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A Common Discrete Resource for Visual Working Memory and Visual Search

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Abstract

Visual search, a dominant paradigm within attention research, requires observers to rapidly identify targets hidden among distractors. Major models of search presume that working memory (WM) provides the on-line work space for evaluating potential targets. According to this hypothesis, individuals with higher WM capacity should search more efficiently, because they should be able to apprehend a larger number of search elements at a time. Nevertheless, no compelling evidence of such a correlation has emerged, and this null result challenges a growing consensus that there is strong overlap between the neural processes that limit internal storage and those that limit external selection. Here, we provide multiple demonstrations of robust correlations between WM capacity and search efficiency, and we document a key boundary condition for observing this link. Finally, examination of a neural measure of visual selection capacity (the N2pc) demonstrates that visual search and WM storage are constrained by a common discrete resource.

Keywords

visual attention, visual memory, evoked potentials, working memory, visual search, ERP, N2pc

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Working memory (WM) is typically defined as an on-line work space where information can be efficiently accessed and updated (Baddeley, 1986; Smith & Jonides, 1999). Thus, it is a natural hypothesis that WM would be required for visual search, an attention-demanding task that requires the rapid apprehension of multi-element displays to find a target. Indeed, virtually every major model of visual search has postulated a role for WM (e.g., Bundesen, 1990; Desimone & Duncan, 1995; Duncan & Humphreys, 1989; Fisher, 1982; Pashler, 1987; Treisman & Gelade, 1980; Wolfe, 1994). A common proposal is that small clusters of items are transferred into WM to enable the parallel evaluation of their target status (e.g., Duncan & Humphreys, 1989; Fisher, 1982; Wolfe, 2005). Critically, these models predict that individuals with higher WM capacity should be able to apprehend a larger number of search elements at a time, and therefore should perform visual search more efficiently. Nevertheless, past efforts have not revealed a link between WM capacity and search efficiency.

Thus far, studies showing a link between WM capacity and search performance have found that higher-capacity individuals identify targets more quickly when it is necessary to overcome distraction from salient irrelevant items (Poole & Kane, 2009; Sobel, Gerrie, Poole, & Kane, 2007). These studies support previous suggestions that WM capacity is critical for resisting distraction (e.g., Engle, 2002; Vogel & Awh, 2008), but because they measured search performance using absolute reaction time (RT)—a measure that is not sensitive to search efficiency—they do not reveal whether WM capacity is critical for search per se. A more direct test was carried out by Kane, Poole, Tuholski, and Engle (2006). They found near-zero correlations between WM capacity and search efficiency using three different search tasks and a sample size of more than 500 subjects. This is a highly significant null result because it casts doubt on a common assumption of major models of visual search, and it challenges a growing body of evidence that similar neural processes underlie internal storage and external selection of visual information (e.g.,

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Awh & Jonides, 2001; Awh, Vogel, & Oh, 2006; Drew & Vogel, 2008; Engle, 2002; Vogel & Awh, 2008). Thus, we were motivated to reexamine this issue.

Here, we present three separate demonstrations of a robust correlation between WM capacity and search efficiency (Experiments 1a, 1c, and 2). Moreover, we offer an explanation of prior null results by defining a key boundary condition for observing this link. In Experiment 2, we tested whether visual selection during search tasks is subject to an item limit by measuring the N2pc, an electrophysiological response that has been shown to track the number of items visually selected (Anderson, Vogel, & Awh, 2011, in press; Drew & Vogel, 2008; Luck & Hillyard, 1994). The N2pc evoked by the search array followed a bilinear function, rising as additional items were included in the search array and reaching a plateau at a set size that predicted both search efficiency and WM capacity. In combination with its link to individual differences in search efficiency, the plateau in selectiondependent neural activity suggests discrete limits in the number of items that can be searched simultaneously. We conclude that a common discrete resource constrains WM storage and search efficiency.

Experiments 1a, 1b, and 1c

Method

Sixty-five undergraduates at the University of Oregon (23, 25, and 17 in Experiments 1a, 1b, and 1c, respectively) completed the experiments for course credit or monetary compensation. All participants gave informed consent according to procedures approved by the University of Oregon institutional review board.

Stimuli were generated in MATLAB using the Psychophysics Toolbox extension (Brainard, 1997; Pelli, 1997) and were presented on a 17-in. flat CRT computer screen (120-Hz refresh rate). The viewing distance was approximately 77 cm. Participants first performed a WM task and then a visual search task.

WM task. Participants fixated a central dot $(0.37^{\circ} \times 0.37^{\circ})$ and were instructed to remember the orientation of six randomly positioned discs (radius = 0.93°), each of which had a prominent rectangular gap (randomly oriented across 360° of stimulus space; Fig. 1a). Memoranda were presented within a 9.6° × 9.6° region, with a minimum separation of two thirds of an object.

Within a single trial, a 750-ms fixation point was followed by presentation of the memoranda for 200 ms, a 1,000-ms delay period, and finally a probe display of rings that appeared in the same positions as the memoranda. In the probe display, one ring was thicker than the others. Subjects made an unspeeded click on this ring to

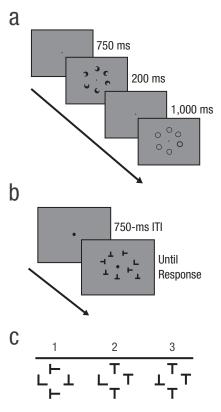


Fig. 1. Illustration of the tasks and search displays in Experiment 1. In the working memory task (a), participants were instructed to maintain fixation and to remember the orientation of all six objects presented in the display. After a short delay, six probe rings were presented, and participants clicked on the thicker ring to report the position of the gap in the sample item that had appeared in that position. In the visual search task (b), participants maintained fixation and were instructed to identify the direction (right or left) of the target letter L. Set sizes ranged from 1 to 8. Participants used the left or right arrow key to indicate whether the vertical segment of the L was on the left or right, respectively. Target-distractor similarity and distractor variability were manipulated (c). In Experiment 1a and one condition of Experiment 1c, both target-distractor similarity and distractor variability were high (Example 1). In Experiment 1b, target-distractor similarity was lower than in Experiment 1a (the relative position of the vertical segment was always different in targets than in distractors), and distractor variability was low (Example 2). Finally, in Experiment 1c, the vertical segment of the L was shifted inward, so that target-distractor similarity was even higher than in Experiment 1a, but grouping was still encouraged by low distractor variability (Example 3). Distances are not to scale. ITI = intertrial interval.

indicate the position of the gap in the corresponding sample item. Each response was followed by a 750-ms blank intertrial interval.

To estimate WM capacity, we fitted a mixture model (Zhang & Luck, 2008) to the distribution of each observer's response errors (the difference between the response and the angle of the probed stimulus) using maximum likelihood estimation. The fitted mixture model was then decomposed to produce a von Mises distribution, corresponding to target-related responses, and a uniform

distribution, corresponding to the proportion of trials in which subjects failed to store the probed item (P_f) . The probability that the critical item was stored $(1 - P_f)$, was our operational definition of WM capacity.

Visual search task. Search displays contained a target L shape (facing left or right) and a variable number of distractor T shapes (Fig. 1b), and were presented within a square $9.6^{\circ} \times 9.6^{\circ}$ region. Search elements $(1.1^{\circ} \times 1.1^{\circ})$ were composed of line segments $(0.2^{\circ}$ thick) and were randomly positioned with the constraint that all objects were separated by at least two object widths.

The key manipulations across Experiments 1a through 1c were *distractor variability* (i.e., uniform vs. varied distractor orientations) and *target-distractor similarity* (determined by whether specific junctions in the *T* and *L* stimuli overlapped). These manipulations allowed us to test whether the putative correlation between WM capacity and search efficiency would be contingent on distractor variability that required the individuation of each search element.

In Experiment 1a (Fig. 1c, Example 1), distractor variability was high because the *T* shapes were presented in four possible orientations (up, right, left, or down). Target-distractor similarity was high because the specific right angle present in the target stimuli was also present in each possible distractor. In particular, it has been argued that high distractor variability increases the need to individuate distractors to determine their target status (Duncan & Humphreys, 1989).

In Experiment 1b (Fig. 1c, Example 2), distractor variability was low, because the distractors were uniform upright *T* shapes. Target-distractor similarity was lower than in Experiment 1a because although all stimuli contained right angles, the relative position of the vertical segment was always different in targets than in distractors. In this experiment, uniform distractors could be grouped and rejected as groups (Duncan & Humphreys, 1989).

One condition of Experiment 1c was the same as in Experiment 1a. In the other condition, uniform distractors were employed, but the target alternatives were made more similar to each other (and to distractors) by positioning the bottom segment of the L partly across the vertical segment (Fig. 1c, third example). Although distractors were still groupable in these displays, search slopes were expected to be steep. This experiment tested whether the steepness of search slopes alone is a critical factor for observing a link between WM capacity and search efficiency.

Set size varied from 1 through 8, inclusive. Eight positions were randomly selected for each trial with the minimum distance requirements already noted, and then a contiguous subset of these positions was selected for the

given set size. For instance, for a trial with a set size of 3, we selected three contiguous positions from within eight positions that met the minimum distance requirements. This strategy (along with fixation instructions) ensured that interitem distances—and therefore visual crowding—were equated across set sizes.

During each trial, subjects first saw a central fixation point, followed by the search display (presented until response). They were instructed to respond as quickly and accurately as possible by pressing the left or right arrow key to indicate whether the vertical line of the $\it L$ was on the left or right, respectively. A 750-ms blank intertrial interval followed each response.

RT measurements were excluded if the search response was incorrect or RT was 3 standard deviations (or more) above or below the mean. Average RT was calculated for each set size, and search efficiency was operationalized as the slope of the RT-by-set-size function.

Results and discussion

Experiment 1a: WM capacity correlates with search efficiency when individuation is required. There was a significant effect of set size on RT in this experiment (Fig. 2a), F(7, 16) = 67.08, p < .001. Set size had no effect on accuracy, F(7, 16) = 1.55, p = .22—evidence against a significant speed-accuracy trade-off. The slope of the RT-by-set-size function (25.8 ms/item) indicated relatively inefficient search (Wolfe, 1998), and split-half reliability was strong (.87). The critical result was a robust correlation between WM capacity and search efficiency (Fig. 2b), $R^2 = .63$, p < .0001, such that slopes were shallower for higher-capacity observers. By contrast, WM capacity did not predict the intercept of the RT-by-setsize function, $R^2 = .013$, p > .60, which suggests that highcapacity subjects had an advantage in search efficiency per se rather than a more general advantage in processing speed or better maintenance of the task set.

Experiment 1b: distractor grouping masks the link between WM capacity and search efficiency. RT rose with set size in Experiment 1b (Fig. 2c), F(7, 18) = 132.79, p < .001. Accuracy did not vary across set sizes, F(7, 18) = 0.67, p = .42, which again indicated the absence of a significant speed-accuracy trade-off. The slope of the RT-by-set-size function (15.3 ms/item) indicated more efficient search than in Experiment 1a. Critically, however, we observed no relationship between WM capacity and search efficiency (Fig. 2d), F(7, 18) = 1.56, or search intercept, F(7, 18) = 1.56, or search

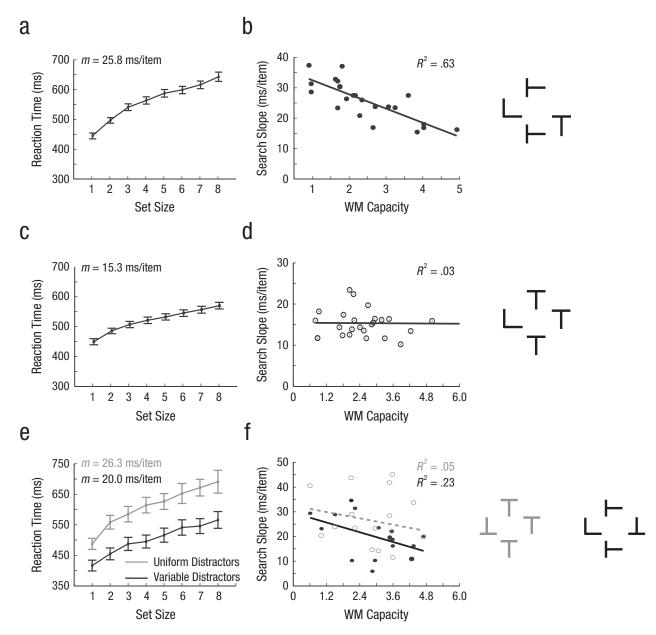


Fig. 2. Results from Experiment 1. The graphs on the left show mean reaction time (RT) as a function of set size in (a) Experiment 1a, (c) Experiment 1b, and (e) Experiment 1c. Also shown is the slope (m) of each function. Error bars represent 95% confidence intervals. The graphs on the right show individual participants' search slopes (with best-fitting regression lines) as a function of working memory (WM) capacity in (b) Experiment 1a, (d) Experiment 1b, and (f) Experiment 1c. Illustrations of the stimulus configurations for the experiments are displayed to the right of the scatter plots; in (f), stimuli for the uniform- and variable-distractor conditions are illustrated in gray and black, respectively.

Experiment 1c: difficult search alone does not reveal the link between WM capacity and search efficiency. An alternative interpretation of the null result from Experiment 1b is that the correlation was masked because the search task was easier (and the range of slopes was reduced). To test this possibility, we made the target alternatives in the uniform-distractor condition of Experiment 1c harder to discriminate and more similar to the distractors (Fig. 1c, third example). Search slopes increased markedly in this condition, perhaps because

observers needed more time to reject each distractor. Nevertheless, the uniform distractors still facilitated grouping. If lower search slopes per se masked the correlation in Experiment 1b, then this more challenging search task might reveal a link between WM capacity and search efficiency. By contrast, if distractor grouping was responsible for masking the correlation, then we would not find any correlation in this condition either. Experiment 1c also included separate blocks of a condition that replicated Experiment 1a (variable-distractor condition).

There was a main effect of condition on accuracy, F(1, 16) = 13.6, p < .01. Accuracy was higher in the variable-distractor condition than in the uniform-distractor condition, presumably because the target alternatives were more similar in the latter condition. There was no effect of set size on accuracy, F(7, 10) = 1.55, p = .78—evidence against a significant speed-accuracy trade-off. No significant interaction between condition and set size was observed for accuracy (p = .9).

Analyses of the RTs revealed significant effects of condition, F(1, 16) = 51.6, p < .001, and set size, F(7, 10) = 30.2, p < .001 (Fig. 2e), and a marginally significant interaction, F(7, 10) = 2.8, p = .07. Search was relatively inefficient in both the variable-distractor blocks (20.0 ms/item) and the uniform-distractor blocks (26.3 ms/item). Slopes were higher in the latter than in the former condition, t(16) = 4.65, p < .001. Split-half reliability estimates were strong for both conditions (> .91).

Just as in Experiments 1a and 1b, WM capacity was uncorrelated with the intercept of the RT-by-set-size function, for both the variable-distractor condition, R^2 = .012, p = .67, and the uniform-distractor condition, $R^2 =$.0003, p = .93. The key result of Experiment 1c was that we observed a reliable correlation between WM performance and search efficiency in the variable-distractor condition ($R^2 = .23$, p < .05), but no evidence of this link in the uniform-distractor condition ($R^2 = .05$, p = .39; Fig. 2f). A Hotelling-Williams test showed that the correlation was significantly larger in the variable-distractor condition, t(14) = -3.28, p < .01. The null correlation between WM capacity and search efficiency in the uniform-distractor condition shows that the null result from Experiment 1b was not caused by faster search slopes per se. Instead, we conclude that groupable distractors mask the link between WM capacity and search efficiency.

Summary of Experiments 1a, 1b, and 1c. Experiments 1a through 1c show that WM capacity is a robust predictor of search efficiency. Observing this link, however, requires search displays that minimize distractor grouping. When distractors were uniform and groupable, the correlation was not observed, even when difficult-to-discriminate target alternatives elicited steep search slopes. We propose that distractor grouping can mask the correlation between WM capacity and search efficiency because grouping changes the effective set size of the search display, producing a disconnect between WM capacity and the number of search elements that can be apprehended simultaneously.

In line with past proposals (e.g., Duncan & Humphreys, 1989; Fisher, 1982; Wolfe, 2005), our working hypothesis is that WM capacity predicts search efficiency because WM capacity determines the number of items that can be

searched simultaneously. An alternative interpretation, however, is that higher-capacity subjects search individual items more quickly rather than searching more items at a time. Experiment 2 provides direct evidence that the number of items simultaneously selected during search is linked to WM capacity, but the data thus far already are evidence against a general link between processing speed and WM capacity. Specifically, no correlation between WM capacity and absolute RT (operationalized by the intercept of the RT-by-set-size function) was observed even though a general processing-speed advantage predicts precisely this finding. Another alternative interpretation is that higher-capacity subjects were simply more attentive to a challenging task, but superior attention to the task at hand should have given them an advantage in all search tasks, not just the ones that minimized distractor grouping. Our conclusion is that search efficiency per se is better among subjects with higher WM capacity.

Experiment 2

The hypothesis that WM capacity limits the number of search items that can be selected simultaneously presumes that visual search is indeed constrained by an item limit. Experiment 2 tested this assumption by measuring the amplitude of the N2pc waveform, a phasic negative deflection in event-related potential (ERP) amplitude over posterior electrodes contralateral to visually selected items (Luck, Girelli, McDermott, & Ford, 1997; Luck & Hillyard, 1994). Recent work has shown that N2pc amplitude provides a sensitive index of the number of items selected (Anderson et al., 2011, in press; Drew & Vogel, 2008; Pagano & Mazza, 2012). Thus, if there is a discrete limit in the number of items an observer can select during search, then N2pc amplitude should reach a plateau when the number of items to be searched exceeds the observer's selection capacity. In turn, if the N2pc provides a valid measure of visual selection capacity, then it should predict individual differences in search efficiency. We tested these predictions and also examined whether the same neural measure would predict WM capacity.

Method

Thirty undergraduates at the University of Oregon completed the experiment for course credit or monetary compensation. All participants gave informed consent according to procedures approved by the University of Oregon institutional review board.

Viewing distances were approximately 100 cm. The WM task and modeling procedures were the same as in Experiment 1.

The visual search task was identical to the task in Experiment 1 except as noted here. Search elements (Fig. 1c, Example 1) were presented within two imaginary rectangles $(6.3^{\circ} \times 4.9^{\circ})$, each centered 4.0° to the left or right of a central diamond fixation $(0.57^{\circ} \times 0.57^{\circ})$. During each trial, subjects fixated a central cue (duration = 500 ms) that was blue on one side and yellow on the other. After a 500-ms interstimulus interval, the search array was presented. Subjects were instructed to attend the side of the screen indicated by one of the two fixation colors (counterbalanced across subjects), and to indicate the target's identity quickly and accurately. On the unattended side, an irrelevant display of the same set size was presented (to match visual stimulation across the two hemifields).

ERPs were recorded using our lab's standard recording and analysis procedures, including rejection of trials contaminated by blocking, blinks, or large (> 1°) eye movements (McCollough, Machizawa, & Vogel, 2007; Vogel, Luck, & Shapiro, 1998). Subjects with trial rejection rates greater than 20% were excluded from the sample.

The N2pc was measured at parietal, posterior parietal, and lateral occipital sites as the difference in mean amplitude between the ipsilateral and contralateral waveforms during the period 200 to 275 ms after the onset of the visual search display. The electroencephalogram and electrooculogram were amplified with an SA Instrumentation (San Diego, CA) amplifier with a band pass of 0.01 through 80 Hz and were digitized at 250 Hz in LabView 6.1 (National Instruments, Austin, TX) running on a PC.

Results and discussion

Visual search performance. There was a significant effect of set size on RT (Fig. 3a), F(7, 21) = 25.00, p < .001, and no effect of set size on accuracy, F(7, 21) = 2.05, p = .1, which indicated that there was not a significant speed-accuracy trade-off. Search was relatively inefficient (17.70 ms/item).

Behavioral link between WM capacity and search efficiency. As in Experiments 1a, and 1c, we observed a strong relationship between WM capacity and search efficiency (Fig. 3b; $R^2 = .30$, p < .0001). Once again, however, WM capacity was uncorrelated with the intercept of the RT-by-set-size function ($R^2 = .01$, p = .57), which suggests that WM capacity is correlated with search efficiency per se rather than with general processing speed.

Linking a neural measure of visual selection with visual search performance. The N2pc was measured by subtracting ipsilateral from contralateral amplitudes from the OL and OR electrodes 200 to 275 ms after the

onset of the search array (Fig. 3c). N2pc amplitude rose monotonically and then reached a plateau at about set size 3 (Fig. 3d)—set size 1 vs. 2: t(29) = 4.4, p < .001; set size 2 vs. 3: t(29) = 2.1, p < .05; set size 3 vs. 4: t(29) = -0.45, p = .66; set size 4 vs. 5: t(29) = 0.76, p = .46; set size 5 vs. 6: t(29) = 0.82, p = .76; set size 6 vs. 7: t(29) = 1.28, p = .21; set size 7 vs. 8: t(29) = -0.74, p = .47. A bilinear function provided an excellent fit to the N2pc-by-set-size function ($R^2 = .97$, p < .0001) and revealed that N2pc amplitude reached a plateau at approximately 2.5 items. This plateau suggests that only a few items could be selected simultaneously when the search array appeared.

If the N2pc provides a valid measure of the number of items each observer could select, then it should predict visual search efficiency. To test whether this was the case, we fit a bilinear model to the data from each observer (average $R^2 = .62$); this fit was superior to that provided by an exponential function (predicted by models that eschew item limits for visual selection). Critically, the inflection point of the bilinear function was strongly correlated with search efficiency (Fig. 3e; $R^2 = .31$, p <.01), a result showing that the N2pc-by-set-size function is sensitive to individual selection capacity. Thus, the plateau in N2pc amplitude across set sizes constitutes evidence for a relatively low item limit constraining visual selection, and the correlation with search efficiency shows that this item limit determines the efficiency of visual search. Finally, we also found a strong correlation between the inflection point of the N2pcby-set-size function in the search task and WM capacity (Fig. 3f; $R^2 = .30$, p < .01), which suggests that a common item limit constrains visual search and storage in WM.

General Discussion

Although influential models of visual search have suggested that WM provides the work space for visual search, previous studies have not found the predicted link between WM capacity and search efficiency (Kane et al., 2006). Here, we have provided three separate demonstrations that this correlation is robust, and we have documented an important boundary condition for observing this correlation. When distractor grouping minimized the need to individuate search elements, the correlation was masked (Experiment 1b and uniform-distractor condition in Experiment 1c). Our hypothesis is that grouping of distractors can obscure the link between WM capacity and search efficiency because variations in grouping efficiency can elicit uncontrolled changes in the effective set size of the search array, leading to a disconnect between WM capacity and the number of search elements that can be apprehended simultaneously. Experiment 2 provided direct evidence that visual search is constrained by an

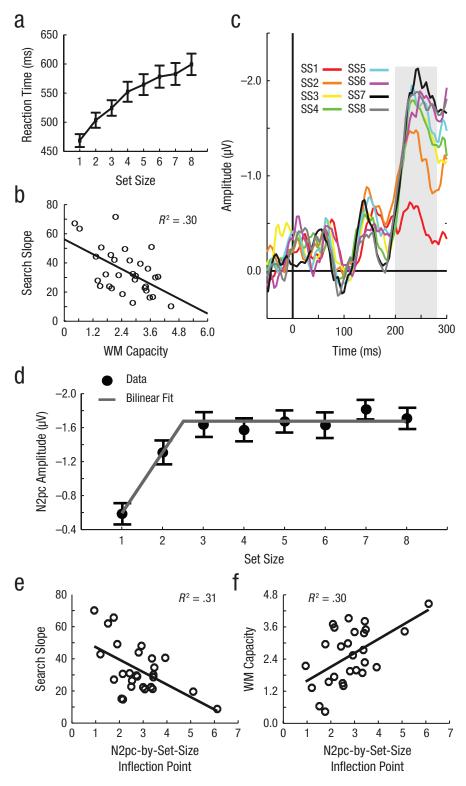


Fig. 3. Results from Experiment 2: (a) reaction time (RT) as a function of set size, (b) individual participants' search slopes (with best-fitting regression line) as a function of working memory (WM) capacity, (c) grand-averaged difference waves (contralateral amplitude – ipsilateral amplitude) from the OL and OR electrodes at each set size ("SS"), (d) N2pc amplitude as a function of set size (with a fitted bilinear function), (e) individual participants' search slopes (with best-fitting regression line) as a function of the inflection point of the N2pc-by-set-size function, and (f) WM capacity (with best-fitting regression line) as a function of the inflection point of the N2pc-by-set-size function. In (a) and (d), error bars represent 95% confidence intervals. In (c), the gray shading indicates the temporal window used to measure N2pc amplitudes.

item limit. Specifically, the amplitude of a neural index of visual selection (the N2pc) rose monotonically as additional items were included in the search array and reached a plateau at a set size that predicted individual search efficiency. Finally, the same N2pc function was also a robust predictor of WM capacity, a finding consistent with the hypothesis that WM and search are constrained by a common item limit.

Of course, it is important to consider how our findings can be reconciled with past studies that have not found a correlation between WM capacity and search efficiency. Grouping of distractors may have played an important role in the near-zero correlations observed by Kane et al. (2006); they employed search displays with large set sizes (up to 19 items) and a small number of unique distractor values, which may have encouraged grouping of the distractors. Furthermore, eye movements were unconstrained, and the area occupied by the search array and therefore the average eccentricity of the search elements—increased with set size. Because crowding strength increases with eccentricity (Bouma, 1970), estimates of search efficiency would have been determined in part by sensitivity to visual crowding rather than by the number of items that could be selected simultaneously (see Cohen & Ivry, 1991). Thus, our efforts to restrict eye movements and control visual crowding across set sizes may have provided a more sensitive measure of the link between WM capacity and search efficiency.

Findings from dual-task paradigms have also challenged whether WM is integral to visual search (Logan, 1978, 1979; Woodman, Vogel, & Luck, 2001). For example, Logan (1978) measured search efficiency while subjects were either given a verbal memory load or not. Search efficiency was equivalent across the two conditions, and Logan concluded that visual search does not require storage in WM (see also Oh & Kim, 2004). One key caveat, however, is that none of these studies provided direct evidence that subjects kept the memoranda active in WM during the search phase of the trial. More recent dual-task work (Unsworth & Engle, 2007) has shown that subjects can perform such tasks by relying on secondary memory to store the memoranda when attention must be directed toward an intervening task. This raises the possibility that subjects in these "dual"-task studies were actually searching in the absence of any active WM load. Given this uncertainty, the implications of these studies will be unclear until further work clarifies whether and when observers "offload" the contents of WM during challenging dual tasks.

Ours is not the first study to support a link between WM and search. For example, there is evidence suggesting that the contents of WM bias visual selection during search (Downing, 2000; Soto, Hodsoll, Rotshtein, & Humphreys, 2008; Woodman & Luck, 2007). In these

studies, search elements were prioritized during selection when they shared similar features with the contents of WM, which suggests that the contents of WM bias selection during search. These WM guidance effects, however, are not directly relevant to the basic question of whether WM capacity constrains the number of items that can be selected during search.

Emrich, Al-Aidroos, Pratt, and Ferber (2009) investigated search while measuring contralateral delay activity (CDA; Vogel & Machizawa, 2004), an electrophysiological component sensitive to on-line storage load. They found that similar CDA activity was observed during visual search and WM tasks, and that CDA amplitudes predicted absolute search RT. These data clearly suggest a role for WM during the lateralized search task, but they leave uncertain the specific role that WM played. For example, rather than indicating the selection of currently searched items, the CDA activity observed by Emrich et al. could have been elicited by the storage of previously searched locations (McCarley, Wang, Kramer, Irwin, & Peterson, 2003; Peterson, Kramer, Wang, Irwin, & McCarley, 2001; but see Horowitz & Wolfe, 1998) or the broader act of attending the relevant and suppressing the irrelevant side of space. Thus, the central value of the present work is to elucidate the way in which WM is integral to visual search. These two processes may call upon a common discrete resource that limits the number of items that can be selected, during either internal storage or external selection.

To conclude, our findings corroborate the long-standing but poorly supported assumption that visual WM provides the on-line work space for the analysis of potential targets during visual search (Bundesen, 1990; Desimone & Duncan, 1995; Duncan & Humphreys, 1989; Fisher, 1982; Treisman & Gelade, 1980; Wolfe, 2005). This finding dovetails with a growing body of research indicating that there are pervasive links between storage in on-line memory systems and the top-down selection of relevant aspects of the environment (Awh & Jonides, 2001; Chun, 2011; Cowan, 2001; Engle, 2002; Gazzaley & Nobre, 2011; Vogel & Awh, 2008). Our working hypothesis is that multiple stages of visual selection, including the initial apprehension and subsequent storage of items in WM, may be constrained by a common resource that determines the number of individuated representations that can be selected simultaneously (Ester, Vogel, & Awh, 2012). This "individuation thread" may explain why similar item limits have been inferred across a wide range of tasks that require internal and external selection, such as multipleobject tracking (Drew & Vogel, 2008; Pylyshyn & Storm, 1988), rapid enumeration (Ester, Drew, Klee, Vogel, & Awh, 2012; Halberda, Sires, & Feigenson, 2006; Pagano & Mazza, 2012), and storage in visual WM (Cowan, 2001; Luck & Vogel, 1997).

Acknowledgments

E. A. and D. E. A. conceived and designed the experiment; D. E. A. collected and analyzed data; E. A., D. E. A., and E. K. V. wrote the manuscript.

Declaration of Conflicting Interests

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

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