional Control to Storage

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THE CAPACITY OF VISUAL WORKING MEMORY

The amount of visual information an individual can actively represent is severely limited; this limitation is known as the capacity of visual working memory (VWM). To estimate an individual's VWM capacity, we present an observer with a memory array containing multiple visual stimuli to remember over a relatively short delay interval, after which we test their memory (Figure 1(a)). When we examine memory performance as a function of the number of stimuli to remember (i.e., set size), we find that healthy young adults can easily retain up to three simple objects (Figure 1(b)), with their performance declining thereafter as the set size increases. Further, when memory performance for a set size larger than three is transformed to an estimate of the number of stimuli retained in VWM, the average VWM capacity estimate (K) is consistently computed as around three objects across a wide range of paradigms (Cowan, 2001; Luck & Vogel, 1997; Zhang & Luck, 2008). Based on such robust findings, the average VWM capacity for healthy young adults is thought to be around three simple objects. To derive a single metric of VWM capacity, we often average the K estimate across set sizes above four guided by the logic that across these large set sizes individuals' VWM stores are equally filled to capacity (e.g., Fukuda & Vogel, 2009; Fukuda, Vogel, Mayr, & Awh, 2010; Vogel & Machizawa, 2004). In this chapter, we call this estimate Kave for the sake of clarity.

Individual Differences in VWM Capacity

Despite this robust estimate of the average capacity in healthy young adults, it is well known that K estimates differ substantially across different subject populations. VWM capacity is known to develop throughout childhood, and it reaches its peak at young adulthood followed by a gradual decline as we age (Brockmole, Parra, & Sala, 2008; Brockmole & Logie, 2013; Cowan, Naveh-Benjamin, Kilb, & Saults, 2006; Riggs, McTaggart, Simpson, & Freeman, 2006). Furthermore, an impaired ability to store information in VWM, inferred by differences in K estimates, is associated with a wide variety of cognitive disorders, such as schizophrenia (Goldman-Rakic, 1994; Lee & Park, 2005), and Parkinson's disorder (Gabrieli, Singh, Stebbins, & Goetz, 1996; Lee et al., 2010). Even in the healthy young adult population, researchers find sizable and reliable individual differences in K estimates (Awh, Barton, & Vogel, 2007; Cowan et al., 2005; Fukuda, Awh, & Vogel, 2010). Some individuals show Kave of four or above, whereas others show Kave of two or less. Interestingly, these individual differences are robustly correlated with a variety of higher cognitive functions such as fluid intelligence (Cowan, Fristoe, Elliott, & Brunner, 2006; Fukuda, Vogel, et al., 2010; Shipstead, Redick, Hicks, & Engle, 2012). Therefore, it is very important to understand what contributes to the individual differences in this capacity estimate.



FIGURE 1 (a) A schematic of a standard change-detection task used to estimate individuals' visual working memory capacity. A memory array consisting of multiple colored squares are presented for a brief time, and participants are asked to hold as many squares as possible in mind. After a short retention interval, one item is presented on a test array, and participants have to indicate whether the test item is the same or different from the memory item presented at the same location. (b) Typical performance during this type of change-detection task. The accuracy is near perfect up to set size 3, and it drops monotonically as a function of a set size. When performance is converted to visual working memory capacity estimate (K) using a standard formula (Cowan, 2001), it increases up to three and stops increasing for higher set sizes.

Why do some individuals have higher Kave than others? One simple explanation would be that the variation in Kave reflects the variation in the size of mental storage space. That is, those with high Kave have enough storage capacity to hold four or more objects in VWM, and others with low Kave have less storage space and can only hold two or fewer objects. However, here we also consider the alternative hypothesis that individuals might have roughly the same amount of storage capacity, but what differs across individuals is the ability to consistently use their capacity to its maximum.

Evidence supporting this alternative hypothesis comes from studies that have investigated the relationship between individuals' VWM capacity and attentional-control ability (Fukuda & Vogel, 2009, 2011; McNab & Klingberg, 2008; Vogel, McCollough, & Machizawa, 2005). A well-established consensus is that individuals with low Kave are poor at exerting attentional control over what gets encoded and maintained in VWM. For example, Vogel and colleagues have shown that low-Kave individuals cannot help but orient their attention to distractors (Fukuda & Vogel, 2009), and thus they end up storing more distractors in their limited-capacity VWM than high Kave individuals (Vogel et al., 2005). Though this individual-differences approach has been successful in highlighting the important link between VWM capacity and attentional control, it still is unclear how attentional-control ability manifests itself in a conventional VWM task in which participants simply remember as many objects as possible.

How would attentional control become relevant in the absence of distractors? The attentional-capture literature suggests a plausible mechanism through which the onset of a large number of task-relevant objects induces an overwhelming competition for the limited VWM resource. It is well known that the objects sharing critical features with the target items serve as potent distractors (i.e., contingent-capture distractors), and their onset automatically demands deployment of attentional resources (Folk, Leber, & Egeth, 2002; Folk, Remington, & Johnston, 1992). If we extend this perspective to VWM tasks, all target items in a memory array would automatically claim their share of VWM resources with their onset. If the set size is equal to or below an individual's VWM capacity, then all items would get a sufficient share of the resources to be encoded into VWM. However, if the set size exceeds one's VWM capacity, then the competition for the resources becomes overwhelming, and VWM storage would require the exertion of attentional control needed to adequately allocate VWM resources, then the number of items successfully retained in VWM could be less than they can actually hold.

Our goal here was to better characterize the nature of individual differences in VWM capacity observed in a standard VWM task (i.e., the change-detection task). We collected a large pool of data (n=495), and analyzed it with the following questions in mind. First, does the capacity estimate systematically change as a function of set size? If K estimates simply reflect the amount of mental storage space, then they should not change as a function of set size so long as the set size exceeds an individual's VWM capacity (e.g., larger than set size 3). On the other hand, if the capacity estimate also reflects an individual's ability to exert attentional control over encoding into VWM, then it might show a decrement at supra-capacity set sizes in which the competition among stimuli for storage overwhelms attentional selection mechanisms. More importantly, if this attentional-control ability to resolve the competition for encoding is a

the key factor in determining an individual's VWM capacity estimate, then we should observe that the low-capacity individuals show a disproportionate drop in K estimates at supra-capacity set sizes. To test this hypothesis, we computed a traditional single metric for VWM capacity for each individual by averaging K estimates across set sizes larger than three (Kave). Based on Kave, we split the participants into high- and low-capacity groups using a median split, and examined how the high- and low-capacity groups performed across set sizes. If the storage-space account holds true, performance differences between groups will emerge as soon as the to-be-remembered set size surpasses their VWM capacity and stay constant across larger set sizes. On the other hand, if attentional control is what differentiates high- and low-capacity individuals, performance differences between groups will groups will grow larger as the set size increases.¹

EXPERIMENT 1

To test the competing theoretical accounts of the individual differences in Kave that we described previously, we accumulated a large pool of data (n = 495) using a standard VWM task (i.e., the change-detection task). In this task, participants were asked to remember a briefly presented memory array that consisted of either four or eight colored squares. After a 1000-ms retention interval, participants had to judge if a single item matched the original item presented at the same location in the previous memory array. Using this large sample size, we tested the following predictions. If the attentional-control account is true, then we should first observe that the K estimates drop from set size 4 to set size 8 (i.e., the 4–8 drop). Next, and more importantly, the distribution of K estimates should be much tighter for set size 4 than for set size 8. The attentional-control account predicts that the increased spread of the distribution should be mainly due to those who show a decrement in K estimates from set size 4 to set size 8. In contrast, if the storage-space account is correct, we should observe stable capacity estimates across set sizes, and the distribution of the K estimates should not show any difference for low-Kave individuals.

Method

Participants

After providing informed consent of procedures approved by the University of Oregon Institutional Review Board, 495 young adults with normal or corrected-to-normal vision participated in the study in return for either course credit in psychology classes or monetary compensation (\$8/h).

Stimuli and Procedure

Participants performed a standard change-detection task. In this task, participants were presented with a memory array that consisted of either four (set size 4) or eight (set size 8) colored squares for 150 ms. The memory array was created from nine highly discriminable colors (red, green, blue, yellow, magenta, cyan, orange, white, and black) that were randomly chosen without replacement. Participants were asked to remember as many colored squares as possible across a retention interval of 1000 ms during which the screen remained blank. After the retention interval, a single colored square was presented, and the participants indicated whether or not the test square had the same color as the original one at the same location. Participants used the "z" key on the keyboard to indicate that the color of the test item was the same and the "/" key to indicate that the color of the test item was different in an unspeeded manner. Half of the trials were same trials, and the others were different trials. The sequence of the trials was pseudo-randomly determined, and participants completed 60 trials at each set size. After instructions were given and the subjects were given the opportunity to ask questions the experimental trials began.

Results

Attentional-Control Account of Individual Differences in Kave

The accuracy for each set size was converted to VWM capacity estimate (K4 for set size 4, and K8 for set size 8) using the standard formula (Cowan, 2001; Rouder, Morey, Morey, & Cowan, 2011). Then, each individual's

¹Importantly, we are splitting individuals based on a metric derived by the dependent measure of interest. Therefore, the main effect of group will be meaningless (i.e., high-capacity individuals have higher capacity estimate than low-capacity individuals by definition). However, the two models of individual differences in visual working memory capacity make qualitatively different predictions for the interaction between set sizes and capacity groups, and this justifies our approach.



FIGURE 2 (a) A histogram of visual working memory capacity estimate (K) for set size 4 and set size 8. The blue bars depict the distribution of K estimate for set size 4 (K4) and red bars for set size 8 (K8). The black bar represents the mean K4 and K8 scores. As can be seen, the distribution for K8 is wider compared with that for K4. Particularly, there is a substantial increase in the number of individuals toward the lower end of distribution. (b) 4–8 drop for every individual sorted by their traditional visual working memory capacity measure (Kave). For each individual, the difference between K4 and K8 (4–8 drop) was calculated as a measure of the decrement in the capacity estimate from the capacity overload. The figure shows the sorted 4–8 drop for all the participants from the lowest Kave estimate to the largest Kave estimate. Clearly, it was the low-capacity individuals who showed the larger 4–8 drop.

traditional VWM capacity (Kave) was computed by averaging K4 and K8. Based on Kave, individuals were grouped into high- and low-capacity groups by a median split (median Kave=2.53). The resultant data were subjected to a mixed-design repeated-measures analysis of variance (ANOVA) with the between-subject factor of group (high vs low Kave) and the within-subject factor of set size (4 vs 8). There was a main effect of set size (F(1, 492) = 60.15, p < .0001). K4 (mean=2.7) was significantly higher than K8 (mean=2.4) (Figure 2). This finding is consistent with a previous observation by Cusack and colleagues (Linke, Vicente-Grabovetsky, Mitchell, & Cusack, 2011) that K decreases when estimated with larger set sizes. Further, the spread of distribution nearly doubled from set size 4 (SD=0.61) to set size 8 (SD=1.18). This increase in the spread is not entirely driven by the limited range of K estimates at set size 4 because the largest capacity estimate for set size 8 was 5.06 compared with 4 for set size 4, the number of the individuals with K4 less than 1.5 was 22. However, this number showed nearly a five-fold increase (106 individuals) at set size 8. Although we do see a small portion of individuals who showed a K estimate greater than 4 in set size 8 (8% of the sample), the pattern of the data is largely consistent with the attentional-control account as opposed to the storage-space account in which K estimates should remain fixed once the capacity is reached for an individual.

Our next observation was that there was a significant interaction between set size and capacity group (F(1, 492) = 213.06, p < .0001), suggesting that the drop in the capacity estimate for the supra-capacity set size was primarily driven by the low-capacity individuals. To further decompose this interaction, we calculated the drop in the K estimates at the supra-capacity set size (i.e., K4–K8, or the 4–8 drop). If this is the main source of individual differences in the standard VWM capacity estimates (Kave = the average of K4 and K8), we should expect that the individuals with low Kave should show a larger 4–8 drop than those with high Kave. When low- and high-Kave groups were compared, high-Kave individuals showed a modest increase from K4 to K8 (M = +0.25), whereas low-Kave individuals showed a sizable 4–8 drop (M = -0.83). This resulted in a larger group difference in K8 than in K4. A correlational analysis buttressed this observation by showing a strong negative correlation between individuals' Kave and the size of the 4–8 drop (r = -0.64, p < .0001). Taken together, these findings support the attentional-control account of individual differences in VWM capacity. That is, our findings suggest that the individual differences in Kave are heavily affected by how good individuals are at regulating the competition induced by more task-relevant information than they can represent in their limited VWM capacity. More specifically, it is the low-Kave individuals who are negatively affected by an excessive information load, and as a result, they store less information than their VWM could actually hold.

Time Invariant Nature of the Visual Working Memory Capacity Estimate within a Session

The previous findings show that estimated capacity changes with the set size of the to-be-remembered array, and this change strongly drives the individual differences in VWM capacity estimates. One unexplored hypothesis is that these individual differences change their structure over time. One plausible scenario is that early on in the

experiment, high-capacity individuals might also show a similar K deficit for the supra-capacity set size as exhibited by the low-capacity individuals. However, high-capacity individuals learn to counteract this memory overload in the course of the experiment, thus leading to stable K estimates across set sizes. This scenario would predict an increase in the individual differences in the K estimate for a supra-capacity set size over time. Another plausible scenario is that the K deficit resulting from memory overload for low-capacity individuals might be only observable in the early part of the experiment, and as they learn how to attentionally select the manageable set of items, this deficit might disappear. This scenario, on the other hand, would predict a decrease in the individual differences in the K estimate for a supra-capacity set size over the course of the experiment. Or alternatively, the individual differences in K estimates are very robust and its structure might not change at all over the course of the experiment.

Recently, Luck and colleagues examined a similar question using a single set size to measure VWM storage as the experiment unfolded. They found that the VWM capacity estimate measured in a standard change-detection task is not influenced by proactive interference, as evidenced by the fact that average performance did not change across the experiment or across trials with a specific type of stimulus (Lin & Luck, 2012). They interpreted these observations as indicating that the standard change-detection task is insensitive to the accumulation of representations in long-term memory over the course of the experiment, and thus K provides a pure measure of the amount of information actively held in VWM at a given moment, uninfluenced by storage in other memory systems. One thing that Luck and colleagues did not directly point out in this study is the time course of the individual differences. Thus, we examined the metric of individual capacity across the experiment in the following analysis. To address the question of the stability of individual differences in K measures, we calculated K estimates for every temporal order for each set size by pooling single trial data from all individuals in each capacity group (e.g., performance of all low-capacity individuals on the first trial of set size 4 condition, the second trial, the third, etc.). We first separately sorted set size 4 and 8 trials in the temporal order that they occurred for each individual. This resulted in trial one through 60 for each set size for each individual. Then, individuals were divided into high- and low-capacity groups by median split based on the standard VWM capacity estimate (i.e., Kave = the average of K4 and K8). Last, performance for each trial order was pooled within high- and low-capacity group to calculate the group capacity estimate for each trial order. Figure 3 shows the temporal fluctuation of the K estimate for each set size. As can be seen, there was no systematic change in the K estimate over time for both set sizes for both groups (absolute rs < 0.14, not significant). This clearly



FIGURE 3 The fluctuations of K estimates across the experiment. (a) The temporal fluctuation of K estimates for the high-capacity group. The blue line shows the temporal fluctuation of the K estimate for set size 4 (K4); the red line shows that for set size 8 (K8). K4 and K8 are nearly identical throughout the time course of the experiment. (b) The temporal fluctuation of K estimates for the low-capacity group. The blue and red lines represent the fluctuation of K4 and K8, respectively. K4 is consistently higher than K8 throughout the experiment, and the difference does not change over time. indicates that the individual differences reflected in this capacity estimate are not malleable over the course of the experiment and that K is a stable and reliable metric of individual differences in information processing.

Discussion

The results from Experiment 1 strongly supported the attentional-control account of the individual differences in VWM capacity estimates. Unlike the prediction of the space account, the capacity estimate was significantly smaller for a supra-capacity set size (i.e., set size 8) than for a near capacity set size (i.e., set size 4). This suggests that the onset of excessive task-relevant information causes an overwhelming competition for the limited VWM capacity. Additionally, the decrement in the capacity estimates with the supra-capacity set size was strongly driven by low-capacity individuals, and in turn, it showed a significant contribution to the standard VWM capacity estimates. Further, our large dataset uniquely enabled us to estimate the fluctuation of VWM capacity estimates from trial to trial. The time-course analysis of the capacity estimates revealed that the individual differences are time invariant and can be reliably measured at any point in time. This finding also may suggest that the contribution of the attentional control to memory storage is rather constant over the course of the experiment.

However, one glaring limitation in Experiment 1 was that we drew our inferences about the number of items held in VWM based solely on participants' behavioral report of a match between the memoranda and the test item. We know that VWM representations are not perfect, and their precision worsens as the number of items increases (Anderson, Vogel, & Awh, 2011; Bays & Husain, 2008; Zhang & Luck, 2008). Further, if the representations are not precise enough, individuals are prone to committing errors when comparing the test item with the memoranda. These comparison errors alone can be responsible for a pronounced decrement in the behavioral capacity estimate (Alvarez & Cavanagh, 2004; Awh et al., 2007). It could have been these comparison errors that induced the decrement in the K estimate for the supra-capacity set size. Thus, behavioral data alone do not provide definitive evidence for a decrease in the number of items represented in VWM.

EXPERIMENT 2

In Experiment 2, we used a neural measure to more directly test the predictions of the competing storage-space account and attentional-control account of VWM capacity limitations. Neural measures obtained during VWM maintenance have the distinct advantage of measuring storage without contamination by comparison errors, output interference, and simple breakdowns in late-stage response selection. The contralateral delay activity (CDA) is an electrophysiological measure of the number of items actively represented in VWM (Vogel & Machizawa, 2004). That is, the amplitude of CDA provides a direct measure of the number of items actively maintained in VWM without the complications inherent in basing our conclusions on behavioral output. The CDA is an event-related potential (ERP) component defined as a sustained negative voltage over the parieto-occipital channels that are contralateral to the hemifield in which memory items are presented. It onsets approximately 300 ms after the onset of memory items, and it lasts until the end of the retention interval. In previous experiments that parametrically manipulated memory set size, the amplitude of the CDA showed a monotonic increase until the set size reached an individual's VWM capacity, with no further increase after set size reached K (Anderson et al., 2011). Furthermore, the differences in the CDA amplitudes between a subcapacity set size (e.g., set size 2) and a supra-capacity set size (e.g., set size 4 or more) was shown to strongly correlate with VWM capacity estimates (Anderson et al., 2011; Tsubomi, Fukuda, & Vogel, 2012; Vogel & Machizawa, 2004). In the first CDA article that showed the link between the CDA amplitude and VWM capacity (Vogel & Machizawa, 2004), higher asymptotic CDA amplitudes were found in the high-capacity individuals. This finding was interpreted as evidence that these individuals have more storage space than low-capacity individuals. In the present experiment, we return to this issue and used this neural signature of VWM capacity to directly distinguish between the originally assumed storage-space account (Vogel & Machizawa, 2004) and the attentionalcontrol account of individual differences in VWM capacity.

In this experiment, we had participants perform an ERP version of the change-detection task while we manipulated the set size between 1 and 8 items across trials. In this version, we controlled for the electrophysiological responses to the stimulus onset per se by presenting the same number of items on both sides of the screen. As in the typical paradigm used to measure the CDA, we instructed participants to remember the items presented on the precued side only (e.g., Vogel & Machizawa, 2004). The CDA amplitude was characterized as the difference in the parieto-occipital ERP amplitude between the contralateral and ipsilateral channels relative to the hemifield where the to-be-remembered stimuli were presented. If the space account of individual differences in VWM capacity is

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correct, then we should observe that the differences in the CDA amplitudes between high- and low-capacity individuals stay constant once the set size surpasses their VWM capacity (i.e., set sizes higher than 3). Alternatively, if the attentional control-account is correct, then we should observe the following. First, all the individuals should show a rise in the CDA amplitude up to their capacity limit. However, when the set size surpasses their capacity, low-capacity individuals should show a decrease in the CDA amplitude, whereas high-capacity individuals should show sustained amplitudes.

Method

Participants

After providing informed consent of procedures approved by the University of Oregon Institutional Review Board, 36 neurologically normal young adults with normal or corrected-to-normal vision participated in the study in return for monetary compensation (\$10/h).

Stimuli and Procedure

An example trial is shown in Figure 4(a). Participants were first presented with a central arrow cue that indicated which hemifield (i.e., left or right) to remember. Participants were instructed to remember the colored squares in the cued hemifield. Five hundred milliseconds after the cue presentation, a bilateral memory array consisting of one through eight colored squares ($1^{\circ} \times 1^{\circ}$ each) on each side was presented for 100 ms. The minimum distance between



FIGURE 4 (a) A schematic of the bilateral change-detection task. In this task, participants were first presented with a central arrow cue indicating which side they should shift their attention to while holding a central fixation. Five hundred milliseconds after the onset of the cue, a memory array consisted of the same number of items on both sides were presented for 150 ms, and participants remembered items presented on the cued side while ignoring those on the other side. After a 900-ms retention interval, a test array that is either identical or different by one item on the cued side was presented, and participants indicated whether it was the same or different compared with the memory array by a button press. (b) Set size functions of K estimates. The red and blue lines represent the set size functions of K estimates for low- and high-capacity groups, respectively. The error bars indicate the within-subject 95% confidence intervals. The green diamonds show the mean K estimate across all individuals. Consistent with the results of Experiment 1, K estimates for the low-capacity group showed a continuous decline above set size 4, whereas those for the high-capacity group remained constant. (c) Set size function of the CDA amplitudes. The blue and red lines represent the set size functions of the CDA amplitudes for low- and high-capacity groups, respectively. The error bars indicate the within-subject 95% confidence intervals. The green diamonds show the mean CDA amplitudes across all individuals. Much like the K estimates, the low-capacity group showed a monotonic decline in the CDA amplitude after set size 4, whereas the high-capacity group showed stable amplitudes.

squares was 2° , each as at least 2.5° from fixation, but no more than 6.5° from fixation. The colors were randomly chosen from six highly distinguishable colors (i.e., red, blue, yellow, green, magenta, and black), allowing one repetition of each color. After a 900-ms blank retention interval, the test array was presented. The test array was either identical to the memory array or different by one colored square, and participants had to press the key indicating same or different ("z" or "/" on the keyboard, respectively). The test array was available until participants made a response. After responding, participants were allowed to blink or make eye movements for 1s before the next trial started. The set size was pseudo-randomly changed throughout the experiment, and each participant performed 200 trials with each of the 8 set sizes.

Electroencephalogram Recording

ERPs were recorded in each experiment using our standard recording and analysis procedures, including rejection of trials contaminated by blinks or large (>1°) eye movements, movement artifacts, or amplifier saturation (Vogel & Machizawa, 2004). We recorded from 22 standard electrode sites spanning the scalp, including International 10/20 sites F3, F4, C3, C4, P3, P4, O1, O2, PO3, PO4, P7, P8, PO7, and PO8.² Trials containing ocular artifacts, movement artifacts, or amplifier saturation were excluded from the averaged ERP waveforms. Participants who had more than 20% of trials rejected in any condition were replaced (five subjects replaced).

Measuring the Contralateral Delay Activity

As is now standard procedure for measuring the CDA (Vogel & Machizawa, 2004; Vogel et al., 2005), ERPs recorded at posterior parietal, lateral occipital, and posterior temporal electrode sites (PO3, PO4, T5, T6, OL, and OR) were first binned as either contralateral side or ipsilateral side with respect to the memorized hemifield. Because each pair of electrode sites showed the CDA, we maximized the signal-to-noise ratio of our measurements by averaging the channels for each bin to make a single pair of the contralateral and the ipsilateral channels. The CDA amplitude was calculated as the difference between the mean amplitude for the contralateral and the ipsilateral activity in 300–1000 ms time window after the onset of the memory array.

Results

Behavioral Results

As shown in Figure 4(b), the accuracy for each set size was first transformed into the standard capacity estimate, K. To obtain a single metric of VWM capacity (Kave), we averaged the estimates from set size 4 through set size 8 for each individual. Then based on Kave, we divided the participants into high-Kave (M=2.8) and low-Kave (M=1.4) groups using a median split. A mixed-model repeated-measures ANOVA with the between-subject factor of capacity group (high vs low) and the within-subject factor of set size (1 through 8) on the accuracy data revealed that there was a main effect of set size (F(7, 28) = 47.73, p < .0001). As typical in this design, the estimates increased monotonically up to set size 4 (K4=2.4), and showed no further increase. More importantly, there was a significant interaction between capacity group and set size (F(7, 196) = 22.34, p < .001). In contrast to high-Kave individuals who showed relatively stable capacity estimates across set size 4 through set size 8, low-Kave individuals showed a monotonic decrease in the capacity estimates as the set size increased. This interaction was further supported by the strong correlation between individuals' VWM capacity estimate (Kave) and the size of drop in the capacity estimates from set size 4 to set size 8 (r = -0.83, p < .001). Thus, the behavioral findings of Experiment 1 even while using different memory and test arrays and requiring fixation.

ERP Analyses

The CDA Amplitude

First, we analyzed the standard CDA waveforms across set sizes, as shown in Figure 4(c). A mixed-model repeated-measures ANOVA was run with capacity group as the between-subject factor and set size as the within-subject factor. Replicating the previous observations, the CDA amplitude increased monotonically up to set size 3

²P7, P8 PO7, and PO8 are identical to T5, T6, OL, and OR, respectively, in the previous CDA literature.

and showed no further increase as a function of the set size (F(7, 28) = 43.21, p < .0001). We also replicated the tight relationship between individuals' Kave and the increase in the CDA amplitude from set size 2 to set size 4 (r = -0.56, p < .01).

Most critically for the current hypothesis, there was a significant interaction between Kave and the set size (F(7, 196) = 2.91, p < .01). In contrast to high-Kave individuals who showed stable CDA amplitudes across set size 3 through set size 8, low-Kave individuals showed a monotonic decrease in the CDA amplitudes as the set size increased beyond set size 3. This interaction was supported by a robust correlation between individuals' Kave and the size of drop in the CDA amplitude from set size 3 to set size 8 (r = -0.50, p < .01).

Separating Contralateral and Ipsilateral Activity

The set size function of the CDA amplitudes supported the attentional-control account of the individual differences in VWM capacity estimate (Kave). If attentional control is the key factor that determines whether an individual will have a high or low VWM capacity, then the activity elicited by items presented on the to-be-ignored side should contribute to the relationship between the CDA amplitudes and the behavioral capacity estimates. The paradigm we used in Experiment 2 involved presenting an entire hemifield full of items that need to be filtered out so as not to induce a sensory confound in the ERPs (Drew, McCollough, & Vogel, 2006; Woodman, 2010). It is easy to imagine that the presence of to-be-ignored items further taxed the attentional selection of the manageable subset of items because they shared critical features with the target items in the cued hemifield. If low-capacity individuals are unable to do this, then we should see that the waveforms recorded contralateral to the irrelevant items (i.e., ipsilateral to the to-be-remembered items) would be more negative relative to the waveforms from high-capacity individuals as the CDA is elicited by these irrelevant items. To test this idea, we separately analyzed the contralateral and the ipsilateral waveforms (relative to the to-be-remembered hemifield) across set sizes for the high- and low-capacity individuals. There was a monotonic increase in the negativity of the contralateral potential up to set size 3 and showed no further increase for larger set sizes (see Figures 5(a,b)). This resulted in a significant main effect of set size on these contralateral waveforms (F(7, 28) = 25.86, p < .00001), but the effect of capacity group was not significant (F(1, 28) < 1.0, not significant). Interestingly, the ipsilateral activity revealed a significant interaction between set size and capacity group (F(7, 196) = 2.38, p < .03). More specifically, low-Kave individuals showed a monotonic rise in ipsilateral negativity as a function of a set size, whereas the high-Kave group showed constant amplitudes across all set sizes. In fact, when the difference in the ipsilateral negativity between subcapacity set sizes (i.e., average of set size 1 and set size 2) and supra-capacity set sizes (the average of set sizes above 3) were correlated with the capacity estimates, low-Kave individuals showed a larger difference in the ipsilateral negativity than high-Kave individuals (r = -0.39, p = .03). These analyses suggest that the onset of to-be-ignored items also overload low-capacity individuals' selection mechanisms and they cannot help but allocate VWM resources to them.

Discussion

In Experiment 2, we found evidence from both behavioral and ERP measures consistent with our predictions that low-capacity individuals showed a drop in the amount of task-relevant information represented in VWM as the set size increased beyond their storage capacity. It appears that it is this drop that magnifies the differences between high- and low-Kave individuals. This finding contradicts with the space account of individual differences in VWM capacity, and again supported the attentional-control account by showing that the difference between high- and low-Kave individuals is largely driven by the ability to use their VWM to the fullest when there are more objects than they can maintain in their VWM. We have observed supportive ERP evidence for this interpretation in the literature. The CDA amplitudes showed a similar trend in previous studies (Anderson et al., 2011; Vogel & Machizawa, 2004). One study that employed a task that heavily taxes attentional selection to gate access to VWM capacity (i.e., multiple-object tracking) even reported that the drop in the CDA amplitudes was associated with lower performance (Drew & Vogel, 2008). Thus, it suggests that strong correlations previously observed between the CDA and the behavioral capacity estimates might have been reflecting the underutilization of VWM capacity by low-capacity individuals' when attentional selection was overloaded.

Another interesting finding came from a separate analysis of the ipsilateral activities. If attentional control against the automatic deployment of attention to the onset of an overwhelming large number of targets is what impedes low-Kave individual's performance, we might expect that the neural response to the to-be-ignored side would also differ between high- and low-Kave individuals. It was indeed the case. Low-Kave individuals showed significantly greater ipsilateral negativities for supra-capacity set sizes, which contributed to the decrease in the



FIGURE 5 Findings of the separate analyses of the waveforms measured contralateral to the memoranda versus ipsilateral to the memoranda (and contralateral to the to-be-ignored items). (a) Contralateral and ipsilateral ERP responses for set size 2, 4, and 8. The figures show the contralateral (purple) and ipsilateral (black) response to the onset of the memory arrays. The tick marks on the x axis indicate every 200 ms after the onset of the memory array. The difference between the contralateral responses and the ipsilateral responses in the 300–1000 ms (highlighted by the green bars) time window defines the CDA. The top and bottom rows show the response for set size 2, 4 and 8 for low- and high-capacity groups, respectively. (b) Set size functions of contralateral and ipsilateral responses. The blue and green lines represent the set size functions of the mean amplitudes of the contralateral responses in the CDA time window for low- and high-capacity groups, respectively. The error bars indicate the within-subject 95% confidence intervals. The contralateral responses show similar patterns across capacity groups, but the ipsilateral responses clearly dissociate the capacity groups. The ipsilateral responses for low-capacity group showed monotonic increase in negativity, consistent with what we predicted if these individuals were attempting to store the task-irrelevant items, whereas those for high-capacity group remained constant across set sizes.

CDA amplitudes for supra-capacity set sizes. This nicely matches with our attentional-control account of individual differences in VWM capacity. Our findings extend the potential implications of measuring CDA amplitudes as the marker of the number of items held in VWM. That is, our findings indicate that there is utility in measuring the amplitude of activity at one hemisphere as task demands are manipulated, instead of being constrained to measuring the CDA as a difference between hemispheres to understand the nature of capacity limitations in the brain.

EXPERIMENT 3

The results from Experiments 1 and 2 suggest that the VWM capacity estimate obtained from the standard changedetection task is also sensitive to individuals' ability to use their storage space in the face of an overload of taskrelevant information. Particularly, it is the low-capacity individuals who suffer more from this overload and end up storing fewer usable task-relevant items than their storage space allows. Our current working hypothesis argues that this deficit is triggered by the onset of the supra-capacity load of items that demand attentional selection. Recently, Shapiro and colleagues have found evidence supporting this explanation by manipulating the presentation of memory items (Ihssen, Linden, & Shapiro, 2010). In their study, they presented eight memory items, either simultaneously or sequentially in two four-item groups. Arguably, in the sequential-presentation condition, the amount of the competition among items in each memory array is substantially reduced. According to our hypothesis, this should

lead to the elimination of the decrement in the capacity estimate associated with supra-capacity set sizes. Indeed, the capacity estimate was higher for the sequential condition than that for the simultaneous condition. More important to our hypothesis, the benefit of the sequential presentation was larger for low-capacity individuals. However, one limitation in this study by Shapiro and colleagues was that sequential presentation could have potentially altered how participants performed the task. For instance, participants could have used different mnemonic strategies (e.g., verbal rehearsal) to retain the initially presented items, and then devoted VWM exclusively to the information in the second display. Alternatively, they could have encoded the initially presented items into offline memory storage (i.e., long-term memory) before the onset of the second display. To eliminate such alternative hypotheses, we sought to diminish the capacity decrement associated with the supra-capacity set size while preserving the simultaneous onset of memory items.

According to attentional-capture literature, resolving involuntary competition for resource deployment requires time for attentional control to be exerted (Folk et al., 2002). More specifically, our recent study demonstrated that it is the low-capacity individuals who take significantly longer to exert proper attentional control to disengage their attention from task-irrelevant distractors that have target properties (Fukuda & Vogel, 2011). If this is the case, we should find that the decrement in the capacity estimates for a supra-capacity set size diminishes when target items are presented long enough for the attentional control mechanisms to resolve the competition. Thus, in Experiment 3, we parametrically manipulated the exposure duration of the memory items and examined the decrement in the capacity set size. Our predictions were straightforward. First, with a typical exposure duration (i.e., 150ms) we should observe that the capacity estimates for a supra-capacity set size (i.e., set size 8) are lower than those for a near-capacity set size (i.e., set size 4). Of note, this decrement in the capacity estimates (i.e., the 4–8 drop) should be observed more for low-capacity individuals than high-capacity individuals. Most critically, this 4–8 drop should decrease at longer exposure durations.

Method

Participants

After providing informed consent of procedures approved by the University of Oregon Institutional Review Board, 36 young adults with normal or corrected-to-normal vision participated in the study in return for course credit in psychology classes.

Stimuli and Procedure

Participants performed a variant of the standard change-detection task used in Experiment 1. In this task, participants were presented with a memory array that consisted of either four (set size 4), or eight (set size 8) colored squares. These memory arrays were presented for 150 ms (short), 300 ms (medium), or 450 ms (long). The other aspects were identical to Experiment 1. The types of trials were pseudo-randomly determined, and participants completed 60 trials for each set size and exposure duration combination.

Results

Similar to Experiments 1 and 2, performance at each set size and exposure duration was transformed to K estimate using the standard formula (Figure 6). Then, individuals were classified as high- or low-capacity using a median split based on the mean K estimate across set size 4 and 8 (i.e., Kave=the average of K4 and K8) using the short exposure duration condition. A mixed-design repeated-measures ANOVA with three factors (exposure duration × set size × capacity group) revealed the following. First, there were main effects of set size and exposure duration. The K estimates were significantly smaller for set size 8 than for set size 4 (mean K4=2.7, mean K8=2.3, F(1, 34)=7.68, p<.01). Also, the K estimates increased as the exposure duration increased (short Kave=2.49, medium Kave=2.67, long Kave=2.80; F(2, 68)=5.11, p<.01) In addition, there were two significant two-way interactions, namely between set size and capacity group (F(1, 34)=15.60, p<.001) and between exposure duration and capacity group (F(2, 68)=5.36, p<.01). The first interaction was driven by a larger difference in K estimates for set size 8 than for set size 4 between high- and low-Kave groups. The second interaction was driven by the low-Kave group showing a larger improvement in Kave at longer exposure durations. Critically, we observed a significant three-way interaction across capacity group, set size, and exposure duration (F(2, 68)=3.39, p<.05). This shows that the selective improvement of the traditional capacity estimate due to increased exposure duration was primarily driven by the increase in low-capacity individuals' K8.

FIGURE 6 The effect of exposure duration on visual working memory capacity estimate (K). The blue and red line indicates the K estimate for set sizes 4 and 8 for the low-capacity group, respectively. The green and magenta line indicates the K estimate for set sizes 4 and 8 for the high-capacity group, respectively. The error bars represent the within-subject 95% confidence interval. In a stark contrast to the high-capacity group that showed a stable capacity estimate across set sizes and exposure durations, the low-capacity group's K8 was significantly smaller than K4 at a 150-ms exposure. However, the difference diminished as exposure duration increased mainly from a monotonic increase in K8.



Discussion

In Experiment 3, we sought to investigate the nature of the decrement in the capacity estimates for supra-capacity set sizes. If the decrement is due to the failure in exerting attentional control over the overwhelming competition amongst an excessive number of task-relevant items, we should be able to decrease or eliminate such a decrement by providing enough time for attentional control to resolve the competition. To directly test this hypothesis, we manipulated the interval in which memory stimuli were available for encoding. Consistent with this prediction, we found that increasing the exposure duration of the memory arrays systematically decreased the drop in K to the point that it did not occur at the longest exposure duration. One important observation to note is that the extended exposure only benefitted the performance for low-capacity individuals, particularly in the supra-capacity set size. This critically argues against the alternative hypothesis that the extended exposure encouraged individuals to engage in additional strategies (e.g., verbal re-encoding of stimuli) because it should lead to performance improvement across all set sizes for both high- and low-capacity individuals. In addition, it is also inconsistent with an alternative hypothesis that low-capacity individuals are simply slower at perceiving color information because this hypothesis would also predict an equal, if not larger, amount of increase in the K estimate for the near-capacity set size (i.e., set size 4). Our finding that low-capacity individuals are as quick as high-capacity individuals at identifying a colored target embedded in a rapid-serial-visual presentation is also inconsistent with this alternative account (Fukuda & Vogel, 2009; Experiment 4). Thus, the results from Experiment 3 confirm that a large portion of individual differences in the standard VWM capacity estimate is due to differences in the individuals' ability to exert attentional control in the face of overwhelming competition for the limited representational space in VWM.

GENERAL DISCUSSION

Our ability to actively hold multiple objects in VWM is critically involved in many aspects of our visual cognition (see Luck & Vogel, 2013 for a recent review). At the same time, it is well known that the capacity of VWM reliably and significantly varies among individuals. Numerous studies have investigated why individuals differ in this fundamental cognitive ability, and it has been shown that low-capacity individuals tend to have poor attentional control in allocating VWM to a manageable set of task-relevant objects. However, such observations have been established by examining the correlations among a set of tasks, and it has been unclear how the attentional control component manifests itself in the measure of VWM capacity.

In this study, we sought to examine the contribution of an individual's attentional-control ability to their VWM capacity estimate itself. In Experiment 1, we analyzed a data set based on a sample size of 495 subjects, which enabled a detailed examination of the nature of individual differences in visual short-term memory performance. We found that the capacity estimate systematically changed as a function of a set size. More precisely, the capacity estimate was significantly lower for a supra-capacity set size (i.e., set size 8) than a near-capacity set size (i.e., set size 4). Critically, this decrement in the capacity estimate was primarily driven by low-capacity individuals. These findings support the

GENERAL DISCUSSION

view that the traditional VWM capacity estimate is not only a measure of an individual's maximum storage space in VWM, but is sensitive to an individual's ability to exert attentional control when faced with overwhelming competition induced by an excessive number of task-relevant objects. In Experiment 2, we used the CDA, a well-established neural marker of VWM capacity, to confirm that the decrement in the behavioral capacity estimates for supra-capacity set sizes is not caused by a failure in the postmaintenance comparison processes, but caused by a failure in maintaining manageable amounts of the correct information. Analyses of the waveforms contralateral to the to-be-ignored items revealed that low-capacity individuals processed the task-irrelevant information so that it interfered with the usable task-relevant information as measured with the CDA amplitude. In Experiment 3, we attempted to obtain further evidence for the contribution of the attentional-control component in memory tasks by selectively eliminating the capacity decrement induced by a supra-capacity set size (i.e., the 4–8 drop). We hypothesized that given enough time low-capacity individuals should also be able to exert proper attentional control to resolve the overwhelming competition (Fukuda & Vogel, 2011). Indeed, we successfully eliminated the 4–8 drop for low-capacity individuals by simply extending the exposure duration. Consistent with our hypothesis, the benefit of extended exposure was primarily observed with a supra-capacity set size in low-capacity individuals. This observation rules out the alternative hypothesis that extended exposure led individuals to engage in other mnemonic strategy (e.g., verbal coding). Given these findings, we conclude that the VWM capacity estimate derived from a standard change-detection task is not a pure measure of the size of the storage space, but rather, it is also a measure of how well individuals can attentionally regulate the allocation of the limited storage space in VWM in the face of overwhelming competition.

One favored mechanism of representing multiple items in VWM is that each item is represented by recurring synchronous firing of feature-coding neurons for that item. The recurring neuronal firing for each representation is desynchronized from one another to avoid the confusion of representations that leads to reduction in the number of successfully stored representations using the phase of a low-frequency carrier wave (i.e., theta~alpha wave) (Lee, Simpson, Logothetis, & Rainer, 2005; Liebe, Hoerzer, Logothetis, & Rainer, 2012; Lisman & Idiart, 1995; Luck & Vogel, 1997, 2013; Raffone & Wolters, 2001; Sauseng et al., 2009; Siegel, Warden, & Miller, 2009). In light of this account, the attentional-control mechanism might be playing a critical role in selecting a manageable subset of items so that each representation can be desynchronized from one another in the limited phase space of the carrier wave.

The results of our study have broad implications for the interpretation of individual differences in VWM capacity. First, our results show why VWM capacity measures are strongly correlated with other attentional-control measures. It has been proposed that variability in VWM capacity is the causal factor in individual variations in attentional control (see Luck & Vogel, 2013 for raising a similar argument). Given that the standard capacity measure is heavily influenced by individuals' attentional-control ability as we show here, it is no surprise that such a measure is strongly predicted by other attentional-control measures. Our findings indicate that we need further refinement of our understanding of the relationship between VWM capacity measures and high-level cognitive constructs such as fluid intelligence and reasoning ability. Is it our amount of storage space, our attentional control abilities, or both, that determine our ability to carry out high-level cognitive functions?

Gaining a better understanding of the individual differences in VWM capacity across the population also has important practical implications. As discussed earlier, reduced VWM capacity is one of the most prevalent cognitive deficits found in a wide variety of mental disorders (e.g., schizophrenia, Alzheimer's disease). Also, it is known that VWM capacity estimates change dramatically over the course of normal development and aging. Indeed, there have been multiple attempts at characterizing the nature of VWM capacity differences in such populations (Cashdollar et al., 2013; Jost, Bryck, Vogel, & Mayr, 2011; Lee et al., 2010; Leonard et al., 2013; Mayer, Fukuda, Vogel, & Park, 2012), but these approaches have exclusively relied on examining the correlations between the performance of different tasks. We believe that this work would benefit from taking an approach like that of this study to manipulate the structure of the VWM task itself to understand the bases of these changes across development and aging. Studying the fluctuations of VWM capacity estimate across set sizes would provide the cleanest method for studying how VWM capacity deficits come about in each population.

Last, knowing the nature of the mechanisms underlying VWM capacity deficits is integral to developing an effective training regimen to reduce the capacity limits of human cognition. Training working memory abilities has been a recent focus of investigation given the intimate relationship between this capacity limit and a variety of cognitive abilities. Though its trainability and the transferability of the training effect is still unclear (Jaeggi, Buschkuehl, Jonides, & Perrig, 2008; Jaeggi, Buschkuehl, Jonides, & Shah, 2012; Shipstead, Redick, & Engle, 2012; Shipstead, Hicks, & Engle, 2012), a part of the issue may well be that the training methods are not tailored to the specific type of problem that a given individual faces when trying to encode and maintain multiple items in VWM. By identifying individuals with low capacities because of breakdowns in attentional control, it may be possible to train these individuals to be more selective in what they try to store in VWM.

9. DIFFERENCES IN VISUAL WORKING MEMORY CAPACITY

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