

# More target features in visual working memory leads to poorer search guidance: Evidence from contralateral delay activity

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The visual-search literature has assumed that the top-down target representation used to guide search resides in visual working memory (VWM). We directly tested this assumption using contralateral delay activity (CDA) to estimate the VWM load imposed by the target representation. In Experiment 1, observers previewed four photorealistic objects and were cued to remember the two objects appearing to the left or right of central fixation; Experiment 2 was identical except that observers previewed two photorealistic objects and were cued to remember one. CDA was measured during a delay following preview offset but before onset of a four-object search array. One of the targets was always present, and observers were asked to make an eye movement to it and press a button. We found lower magnitude CDA on trials when the initial search saccade was directed to the target (strong guidance) compared to when it was not (weak guidance). This difference also tended to be larger shortly before search-display onset and was largely unaffected by VWM item-capacity limits or number of previews. Moreover, the difference between mean strong- and weak-guidance CDA was proportional to the increase in search time between mean strong- and weak-guidance trials (as measured by time-to-target and reaction-time difference scores). Contrary to most search models, our data suggest that trials resulting in the maintenance of more target features results in poor search guidance to a target. We interpret these counterintuitive findings as evidence for strong search guidance using a small set of highly discriminative

target features that remain after pruning from a larger set of features, with the load imposed on VWM varying with this feature-consolidation process.

## Introduction

We search for things hundreds of times each day. Whether it is a car in a parking lot or a cup on a shelf, each time we compare a representation of a target to information in our peripheral vision we are engaging in visual search. Search, however, can be more or less efficient, with increased efficiency believed to reflect better search guidance to a target (Wolfe, 1994). Search guidance has historically been inferred from a measure of search efficiency known as the set-size effect: the slope of the function relating target present/absent reaction time (RT) to the number of items appearing in a search display (e.g., Wolfe, 1998). Shallower set-size effects are believed to reflect fewer movements of covert attention to distractors before reaching the target, thereby yielding stronger guidance to the target and increased search efficiency. Such covert estimates of guidance, however, have been criticized as being indirect and ambiguous with respect to underlying search processes—slopes may be shallow due to fewer movements of attention to distractors or due to a faster rejection of each distractor (Zelinsky & Sheinberg,

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1997). These concerns have led to the increasing adoption of eye-movement measures of search guidance (e.g., Chen & Zelinsky, 2006; Schmidt & Zelinsky, 2011); rather than inferring guidance from search slopes and hypothesized shifts of covert attention, guidance is measured directly in terms of observable behavior. In the present study, we follow this growing trend and quantify search guidance using a variety of eye-movement measures, all of which capture, to varying degrees, how efficiently gaze is directed to a target.

Central to every theory of visual search is the assumption that guidance is mediated by a representation of the target goal (Bundesen, 1990; Wolfe, 1994; Zelinsky, 2008), with the prevailing belief that target templates are maintained in visual working memory (VWM; e.g., Woodman, Luck, & Schall, 2007; see also Olivers, Peters, Houtkamp, & Roelfsema, 2011). One way to test this assumption is to measure the VWM load imposed by the target representation and to observe how it affects later search performance. Contralateral delay activity (CDA) is an event-related potential (ERP) widely considered to be an electrophysiological index of VWM load, and it is therefore perfectly suited to this goal. When stimuli are presented to the left and right of fixation and observers are cued to remember all the objects on one side, activity at posterior electrode sites contralateral to the remembered objects tends to be more negative than activity at posterior sites ipsilateral to these objects. This difference between contralateral and ipsilateral activity increases with VWM load—as VWM load increases, so too does CDA magnitude, becoming more negative (Vogel & Machizawa, 2004). CDA also correlates with individual differences in VWM item-capacity limits, and it approaches an asymptote when item capacity has been reached (Vogel & Machizawa, 2004). This means that CDA is typically found to approach an asymptote sooner for low-capacity observers compared to high-capacity observers. However, by definition, this relationship between CDA and VWM item-capacity limits can only exist at sufficiently high VWM loads; it is only once high-capacity observers maintain more in VWM relative to low-capacity observers that CDA magnitude correlates with VWM item-capacity limits (Vogel & Machizawa, 2004).

Importantly, CDA magnitude is also modulated by the type of features currently maintained in VWM (Gao et al., 2009; Woodman & Vogel, 2008) and not by the number of spatial locations (Gao et al., 2011; Ikkai, McCollough, & Vogel, 2010). For example, remembering the orientation of a conjunction object results in larger CDA than remembering the color (Woodman & Vogel, 2008), and presenting objects sequentially at the same or different locations results in comparably sized CDA amplitudes (Ikkai et al., 2010). Although it has

been questioned whether CDA codes the number of maintained *objects* rather than the number of *features* (Luria, Sessa, Gotler, Jolicoeur, & Dell'Acqua, 2010; Luria & Vogel, 2011a), there is consensus in the literature that CDA is not a neural correlate of spatial working memory (Gao et al., 2011; Ikkai et al., 2010).<sup>1</sup> As well, CDA appears to reflect the actual information content of VWM rather than the perceptual difficulty associated with encoding that information (Ikkai et al., 2010), and CDA magnitude can be modulated, moment by moment, by the number of lateralized targets in a multiple-object tracking task (Drew, Horowitz, Wolfe, & Vogel, 2012; Drew & Vogel, 2008). This demonstration of CDA modulation in a tracking task is particularly interesting in the current context, as it suggests that CDA may index demands on both VWM and attention (e.g., Drew et al., 2012), although it is also possible that attended objects may be temporarily stored in VWM (Emrich, Al-Aidroos, Pratt, & Ferber, 2009, 2010). Taken together, these studies suggest that CDA amplitude provides a reliable estimate of VWM load and is therefore a useful tool to measure how the VWM load imposed by a target representation affects later search performance.

Given the many studies showing that CDA indexes VWM load, and the widely held belief that the features used to guide search are represented in VWM, it follows that search guidance should be modulated by target-related CDA in a search task. Several studies have measured CDA in response to the search display for the purpose of evaluating the role of VWM in the search process (e.g., Emrich et al., 2009; Luria & Vogel, 2011b), but fewer studies have related CDA elicited by the target to later search performance (Carlisle, Arita, Pardo, & Woodman, 2011), and none have related it to later search guidance.

One possible relationship between target-elicited CDA and search guidance would predict that guidance should improve as the number of features in the target representation increases, provided that these additional features accurately represent the target. This relationship, one that is consistent with most models of search, follows from the assumption that more target features will lead to a larger signal-to-noise ratio and therefore to more efficient target detection in a search context (e.g., Wolfe, 1994; Zelinsky, 2008). Indeed, Carlisle et al. (2011) have argued recently for exactly this relationship, showing that observers who had larger CDA magnitudes also had faster search RTs.

Another possible relationship implicates the role of VWM in the actual search process rather than in the creation and maintenance of the search target. Consistent with this possibility, Anderson, Vogel, and Awh (2013a) found that high-capacity observers had shallower search slopes compared to low-capacity observers, a finding they attributed to high-capacity

observers' being able to load a greater number of search objects into VWM for comparison to the target. Extrapolating from this relationship, it follows that search may be optimized to use low-load target representations in an effort to minimize the demands placed on a limited-capacity VWM; devoting less VWM to the target template would leave more available to efficiently search through the display items. This hypothesis predicts the opposite relationship between target-related CDA and search guidance—guidance should be best with a low-load target representation, as this would enable a greater number of search items to be processed in parallel (Anderson et al., 2013a; Emrich et al., 2009; Luria & Vogel, 2011b).

## Experiment 1

To investigate the relationship between the VWM representation of a search target and search guidance, we measured CDA during a retention interval after target designation but before search-display onset and related this to measures of gaze direction to a target. We also analyzed the temporal expression of CDA throughout this time window to examine changes in the target representation over time (Schmidt & Zelinsky, 2011). If having more target features in VWM leads to better guidance, CDA magnitude measured during the retention interval should be greater when search is later found to be strongly guided to a target compared to when guidance is weak. However, if VWM is optimized to process search items rather than to maintain a high-load target representation, the opposite relationship might be expected: Increased target-related CDA magnitude might predict weaker, not stronger, search guidance.

## Methods

### Participants

Sixteen undergraduate students from Stony Brook University participated for course credit. All had normal or corrected-to-normal vision, and were native English speakers, by self-report.

### Stimuli, apparatus, and data recording

Each observer participated in two behavioral tasks: a VWM pretest, followed by the main search experiment. We administered the VWM pretest to independently assess VWM item-capacity limits and to screen for an observer's ability to remain fixated during the preview and delay periods. This test used a memory array and a test array. Memory arrays consisted of 6 or 10 (out of a

possible 11) colored  $0.5^\circ \times 0.5^\circ$  squares. No color was presented more than once on a given trial. The squares were lateralized such that three or five squares appeared on each side, all  $3.5^\circ$  from central fixation. Test arrays either were identical or had one colored square swapped with an unused color.

The search task used a four-item target-preview display and a four-item search display (Figure 1). Target-preview displays consisted of four random-category real-world objects, each subtending  $1.35^\circ$  and appearing  $3.5^\circ$  from central fixation. Search displays were presented on a white background and consisted of three distractors and one of the previewed targets. All objects were obtained from the Hemera Photo Objects collection or various Web sources. Search objects were arranged into a square, with one object appearing in each quadrant at  $14.5^\circ$  from central fixation. Each search object also subtended  $1.35^\circ$  (the same size as the target preview), and target positions were balanced over screen locations. Targets and distractors repeated once in new pseudorandom pairings halfway through the experiment. Except for this single repetition, each trial depicted a target at a different basic level category; distractors were selected randomly, with the constraint that no distractor overlapped with any of the target categories.<sup>2</sup>

Stimuli were presented at a screen resolution of  $1680 \times 1050$  pixels using a 22-in. LCD ViewSonic VX2268wm monitor operating at a refresh rate of 120 Hz. The experiment was created and controlled using the Experiment Builder software package (SR Research Ltd., version 1.10.165), running on an Intel Core 2 Duo 3.0-GHz PC with Windows XP. Eye position was sampled at 1000 Hz using an EyeLink 1000 eye tracker with default saccade detection settings. The head position and viewing distance for each observer was fixed at 81 cm using a chin rest. All manual responses were made using a game-pad controller (Microsoft Sidewinder 1.0) by pressing the left and right index-finger shoulder triggers; trials were initiated by pressing the X button operated by the right thumb.

Continuous electroencephalogram (EEG) data were recorded from 64 scalp electrode sites (standard 10-20 configuration) using a BioSemi Active Two system. Two additional electrodes were placed on the left and right mastoids, and the electrooculogram (EOG) generated from eyeblinks and eye movements was recorded from four facial electrodes.<sup>3</sup> Vertical eye movements and blinks were measured using two electrodes, placed 1 cm above and below the right eye; horizontal eye movements were measured using two electrodes, placed 1 cm beyond the outer edge of each eye. The EEG signal was preamplified at the electrode to improve the signal-to-noise ratio. Data were digitized at 24-bit resolution with a least-significant-bit value of 31.25 nV and a sampling rate of 512 Hz, then

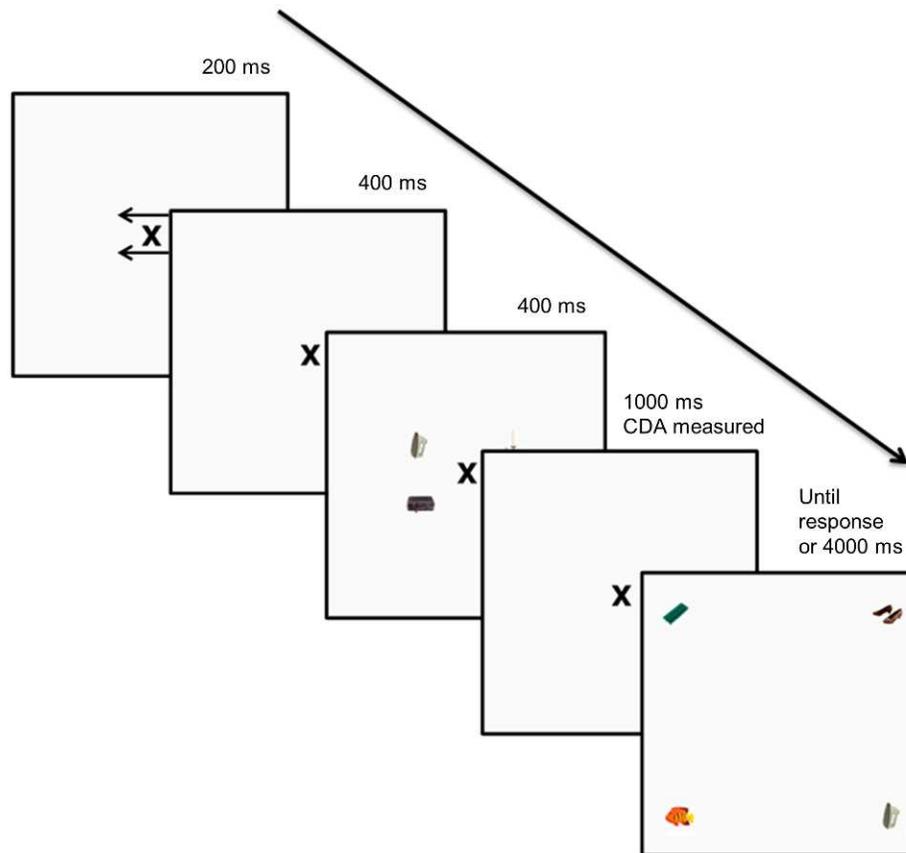


Figure 1. Procedure used for the visual-search task. The arrows cued two potential targets in the preview display, one of which (the iron in this example) always appeared in the search display. See text for additional details.

filtered using a low-pass fifth-order sinc filter with a  $-3$ -dB cutoff point at 104 Hz. The voltage from each active electrode was referenced online with respect to a common-mode-sense active electrode producing a monopolar (nondifferential) channel.

To align the eye-movement and EEG recordings, Experiment Builder was programmed to send an event code at the start of each trial over the parallel port to a computer dedicated to collecting the EEG data. Event markers were saved in the continuous EEG stream and coded for the onset of each visual display, whether the initial saccade during search was directed to the target or a distractor, and for whether the manual response for a trial was correct or incorrect.

### Data analysis

Off-line analyses of the eye-movement data were performed using the DataViewer software package (SR Research Ltd., version 1.11.1) and standard analysis tools. Off-line analyses of the EEG data were performed using Brain Vision Analyzer (Brain Products, Gilching, Germany, version 2.0). EEG data were re-referenced off-line to the average of the two mastoids and band-pass filtered with low and high

cutoffs of 0.01 and 70 Hz, respectively. The EEG was segmented for each trial, beginning 200 ms prior to target-preview onset and continuing for 1500 ms, ending with the onset of the search display. Baseline correction was performed for each trial using the 200 ms prior to preview onset. Artifact analysis identified cases in which there was a voltage step of more than  $75.0 \mu\text{V}$  between samples, a voltage difference of  $150.0 \mu\text{V}$  within a trial, a maximum voltage difference of less than  $0.50 \mu\text{V}$  within 50-ms intervals, and an absolute voltage that exceeded  $\pm 150 \mu\text{V}$ . All segments containing artifacts were discarded. To detect any remaining eye-movement artifacts, a bipolar horizontal electro-oculogram (HEOG) was computed post hoc by subtracting the left EOG channel from the right EOG channel. Average HEOG activity was analyzed separately for the cue and delay windows. Observers generally had less than  $\pm 4 \mu\text{V}$  of HEOG activity in both the “cue left” and “cue right” conditions during both the cue and delay windows. One observer was replaced due to excessive HEOG activity, and another two observers had average HEOG activity of 4.5 and  $5.7 \mu\text{V}$  in a single cue-condition time window. All other observers were below the noted cutoff. We also assessed pre-search eye-movement activity by analyzing the data

from the eye tracker. Eye movements during the preview and retention interval did not differ in number or mean saccade amplitude between the strong- and weak-guidance conditions, all  $t(15) \leq 0.74$ , all  $p \geq 0.35$ .

CDA, quantified as the amplitude difference in electrode sites contralateral and ipsilateral to the cued objects (contralateral minus ipsilateral), was computed at all lateralized parietal and occipital electrode pairs (P1/2, P3/4, P5/6, P7/8, P9/10, PO3/4, PO7/8, O1/2) from 400 to 1300 ms following preview onset. This window corresponded to the first 900 ms of the retention interval separating preview offset from search-display onset.<sup>4</sup>

### Design and procedure

Both the VWM and search tasks began with a 13-point calibration routine used to map eye position to screen coordinates. A calibration was not accepted until the average error was less than  $0.49^\circ$  and the maximum error was less than  $0.99^\circ$ . Observers were recalibrated halfway through each task and as needed during testing. Following the initial calibration were practice trials, 32 in the VWM task and 8 in the search task. Trials began with observers fixating a central point and pressing the X button on the game pad. In addition to initiating the trial, this served as a “drift check” for the eye tracker to record any shift in gaze position since calibration. The fixation point was then replaced by a centrally presented  $\times$  and two arrows, above and below central fixation (Figure 1), both pointing to either the left or right side of the screen. The arrow cue was presented for 200 ms and was followed by a 400-ms delay showing just the fixation cross until the onset of the first task display.

### VWM task

A standard delayed match-to-sample task (Vogel & Machizawa, 2004) was used to calculate the  $k$ -scores used to estimate VWM capacity. Following the arrow cue and the subsequent 400-ms delay, three or five colored squares appeared for 100 ms on each side of central fixation. This was followed after a 1000-ms delay by the presentation of either the identical display or a display in which a change was made to one colored square on the cued side. Observers had 2500 ms to make a same-or-different judgment. A trial was immediately terminated if the observer blinked, if a saccade greater than  $0.75^\circ$  was detected, or if the eye position deviated by more than  $1.25^\circ$  from central fixation, as determined by the eye tracker, before the test array appeared. If any of these events was detected, feedback was given to the observer instructing him or her not to blink or make an eye movement during that time window. Observers were excused from the

experiment if they failed to remain centrally fixated during the cue, memory, or delay windows on at least 80% of the trials. Additionally, feedback was given if observers made an incorrect response or if no response was made within the 2500-ms response window. A variable intertrial interval (ITI) of 100–500 ms followed the feedback or response. There were two test blocks, each containing 60 trials, for a total of 120 test trials. Cue direction and set size were interleaved within block.

### Search task

Figure 1 shows the procedure for the search task, which was identical to the VWM procedure with the following exceptions. Rather than colored squares, the target-preview display depicted two images of real-world objects on each side of central fixation, with the preceding arrow cue indicating which pair of objects were potential targets. This cuing procedure was needed, given that objects had to appear in both visual hemifields; a balanced bilateral display helps to control for hemispheric differences in the EEG signal related to perception. Observers were instructed to encode both of the cued objects because either could be the target. The duration of the target-preview display was also changed to 400 ms, increased from the 100-ms duration of the memory array used in the VWM task. This was done to enable a more complete encoding of the visually complex targets. After a 1000-ms retention interval, a search display appeared, which showed one of the two potential targets with three distractors. Observers had to localize the target, indicated by pressing a button while fixating the object. The search display remained visible until the response or until 4000 ms had elapsed. If a response was not made within this time window, or if observers were looking at a nontarget object when they pressed the button, the trial was flagged as an error and feedback was provided. A variable ITI of 1500–2000 ms followed the feedback or response. There were 416 test trials distributed over eight blocks. Cue direction was interleaved, and guidance condition was determined online based on performance.

### Results

The first step in relating the target representation in VWM to search guidance is to define strong- and weak-guidance conditions. We operationally defined strong-guidance trials as those in which the initial saccade during search was directed at the target, and weak-guidance trials as those in which the initial saccade of the search task was directed at a distractor. Such dichotomizing of data based on behavioral perfor-

	% initial saccade directed to target	Initial saccade latency, ms	Time-to-target, ms	Target dwell time, ms	RT, ms	% correct
Overall	54 (2)	230 (9)	525 (15)	461 (39)	1078 (53)	94 (1)
Strong guidance	100 (0)	233 (9)	366 (13)	445 (38)	894 (49)	97 (0)
Weak guidance	0 (0)	225 (9)	693 (19)	481 (39)	1274 (59)	90 (2)

Table 1. Oculomotor and manual search measures in Experiment 1. *Notes:* Values in parentheses indicate standard error of the mean. RT = reaction time.

mance is a well-established practice in the ERP memory literature; ERPs corresponding to the encoding of later remembered words or objects are often compared to the ERPs corresponding to the encoding of later forgotten words or objects, the so-called difference due to memory or DM effect (e.g., Friedman & Sutton, 1987; Sanquist, Rohrbaugh, Syndulko, & Lindsley, 1980). Our breakdown of CDA by strong and weak guidance is conceptually identical to this accepted practice. The overall guidance data, strong-guidance data, weak-guidance data, manual search times, and data from other oculomotor measures are reported in Table 1. Incorrect trials, no-response trials, and trials aborted due to a blink or an eye movement were excluded from all analyses. Out of the remaining test trials, on average, 54% were strong guidance and 46% were weak guidance (Table 1).<sup>5</sup> Strong-guidance trials were accompanied by significantly longer initial saccade latencies, shorter times to fixate the target (time-to-target), shorter target dwell times, shorter manual RTs, and more accurate responses compared to weak-guidance trials, all  $t(15) \geq 2.50$ , all  $p \leq 0.03$ . The fact that differences between strong and weak guidance were found in so many manual and oculomotor measures, and that these differences were quite large in some cases, suggests that the direction of the initial saccade profoundly impacted search performance in this task.

To investigate the target representation maintained in VWM, we computed mean CDA difference waves during the retention interval after preview offset but before search-display onset. Figure 2 shows head maps indicating overall CDA, as well as CDA grouped by strong and weak guidance. Consistent with prior work, CDA was maximal over occipital and parietal electrode sites (e.g., Vogel & Machizawa, 2004). CDA magnitude was largest at PO7/8, all  $t(15) \geq 2.8$ , all  $p \leq 0.01$ ; however, in the overall data the difference wave was significantly more negative than zero at all occipital and parietal sites, all  $t(15) \geq 2.4$ , all  $p \leq 0.03$ , except at P1/2 and P3/4. The presence of target-elicited CDA suggests that target features were maintained in VWM for the purpose of search and is consistent with earlier reports of CDA in a search task (Carlisle et al., 2011). Significant CDA was also found for weak-guidance trials at all occipital and parietal sites (except P1/2 and P3/4),  $t(15) \geq 2.13$ , all  $p \leq 0.05$ , and for strong-

guidance trials at all occipital and parietal sites (except P1/2 and P9/10), all  $t(15) \geq 2.35$ , all  $p \leq 0.04$ . These latter two analyses suggest that target features were likewise maintained on both strong- and weak-guidance trials.

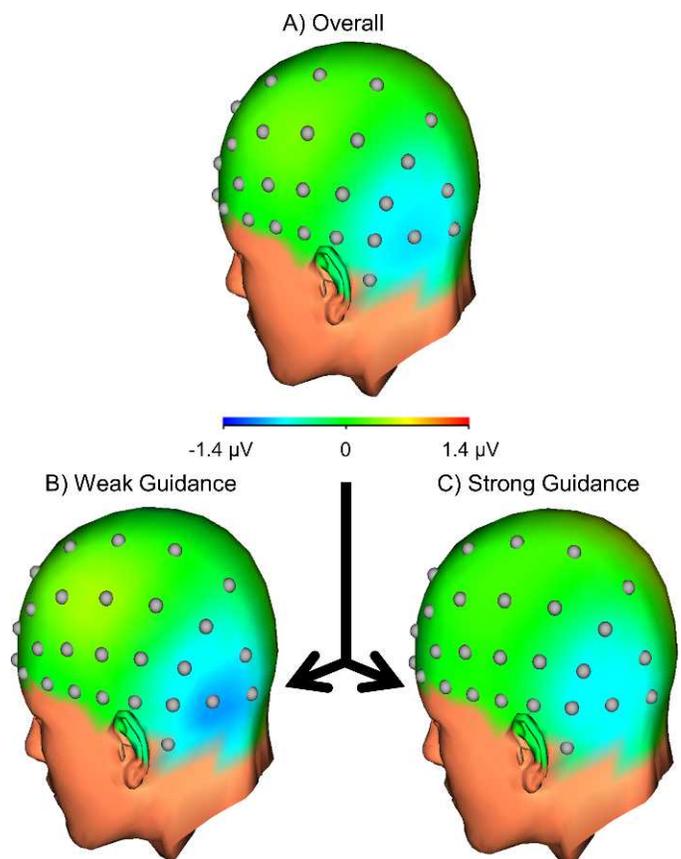


Figure 2. Head maps for Experiment 1 showing the topographic distribution of voltage differences for electrodes contralateral minus ipsilateral relative to the target position in the preview display. CDA was measured for 900 ms during the retention interval after preview offset but before search-display onset; deeper blue indicates a more negative value and greater CDA magnitude. (A) Overall activity from all trials, not segregated by strong versus weak guidance. (B) Activity from only the weak-guidance trials, in which the initial search saccade was directed at a distractor rather than the target. (C) Activity from only strong-guidance trials, in which the initial search saccade was directed at the target.

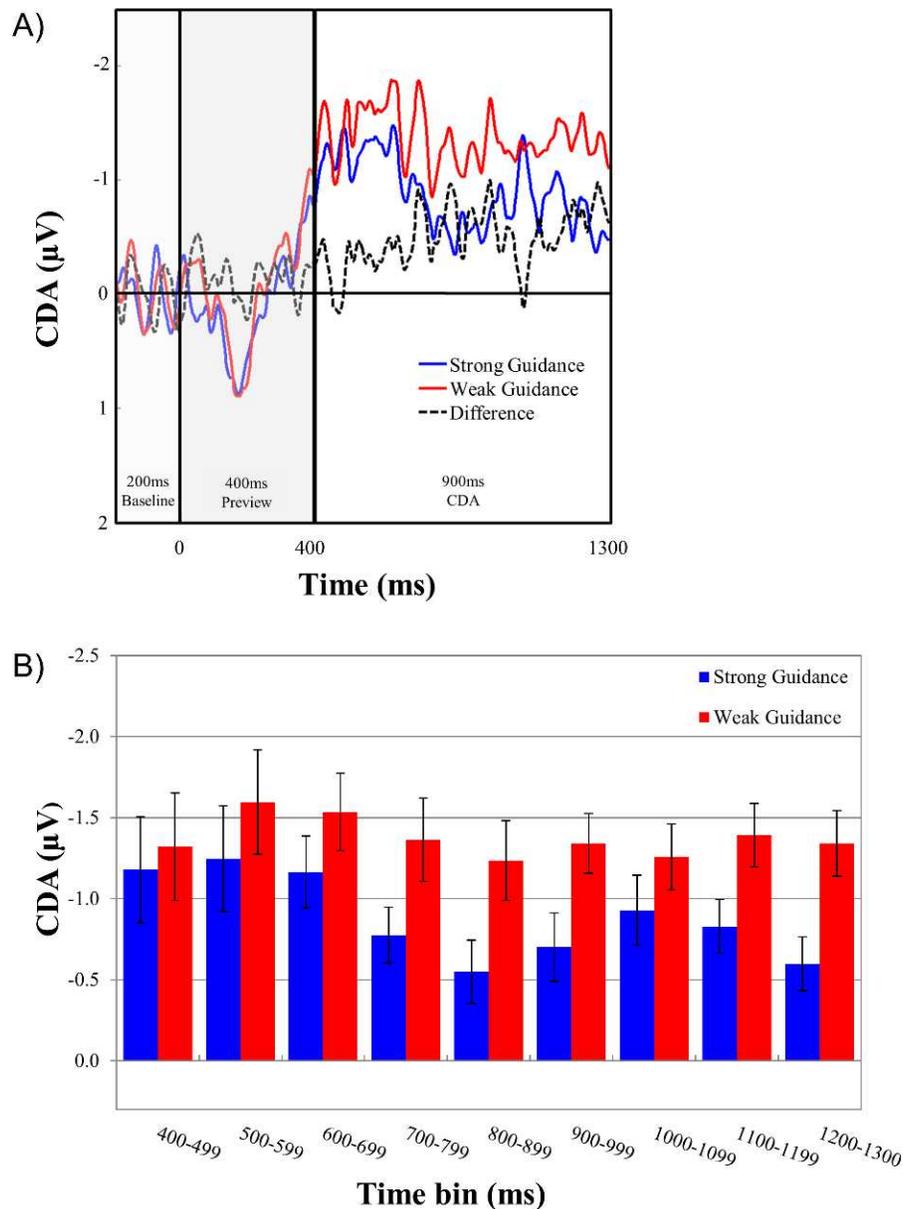


Figure 3. CDA activity over time for Experiment 1. (A) Waveforms showing CDA from PO7/8 in the strong-guidance (blue) and weak-guidance (red) conditions, as well as the wave produced by taking the difference of the two (dotted black). (B) Mean CDA binned into 100-ms intervals from PO7/8 in the strong- (blue) and weak-guidance (red) conditions. Error bars indicate one standard error of the mean. Note that negative values are plotted up in both figures.

To examine the relationship between the target representation in VWM and later search guidance, and to characterize how this relationship changes over time, we partitioned CDA into nine 100-ms time bins, with a mean CDA value computed for each bin, and compared CDA magnitude on strong-guidance and weak-guidance trials (Figure 3A, B). Confining this analysis to PO7/8, where the CDA difference wave was maximal, we found a main effect of guidance. Weak-guidance trials produced significantly greater CDA than strong-guidance trials,  $F(1, 15) = 6.38, p = 0.02$ ;

target-related CDA was significantly more negative when the initial eye movement during search was *not* directed to the target. Contrary to the predictions of most models of search and the findings of Carlisle et al. (2011), this finding suggests that a larger CDA magnitude, indicative of additional target features maintained in VWM, results in a weaker guidance signal and poorer search performance. This latter conclusion is supported by the fact that weaker search guidance also led to longer time-to-target, longer target dwell times, longer RTs, and less accurate manual

responses (Table 1). We also found that the difference between strong- and weak-guidance conditions was larger (except for the 1000–1099-ms time bin) in the later time bins compared to the earlier time bins (Figure 3B). This was confirmed by a significant interaction of guidance (strong versus weak)  $\times$  time,  $F(8, 120) = 2.06$ ,  $p = 0.05$ , that was driven by a reduction in strong-guidance CDA over time and relatively stable weak-guidance CDA. Supporting this relationship between time and the load imposed by the target representation, we found pronounced correlations between strong- and weak-guidance CDA in the first four time bins following preview offset,  $r(16) \geq 0.62$ , all  $p \leq 0.05$ ; however, this relationship weakened over time such that the remaining time bins did not show significant correlations,  $r(16) \leq 0.33$ , all  $p \geq 0.20$ . Taken together, this shows that target representations formed early after preview offset produced CDA for both weak-guidance and strong-guidance trials, but that CDA later during the retention interval faded when guidance was strong but remained when guidance was weak. We interpret these findings as indicating a search process that can reduce the load imposed by a target representation over time, with strong or weak search guidance predicted by the efficiency of this process. The fact that strong and weak guidance became less correlated in the later time bins also suggests that observers differed in their ability to reduce this target-related VWM load on strong-guidance trials.

Does this relationship between weak guidance and greater CDA magnitude also explain differences in performance across individual observers? To answer this question, for each observer we subtracted mean CDA on strong-guidance trials from mean CDA on weak-guidance trials, giving us a CDA difference score with respect to search guidance. We computed a similar guidance-based difference score for time-to-target and RT, again by subtracting strong-guidance mean time-to-target and RT from weak-guidance mean time-to-target and RT, respectively. We then correlated across observers the CDA difference scores with the difference scores for both time-to-target and RT. These analyses revealed significant correlations between CDA and both time-to-target and RT, both  $r(16) \leq -0.52$ , both  $p \leq 0.04$  (Figure 4). Those observers who showed the largest increase in CDA on weak-guidance trials, suggesting they coded the most additional target features, also showed the largest decrement in search performance (as measured by time-to-target and RT) after their misdirected initial saccade. Given that the time-to-target and RT measures capture search performance throughout the task, these findings suggest that the impact of the target representation on search is not limited to the accurate direction of the initial saccade to the target.

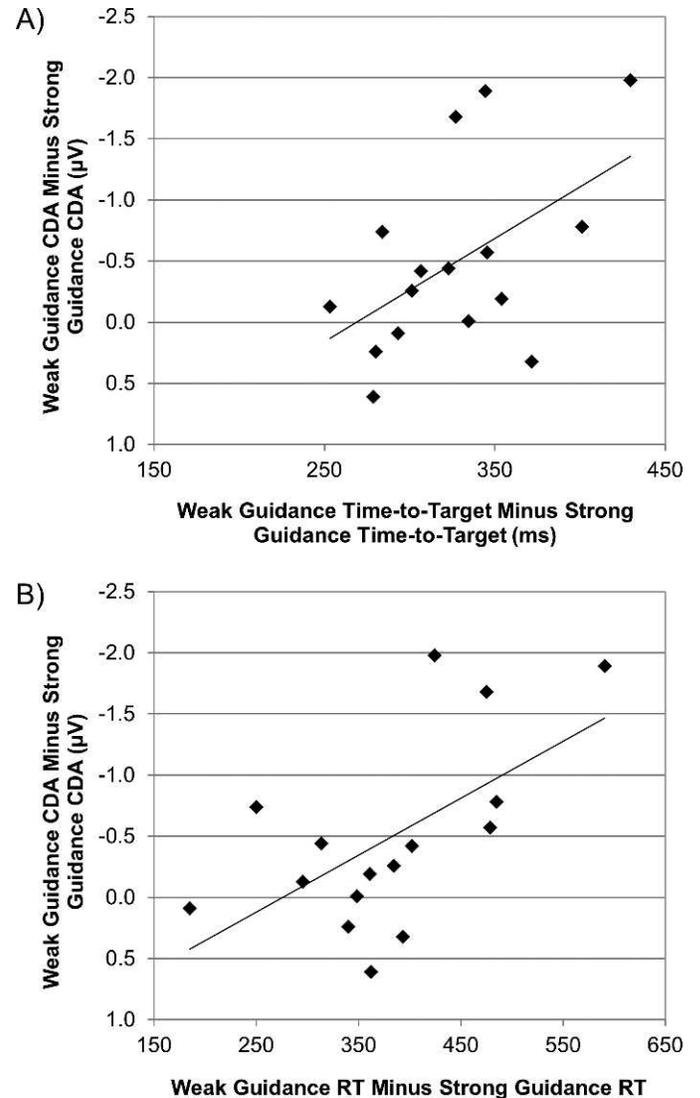


Figure 4. Scatterplots for Experiment 1 depicting the relationship between strong- minus weak-guidance CDA magnitude to (A) strong- minus weak-guidance time-to-target and (B) strong- minus weak-guidance RT. Each black dot indicates data from one observer; a best-fit line shows the relationship across observers. Note that the positive slope of this line indicates a negative correlation, because negative values are plotted up. See the text for additional details.

Does the relationship between CDA magnitude and guidance change with VWM item-capacity limits? Previous work has demonstrated that CDA correlates with VWM item capacity, showing that it approaches an asymptote when capacity has been reached (Vogel & Machizawa, 2004). More specifically, the difference between contralateral and ipsilateral electrode sites approaches an asymptote sooner for low-capacity observers than it does for high-capacity observers, suggesting that there exists some number of features that fill VWM for low-capacity observers, leading to

	% initial saccade directed to target	Initial saccade latency	Time-to-target	Target dwell time	RT	% correct
VWM item capacity ( <i>k</i> -scores)	$r = 0.22,$ $p = 0.44$	$r = 0.43,$ $p = 0.10$	$r = 0.30,$ $p = 0.27$	$r = 0.23,$ $p = 0.40$	$r = 0.30,$ $p = 0.27$	$r = 0.77,$ $p < 0.001$

Table 2. Correlations of VWM item capacity with oculomotor and manual measures of search performance in Experiment 1. Notes: RT = reaction time.

asymptotic CDA, while allowing high-capacity observers to still add features to their VWM, leading to increasing CDA magnitude. If the negative relationship between CDA and guidance reported in the present study is due to the absolute number of features in the target representation, rather than the number of features that can be maintained relative to an observer's capacity limit, we might expect an interaction between observer capacity and strong- versus weak-guidance CDA—the difference between strong- and weak-guidance CDA should be larger for high-capacity observers, as these observers would be maintaining more features. We found that overall CDA correlated significantly with the *k*-scores computed from the observers' VWM capacity pretest,  $r(16) = -0.72$ ,  $p < 0.001$ , replicating Vogel and Machizawa's (2004) results. This suggests that high-capacity observers indeed maintained more target features in VWM. However, a regression analysis revealed that VWM capacity and CDA in the strong- and weak-guidance conditions did not interact,  $t = 1.22$ ,  $p = 0.24$ . This suggests that the relationship between strong- and weak-guidance CDA was not affected by item-capacity limits, despite the fact that high-capacity observers had substantially larger overall CDA. We interpret this finding as evidence that search guidance is modulated not by the absolute number of maintained features but rather by the relative number of features specific to a given observer's capacity and the quality of information that is coded by these features.

Although strong- and weak-guidance CDA did not interact with estimates of VWM item capacity, capacity effects might still be expressed in other measures of search performance. Contrary to the suggestion that high-capacity observers have shallower search slopes (Anderson et al., 2013a), we observed no significant relationships between VWM item-capacity estimates and any of the oculomotor or RT measures reported in Table 2, all  $r(16) \leq 0.43$ , all  $p \geq 0.10$ , although manual responses were more accurate for the high-capacity observers,  $r(16) = 0.77$ ,  $p < 0.001$ . Despite high-capacity observers' maintaining more target features in VWM, differences in VWM item-capacity limits were not expressed in the behavioral measures considered in this study, just as they were found not to interact with the difference between strong- and weak-guidance CDA. We again interpret these findings as suggesting that search performance is modulated not by the

absolute number of target features but rather by how efficiently these features code the information needed to discriminate a target from distractors.

## Discussion

We used CDA to assess the representation of a search target when guidance would later be either strong or weak, and found that strong search guidance was associated with lower CDA magnitude. This suggests that search performance benefits from having fewer, not more, features in the target representation. But before we consider the implications of this finding for search theory, the counterintuitive nature of this relationship requires that alternative interpretations be thoroughly considered.

One potential explanation for our results is that some target objects were less complex than others and that these less complex targets resulted in both a lower VWM load and stronger search guidance. As in the case of the ERP memory literature (e.g., Friedman & Sutton, 1987; Sanquist et al., 1980), the performance-based segregation of trials into strong- and weak-guidance groups in the present study necessarily meant that different targets would constitute the two guidance conditions. If some target objects were simply easier to maintain and search for than others, then easy search targets might lead to a lower VWM load and stronger search guidance, while more difficult targets might lead to a higher VWM load and weaker search guidance. This explanation, however, would predict that many of our targets should be consistently associated with either strong or weak guidance. To test this hypothesis, we analyzed the number of observers showing strong search guidance by target item, and found that guidance was normally distributed over targets (Shapiro–Wilk,  $p = 0.08$ ; Kolmogorov–Smirnov,  $p = 0.20$ ; skewness = 0.85, kurtosis = -0.79).<sup>6</sup> This suggests that the vast majority of target items did not consistently produce either strong or weak guidance, making a purely stimulus-based explanation of our findings highly unlikely. Future work may seek to use a smaller set of target objects so that CDA magnitude on strong- and weak-guidance trials can be compared using an identical set of stimuli.

Another possible explanation for our results is that search guidance may be related to the number of

targets maintained in VWM. Our assumption was that observers were following instructions and attempting to encode both of the objects on the cued side of the display into their VWM, but this may not have been the case. On some trials, observers may have gambled by picking only one of the two cued targets to maintain in VWM, thereby retaining very little about the second object. To the extent this happened, it might result in strong search guidance when the selected object was the target and weak search guidance when it was not. In both cases, low CDA magnitude would be expected, because only one object would be maintained in VWM. It also follows that on trials in which observers maintained both objects in VWM, search guidance should be weaker and CDA magnitude should be relatively high. Thus, trials with strong guidance and low CDA may be associated with the maintenance of only one object, and trials with weak guidance and high CDA may be associated with the maintenance of both objects. Note that this explanation would also predict weak guidance and low CDA on those trials in which the wrong object was selected and maintained, a pattern that is inconsistent with our data, given that it predicts little change in CDA amplitude when correct target selections are also considered; but it is possible that these trials contributed disproportionately to errors and were therefore not included in the analyses. Moreover, although this alternative interpretation cannot explain the observed interaction of strong- and weak-guidance CDA over time or the correlation between strong and weak guidance in early but not late time bins, it might nevertheless explain our core finding—that search guidance is inversely related to CDA magnitude. We therefore conducted a second experiment, in which only a single target appeared on the cued side, to rule out this interpretation.

## Experiment 2

### Methods

#### Participants

Eighteen undergraduate students from Stony Brook University participated for course credit. All had normal or corrected-to-normal vision, and were native English speakers, by self-report. None had participated in Experiment 1.

#### Design and procedure

All stimuli, apparatus, data recording, analyses, and procedures were identical to those in Experiment 1, except the target-preview display now depicted one object on each side of central fixation rather than two.

The CDA analysis window was also extended by 100 ms to include the full 1000-ms retention interval. Given that only one object now appeared at preview (with the task being to fixate the target and press a button, as in Experiment 1), any uncertainty about the number of objects maintained in VWM is removed.

### Results

Given the reduction in the number of targets in Experiment 2 relative to Experiment 1, we expected that this lower load would result in behavioral and electrophysiological differences between the experiments. This is precisely what we found. Searching for one target compared to two resulted in a greater proportion of initial saccades directed at the target, shorter overall mean RT, shorter time-to-target, and increased detection accuracy, all  $t(32) \geq 3.12$ , all  $p \leq 0.004$ , despite the use of identical search displays between the experiments. We also found that CDA magnitude was numerically smaller in Experiment 2 ( $-0.75 \mu\text{V}$ ) compared to Experiment 1 ( $-1.13 \mu\text{V}$ ), although this trend was not statistically significant,  $t(32) = 1.54$ ,  $p = 0.13$ . Had the load manipulation been the focus of this study, we would have made it a within-subjects factor (as is typical with load manipulations), and this likely would have resulted in significant differences in overall CDA as well. Taken together, the totality of our data suggests that observers were representing the target information differently between the two experiments.

More central to the aim of the experiment was how the removal of a potential target gambling strategy might affect search guidance. As in Experiment 1, trials were segregated into strong-guidance (69%) and weak-guidance (31%) conditions based on the direction of the initial search saccade in relation to the target. The overall guidance data, strong- and weak-guidance data, manual search times, and data from other oculomotor measures are reported in Table 3. Perfectly replicating the results of Experiment 1, strong-guidance trials showed significantly longer initial saccade latencies, shorter time-to-target, shorter target dwell times, shorter overall RTs, and more accurate responses compared to weak-guidance trials, all  $t(17) \geq 3.00$ , all  $p \leq 0.01$ . This reinforces the use of initial saccade direction as a measure of search guidance and further validates the grouping of data into strong- and weak-guidance conditions.

To test whether higher target-related VWM load results in weaker search guidance, we compared strong-guidance and weak-guidance CDA over time. It is important to note that a single target will generally result in faster and more accurate search, a lower VWM load, and a reduced range of possible CDA

	% initial saccade directed to target	Initial saccade latency, ms	Time-to-target, ms	Target dwell time, ms	RT, ms	% correct
Overall	69 (2)	229 (7)	421 (8)	380 (39)	856 (47)	98 (0)
Strong guidance	100 (0)	233 (7)	342 (9)	372 (39)	769 (45)	99 (0)
Weak guidance	0 (0)	221 (7)	580 (13)	399 (37)	1035 (45)	96 (1)

Table 3. Oculomotor and manual search measures in Experiment 2. Notes: Values in parentheses indicate standard error of the mean. RT = reaction time.

values, thus reducing the effect size and strength of any correlations (see also Carlisle et al., 2011). The main effect of strong- versus weak-guidance CDA was in the same direction as in Experiment 1 but failed to attain significance,  $F(1, 17) = 2.56$ ,  $p = 0.13$  (see Figure 5). However, as was also true for Experiment 1, strong- and weak-guidance CDA interacted over time (Figure 6A, B),  $F(9, 153) = 2.06$ ,  $p = 0.036$ , diverging only in later time bins and explaining the lack of the overall main effect. Consistent with an interaction over time, a strong correlation between strong- and weak-guidance CDA across observers was found for the first time bin after preview offset (400–499 ms),  $r(18) = 0.56$ ,  $p = 0.02$ , but not for any of the later time bins (all remaining time bins),  $r(18) \leq 0.24$ , all  $p \geq 0.34$ . This again suggests that immediately after preview offset, observers having larger CDA on weak-guidance trials also had larger CDA on strong-guidance trials, but that this relationship quickly faded with longer delays. We again interpret this pattern as evidence for CDA shortly before search-display onset reflecting a process designed to optimize the VWM representation of the target to guide search. This generally confirms the results of Experiment 1 and suggests that the reported inverse relationship between search guidance and CDA magnitude was not the result of observers' selectively maintaining a single target object on strong-guidance trials.

Next we sought to confirm that differences in individual observer search performance could be predicted by differences in CDA magnitude. We again computed mean CDA difference scores by subtracting each observer's mean CDA on strong-guidance trials from mean CDA on weak-guidance trials.<sup>7</sup> We also again computed guidance-based difference scores for time-to-target and RT. These correlations between CDA and search-performance guidance differences were in the same direction as those reported for Experiment 1 and approached significance for both time-to-target,  $r(18) = -0.45$ ,  $p = 0.06$ , and RT,  $r(18) = -0.43$ ,  $p = 0.07$  (Figure 7A, B), suggesting that, on weak-guidance trials, those observers who showed the largest increase in CDA also showed the largest decrement in search performance.<sup>8</sup> This generally replicates the results of Experiment 1 and supports the

suggestion that increased target-related CDA results in poorer search.

Given that one target object should generally result in a VWM load below most observers' item-capacity limits, perhaps we would find in this experiment the relationship between strong- and weak-guidance CDA magnitude and VWM item capacity that we failed to find in Experiment 1. To confirm that most observers were indeed below their item-capacity limits, we again correlated VWM item-capacity estimates obtained during a VWM capacity pretest with mean CDA

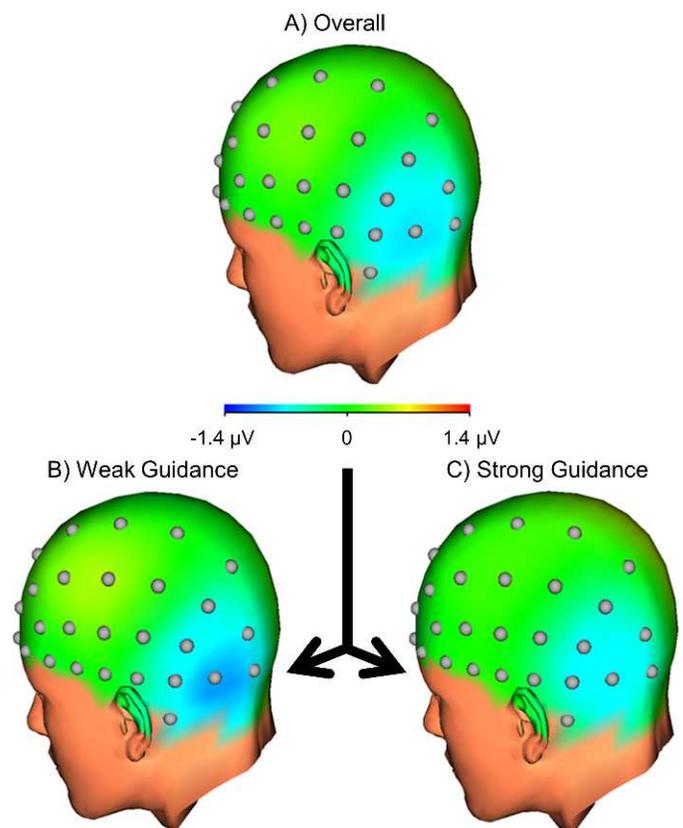


Figure 5. Head maps for Experiment 2 showing CDA measured for 1000 ms during the retention interval after preview offset but before search-display onset; deeper blue indicates a more negative value and greater CDA magnitude. (A) Overall activity from all trials, not segregated by strong versus weak guidance. (B) Activity from only the weak-guidance trials. (C) Activity from only strong-guidance trials.

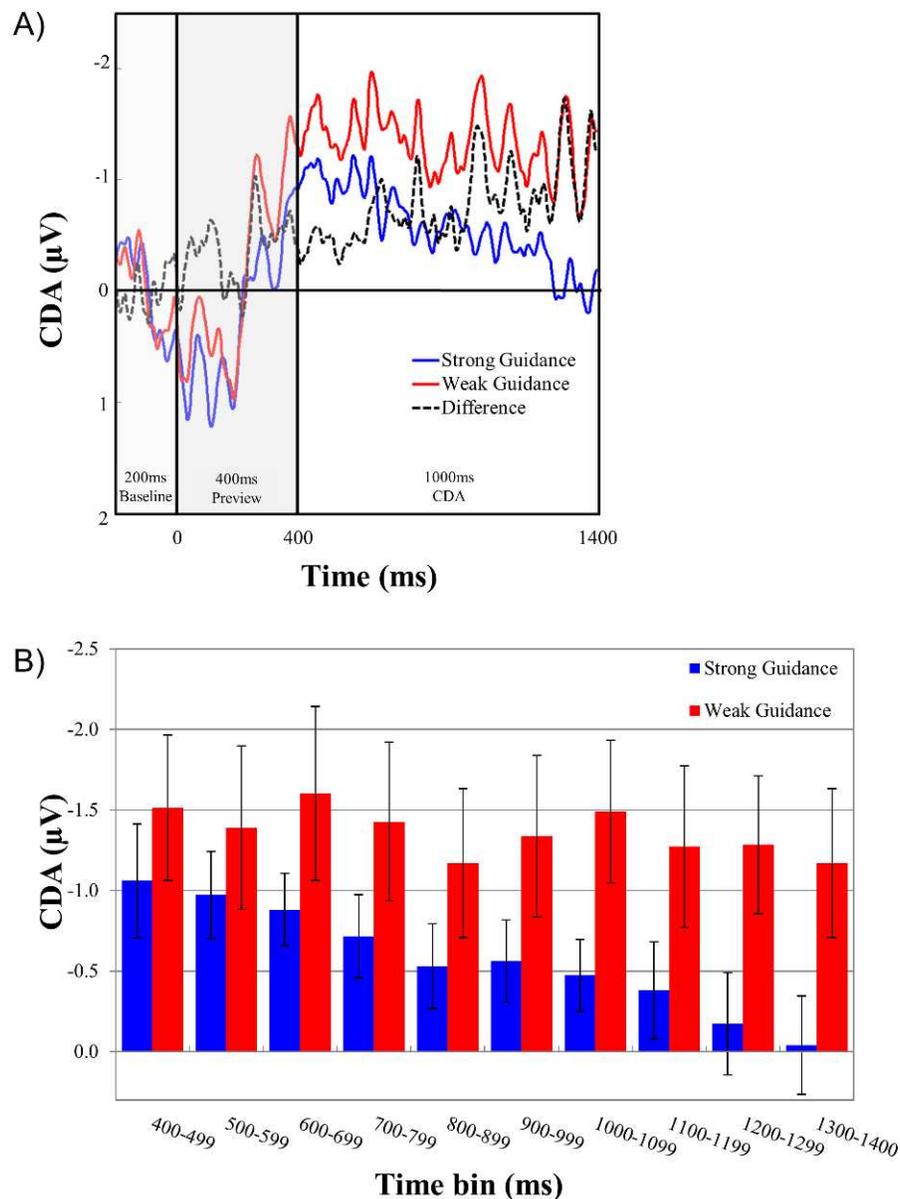


Figure 6. CDA activity over time for Experiment 2. (A) Waveforms showing CDA from PO7/8 in the strong-guidance (blue) and weak-guidance (red) conditions, as well as the wave produced by taking the difference of the two (dotted black). (B), Mean CDA binned into 100-ms intervals from PO7/8 in the strong- (blue) and weak-guidance (red) conditions. Error bars indicate one standard error of the mean. Note that negative values are plotted up in both figures.

amplitude and found no significant relationship,  $r(18) = -0.23$ ,  $p = 0.36$ , suggesting that high-capacity observers were not maintaining more target features in VWM relative to low-capacity observers. We then conducted a regression analysis and found that VWM item capacity and strong- and weak-guidance CDA again failed to interact,  $t = 1.64$ ,  $p = 0.12$ , replicating our finding from Experiment 1. This confirms that the relationship between strong- and weak-guidance CDA was not modulated by VWM item-capacity limits, despite high-capacity observers' not filling VWM to capacity.

Although VWM item capacity failed to interact with strong- and weak-guidance CDA, item capacity might still be expressed in measures of search performance. Specifically, high- and low-capacity observers may be equally likely to exhibit weak search guidance when the target VWM load is high, but there may be fewer trials in which the target fills VWM for high-capacity observers, thus resulting in overall stronger search guidance on average (see also Anderson et al., 2013a). Supporting this suggestion, and contrary to Experiment 1, we found that as capacity increased, so too did the proportion of initial saccades directed at the target,

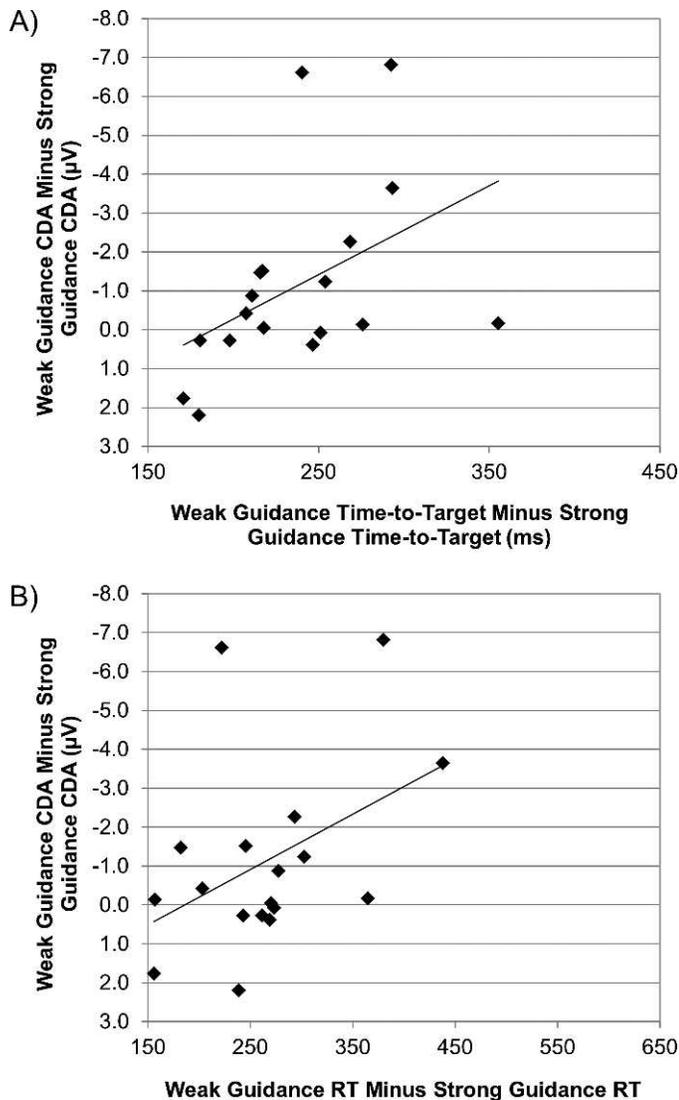


Figure 7. Scatterplots for Experiment 2 depicting the relationship between strong- minus weak-guidance CDA magnitude to (A) strong- minus weak-guidance time-to-target and (B) strong- minus weak-guidance RT. Each black dot indicates data from one observer; a best-fit line shows the relationship across observers. Note that the positive slope of this line indicates a negative correlation, because negative values are plotted up. See the text for additional details.

$r(18) = 0.57, p = 0.02$ . To the extent that high-capacity observers in the study by Anderson et al. (2013a) also exhibited stronger search guidance, this may explain the effect of capacity on search slopes reported in that study. When combined with the results of Experiment 1, this extends the results of Anderson et al. (2013a), suggesting that high-capacity individuals only experience a search benefit when the target VWM load is sufficiently low. However, consistent with the results of Anderson et al. (2013a), in which capacity effects were related to search slopes but not to overall RT, VWM item-capacity estimates failed to correlate significantly

with RT, accuracy, or any of the other oculomotor measures considered in this study, all  $r(18) \leq 0.39$ , all  $p \geq 0.10$  (Table 4). This suggests that when a target representation does not fill VWM item capacity, the stronger search guidance exhibited by high-capacity observers does not necessarily translate into faster or more accurate overall search (see also Anderson et al., 2013a).

## General discussion

We explored the relationship between the VWM representation of a target and later search guidance by measuring CDA after target designation on trials in which search guidance was found to be strong versus weak. Most models of visual search would have predicted a positive relationship between CDA magnitude and search guidance (e.g., Wolfe, 1994; Zelinsky, 2008). This is because theories of visual search widely assume that adding features to the target's representation in VWM should result in an increased signal-to-noise ratio on the map of target evidence, or "priority map" (Bisley & Goldberg, 2010), used to guide search. Contrary to this prediction, in Experiment 1 we found that maintaining more target features in VWM, as indicated by increased CDA magnitude, was accompanied by *weaker* search guidance, not stronger. Experiment 2 generally replicated this finding using a simpler task that depicted only a single target object per trial, thereby removing the potential for guessing strategies to complicate our interpretation. Collectively, these findings also show that CDA can be elicited by visually complex real-world objects, demonstrating an important generalization beyond the simple colored shapes typically used as stimuli in this literature.

We conducted several analyses to clarify our finding of a negative relationship between CDA magnitude and search guidance. First, we showed that this relationship is differentially expressed over time; the difference between strong- and weak-guidance CDA was larger later in the retention interval than earlier. This interaction, found in both Experiments 1 and 2, indicates a target representation that is forming over time and is becoming optimized for the upcoming task of guiding search to the target. Second, we found that the difference in magnitude between strong- and weak-guidance CDA positively correlates with the magnitude difference between strong- and weak-guidance time-to-target and RT; observers who had a large or small difference in one also had a large or small difference in the others. This finding speaks to the robustness of this relationship across different measures of search performance. Third, we found no evidence that strong- and weak-guidance CDA are differentially affected by

	% initial saccade directed to target	Initial saccade latency	Time-to-target	Target dwell time	RT	% correct
VWM item capacity ( <i>k</i> -scores)	$r = 0.57,$ $p = 0.02$	$r = 0.40,$ $p = 0.10$	$r = -0.16,$ $p = 0.53$	$r = -0.38,$ $p = 0.12$	$r = -0.37,$ $p = 0.13$	$r = 0.03,$ $p = 0.89$

Table 4. Correlations of VWM item capacity with oculomotor and manual measures of search performance in Experiment 2. Notes: RT = reaction time.

VWM item capacity, despite a main effect of item-capacity estimates on CDA magnitude in Experiment 1 and the absence of any relationship between item-capacity estimates and CDA magnitude in Experiment 2. This suggests that our pattern of results is not affected by item-capacity limits.

What is it about a low-load target representation that makes it better at guiding search? There are a number of possibilities. One explanation is suggested from recent work by Anderson et al. (2013b). Given the assumption that search is best described as a limited-capacity parallel process (e.g., Pashler & Badgio, 1985), and the assumption that the items that are processed in parallel during search compete for the same limited-capacity VWM resources that are used to construct the target representation, it follows that a low-load target representation should result in greater search efficiency. Conversely, a high-load target representation should result in lower search efficiency. This explanation, however, is unsatisfying in multiple respects. First, it fails to account for our finding of no relationship between target-related strong- and weak-guidance CDA magnitude and VWM capacity. Second, it offers no explanation for the time-varying nature of target-related CDA reported in this study—why, according to this account, does the load imposed by a target representation change over time? Third, this explanation generally discounts the importance of a target representation in guiding search. According to this account, the critical factor in determining search efficiency is the number of search items that can be processed in parallel; as this number increases, so too should search efficiency, with the importance of the target representation reduced to simple target verification or distractor rejection. However, decades of research have implicated the target representation in the actual process of guiding search (for reviews, see Wolfe, 1994, 1998; Zelinsky, 2008). As an explanation of the relationship between guidance and a target representation, which was the focus of the present study, this account is therefore incomplete.

A second possible explanation of our findings appeals to the relationship between the number of features maintained in VWM and the precision of those features. Recent work has suggested that as the number of features maintained in VWM increases, the precision of those features decreases (Anderson, Vogel, & Awh, 2011, 2013b; Bays, Catalao, & Husain, 2009; Bays &

Husain, 2008; Fougne, Asplund, & Marois, 2010; Machizawa, Goh, & Driver, 2012; Wilken & Ma, 2004; Zhang & Luck, 2008). Supporting this relationship, precision has been found to approach an asymptote once VWM item-capacity limits have been reached, presumably because no additional features could be added to VWM (Anderson & Awh, 2012; Anderson et al., 2011, 2013b). Assuming the maintenance of a search target in VWM, this suggests a tradeoff between feature number and precision in the target representation; as the number of maintained target features increases, the precision of those target features must decrease. However, complicating this relationship between precision and VWM load is the fact that high and low-capacity observers appear not to differ in terms of precision (Anderson et al., 2011, 2013b; Awh, Barton, & Vogel, 2007); the loss of precision associated with each additional feature is seemingly unrelated to item-capacity limits, despite high-capacity observers' maintaining more features in VWM (Anderson et al., 2011, 2012; Awh et al., 2007). The clearest test of an effect of feature number would therefore compare high- and low-capacity observers when all observers have filled VWM to capacity, as this comparison should not be confounded with differences in precision. The prediction would be that CDA should increase with the number of target features but that search guidance should decrease due to the lower precision of these features degrading the target representation. We conducted this analysis and found no difference in search performance despite clear differences in CDA magnitude, suggesting an explanation other than the number of features comprising the target representation. It may therefore be that our finding of weaker search guidance with additional target features (i.e., larger CDA) is due to a loss of precision accompanying those additional features and not the number of features per se. Relating the feature precision of a target representation to search performance will be an interesting avenue for future research.

Another possible explanation for our findings follows from recent work suggesting a role of long-term memory (LTM) in the relationship between CDA and search (Carlisle et al., 2011). At first glance, our counterintuitive finding of an inverse relationship between the VWM load imposed by a target representation and search guidance seems inconsistent with the work of Carlisle et al. (2011), who argued for a positive

relationship between CDA magnitude and search performance; those observers who had larger CDA magnitudes also had faster RTs. However, many differences in methodology and analysis may have contributed to these discrepant findings. Their analysis of CDA by observer is more akin to our investigation of capacity rather than our splitting of data into strong- and weak-guidance conditions. Also, their study used simple stimuli and a target present/absent task, with both types of trials combined in their reported correlations. Finally, their quantification of search performance purely in terms of a manual RT dependent measure introduces the possibility that their observed relationship between CDA and search performance was driven by factors related to target verification or distractor rejection rather than search guidance. By defining guidance in terms of the direction of the initial saccade, our study was free of this potential confound.

Perhaps the more relevant observation from the same study (Carlisle et al., 2011) was that target repetition across trials was associated with decreased target-related VWM load as indicated by CDA magnitude. The authors speculated that this decreased reliance on VWM with target repetition reflects an increasing reliance on features from LTM in the target representation. In the context of the present study, the fact that objects repeated halfway through the experiment means that features encoded during the initial presentations might be retrieved from LTM and used to guide search. This role of LTM might be even more pronounced in the present study due to our use of realistic objects; the features of familiar object categories might already exist in LTM. The retrieval of target features from LTM might also explain our observed interaction between search-guidance CDA and time, assuming a temporal dynamic associated with this retrieval process. The idiosyncratic nature of LTM representations could even account for the normal distribution of guidance per target item; one observer might easily retrieve an LTM representation of an object, whereas another observer might have a rather poor LTM representation for that same object. However, it is important to note that Carlisle and colleagues only observed this decreased reliance on VWM with consecutive target repetitions, which never occurred in our study. Moreover, although categorical features from LTM can be used to guide search (Maxfield & Zelinsky, 2012; Schmidt & Zelinsky, 2009; Yang & Zelinsky, 2009), it has not yet been demonstrated that these features can guide search directly from LTM without first being represented in VWM. Specifying the role of LTM in search guidance, and in the VWM load imposed by a target representation, is clearly another important direction for future work.

The interpretation that we believe best explains our data combines ideas of feature precision and LTM retrieval with a process of feature consolidation during the creation of a target representation. The search community has long known that the features comprising a target representation are imprecise. Even when a target is defined by only a single feature, as in the case of an oriented bar, this orientation is represented with surprising imprecision—as either steep or shallow (e.g., Wolfe, Friedman-Hill, Stewart, & O’Connell, 1992). Such observations have been interpreted as evidence for the categorical representation of targets (Wolfe, 1994; Wolfe et al., 1992), the suggestion that targets are represented not by features narrowly tuned to specific objects but by features designed to represent entire object categories. Since this insightful early claim, several recent studies have demonstrated that the visual features of target categories can be learned and used to guide search (e.g., Alexander & Zelinsky, 2011; Zelinsky, Adeli, Peng, & Samaras, 2013; Zelinsky, Peng, Berg, & Samaras, 2013), with these categorical target features presumably residing in LTM. However, this categorical guidance is weak compared to guidance following the preview of a specific target, a finding that can be explained in terms of categorical imprecision—the features optimized to represent a target category may not be optimal with respect to any specific member of that category. To the extent that search targets are represented categorically, one would therefore expect imprecision in those target features, with this imprecision increasing as the category becomes broader and less well defined (Maxfield & Zelinsky, 2012; Schmidt & Zelinsky, 2009). Returning to the present study, we speculate the following dynamic—that upon seeing the target cue, observers filled their VWMs with categorical features retrieved from LTM and other features acquired from the depicted objects, resulting in the formation of high-load categorical target representations shortly after cue offset that we measured as rising CDA magnitude. Because many of these features would be imprecise, weak guidance would be expected from them. This was expressed in our data as a lack of a difference between weak and strong guidance resulting from these early high-load VWM target representations.

This account explains how many imprecise features might come to reside in VWM, but does not explain why the load imposed by the target representation decreases over time and why this change results in better search guidance. Answers to these questions require a process of feature biasing and pruning. We speculate that the target representation consists initially of many features, but that over time the features less useful for search guidance are pruned from the target representation, leaving those features that are better tuned to the specific target properties shown at preview. This pruning process, which is conceptually equivalent

to setting a zero weight on the undesirable features (consistent with biased-competition conceptions of search, e.g., Chelazzi, Duncan, Miller, & Desimone, 1998), would result in a lower VWM load over time and more accurate guidance to the target. To the extent that this process is successful, target-related CDA will be low and search guidance strong; to the extent that it fails, target-related CDA will be high and search guidance weak.

This interpretation is also consistent with models that learn to use features that are discriminative of a target category to guide eye movements during search (Ehinger, Hidalgo-Sotelo, Torralba, & Oliva, 2009; Zelinsky, Adeli, et al., 2013; Zhang, Tong, Marks, Shan, & Cottrell, 2008). Just as discriminative features may be selected for the representation of a target category, they might also be selected from a target representation consisting of imprecise or less useful features. According to this interpretation, underlying good search guidance is a process that weights these discriminative target features and deweights those features that would just add noise to the target representation and reduce search efficiency. This process explains not only our core findings, that there is an inverse relationship between the load of a target representation and search guidance and that this relationship emerges only later during the retention interval, but also the observed effects of VWM capacity on search. CDA magnitude might fail to track guidance differences with capacity because VWM would typically be filled with features, distinctive or not. Despite high-capacity observers' being able to maintain more features, the proportion of these features that were discriminative of the target may have differed between high- and low-capacity observers. High-capacity observers may therefore have had more features through which to prune, but this set may have contained more discriminative features (the more features that are maintained, the more likely that discriminative features would be included in this set), resulting in an unclear relationship between strong- and weak-guidance CDA and capacity.

In conclusion, we contend that what appeared to be a highly counterintuitive finding, that the representation of more target features leads to worse search guidance, might be explained by a relatively simple process of feature consolidation and pruning over time. Early CDA measures may be dominated by VWM load and capacity differences across observers and therefore fail to predict strong or weak guidance; late CDA measures, however, capture these guidance differences following the pruning of less discriminative features from the target representation. Stated more simply, strong-guidance CDA lessens over time, whereas weak-guidance CDA does not. This temporal dynamic highlights the importance of considering the formation

and consolidation of a target representation when interpreting the role that VWM load plays in determining search performance.

*Keywords:* visual search, guidance, target representation, contralateral delay activity (CDA), visual working memory (VWM), visual working memory capacity, event-related potentials (ERPs)

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## Footnotes

<sup>1</sup>We are agnostic with regard to the feature-based or object-based nature of VWM, and will use the term “feature” when referring to the information in VWM indexed by CDA. We will also use the term “feature” when referring to the single-feature objects (e.g., colored boxes and oriented bars) often used in VWM and CDA studies.

<sup>2</sup>We chose to use a large number of nonrepeating real-world objects rather than a small number of repeating single-feature objects for multiple reasons: (a) These objects better approximate real-world search, (b) consecutive target repetition reduces VWM load, thus potentially affecting the relationship between guidance and VWM (Carlisle et al., 2011), and (c) real-world objects likely yield a comparatively high VWM load even with only two targets.

<sup>3</sup>EOG was only used for oculomotor artifact rejection, in order to be consistent with standard methods and practices.

<sup>4</sup>Six observers accidentally completed a version of the task having a shorter preview duration. Given that

no differences were found between these observers and the latter 10 observers on measures of overall CDA, strong-guidance CDA, or weak-guidance CDA, all  $t(12) \geq -1.27$ , all  $p \geq 0.22$ , or on any reported measures of search performance, all  $t(12) \leq 1.08$ , all  $p \geq 0.29$ , we simply shortened the CDA analysis window to 900 ms rather than using the full 1000-ms retention interval.

<sup>5</sup>We operationally defined an initial saccade as the first saccade of  $2^\circ$  or greater made within 500 ms of search-display onset. These criteria resulted in the detection of an initial saccade on more than 97% of trials, on average. When combined with all other rejection criteria, no more than 35% of trials were excluded for any one participant.

<sup>6</sup>The Shapiro–Wilk test and the Kolmogorov–Smirnov test will yield a significant result ( $p < 0.05$ ) when a distribution is non-normally distributed. Likewise, skewness and kurtosis will exceed 2.0 in a non-normal distribution.

<sup>7</sup>Given that only the latter time bins showed significant differences between the guidance conditions, these CDA difference scores were restricted to the mean CDA measured during the last 100 ms of the delay before search-display onset.

<sup>8</sup>As argued by Carlisle et al. (2011; Experiment 1), one-target search generally results in a reduced range of possible behavioral and electrophysiological values and is therefore less likely to produce significant correlations. Moreover, the fact that these correlations failed to attain significance at a  $p = 0.05$  level was largely driven by one aberrant observer. If we were justified in removing this observer, both of these correlations would become significant (time-to-target,  $p = 0.03$ ; RT,  $p < 0.01$ ).

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