

Effects of Search Difficulty on the Selection, Maintenance, and Learning of Attentional Templates

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Abstract

■ Prominent theories of attention claim that visual search is guided through attentional templates stored in working memory. Recently, the contralateral delay activity (CDA), an electrophysiological index of working memory storage, has been found to rapidly decrease when participants repeatedly search for the same target, suggesting that, with learning, the template moves out of working memory. However, this has only been investigated with pop-out search for distinct targets, for which a strong attentional template may not be necessary. More effortful search tasks might rely more on an active attentional template in working memory, leading to a slower handoff to

long-term memory and thus a slower decline of the CDA. Using ERPs, we compared the rate of learning of attentional templates in pop-out and effortful search tasks. In two experiments, the rate of decrease in the CDA was the same for both search tasks. Similar results were found for a second component indexing working memory effort, the late positive complex. However, the late positive complex was also sensitive to anticipated search difficulty, as was expressed in a greater amplitude before the harder search task. We conclude that the amount of working memory effort invested in maintaining an attentional template, but not the rate of learning, depends on search difficulty. ■

INTRODUCTION

Most models of visual search assume that the brain maintains a working memory representation of the search goal, referred to as the attentional template (Bundesen, Habekost, & Kyllingsbæk, 2005; Desimone & Duncan, 1995; Duncan & Humphreys, 1989; Wolfe, Cave, & Franzel, 1989). Neurophysiological and electrophysiological studies using both humans and nonhuman primates have suggested that such attentional templates are indeed maintained in working memory. In these studies, a cue indicated what target to look for in a subsequent search display, which was presented after a blank delay period. During this delay period, single-unit recordings in monkey inferior temporal cortex showed sustained activity to the cue (Chelazzi, Duncan, Miller, & Desimone, 1998; Chelazzi, Miller, Duncan, & Desimone, 1993), whereas in humans, EEG studies have revealed a sustained contralateral delay activity (CDA; Carlisle, Arita, Pardo, & Woodman, 2011; Woodman & Arita, 2011), which is regarded as a direct index of visual working memory maintenance (McCollough, Machizawa, & Vogel, 2007; Vogel & Machizawa, 2004; Klaver, Talsma, Wijers, Heinze, & Mulder, 1999).

Learning an Attentional Template: Role of Long-term Memory in Guiding Search

A recent ERP experiment by Carlisle et al. (2011, Experiment 3) has suggested that, with target repetition, visual

working memory involvement in maintaining the attentional template is reduced. They found that the CDA to the target cue diminished when participants searched for the same target up to seven times in a row. Putatively, target repetition causes the attentional templates stored in working memory to be transferred to long-term memory.

However, in Carlisle et al. (2011), the cue to which the CDA was measured was not strictly necessary to find the target. This was because the target was always defined by a constant, distinct color in the search display. The cue was only necessary to determine whether the target had the correct shape (i.e., it determined the response). Moreover, search is typically very efficient for such color singletons (Theeuwes, 1991, 1992; Duncan & Humphreys, 1989; Treisman & Souther, 1985). Taken together then, the cue in Carlisle et al. (2011) may not necessarily have functioned as an attentional template actively guiding search, although it was required for a correct behavioral response. We hypothesized that, in more effortful search tasks, in which there is no guidance from a distinct color, search relies to a greater extent on an active attentional template, as maintained in working memory. The greater functional importance of the template in effortful search tasks might lead to a slower handoff to long-term memory and, thus, a slower decline of the CDA.

This hypothesis was tested in two experiments that compared the rate of learning (as indicated by a decrease in the CDA amplitude across target repetitions) in pop-out and effortful search tasks. Both tasks are illustrated in Figure 1. Participants were shown a target cue, followed,

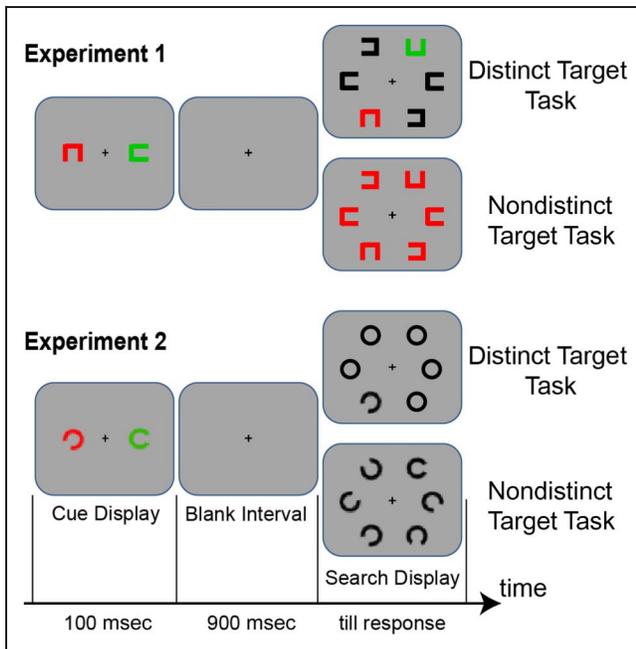


Figure 1. Stimulus sequence in both experiments. The search target was defined by color (red in this example). In Experiment 1 (top), in the distinct target task the search display contained only one red Landolt square, whereas all items were red in the nondistinct target search display. In Experiment 2 (bottom), in distinct target task, the search display had only a single Landolt C, and the distractors were circles, whereas all items were Landolt Cs in the nondistinct target task. In both tasks, the correct response is “present” because all search displays contain the target, that is, the bottom gap Landolt square in Experiment 1 and the bottom-left gap Landolt C in Experiment 2. Note that the sizes and colors are different than the real experiment for illustrative purposes.

after a delay, by a search display. The distinct target task resembled that used by Carlisle et al. (2011), as the target had a unique color relative to the nontargets. This should aid guidance and make visual search easy and efficient. In contrast, in the nondistinct target task, all stimuli had the same color, so the target did not pop out from the display and thus presumably caused search to be more effortful. We ascertained that the two kinds of search indeed differed in efficiency by computing search slopes in each condition.

Other ERP Components of Interest: P170, N2pc, and Late Positive Complex

In addition to the CDA, we investigated three other ERP components: the P170, N2pc, and the late positive complex (LPC). Recently, Woodman, Carlisle, and Reinhart (2013) proposed that the P170 provides a more direct index of the transfer into long-term memory, on the basis of an earlier study linking a reduction in this component to perceptual priming (Voss, Schendan, & Paller, 2010). Consistent with this, Woodman et al. (2013) reported a reduction in P170 amplitude with target repetitions.

Furthermore, if, with target repetition, the attentional template is transferred into long-term memory, then participants might stop attending to the cue, as the memory suffices to do the search. This should lead to a decrease in the N2pc, an index of attentional selection (Hickey, Di Lollo, & McDonald, 2009; Eimer, 1996; for reviews, see Luck, 2012; Luck & Hillyard, 1994). Contrary to this hypothesis, Carlisle et al. (2011) observed no decline in N2pc across target repetitions, suggesting that participants continued selecting the target cue even after it had been stored in long-term memory.

Because the CDA has been reported to be insensitive to task difficulty (Ikkai, McCollough, & Vogel, 2010; McCollough et al., 2007), we also examined a sustained positive component at central-parietal electrode sites, referred to as the sustained P3b, positive slow wave, or LPC (Sutton & Ruchkin, 2006). Although there are different interpretations of the LPC, the findings invariably point toward a relationship between LPC amplitude and the effort required in a working memory task (Polich, 2012; Kok, 2001; Ruchkin, Johnson, Canoune, & Ritter, 1990). It has been shown that the LPC becomes larger with increasing memory set size (Kusak, Grune, Hagendorf, & Metz, 2000; García-Larrea & Cézanne-Bert, 1998; Ruchkin et al., 1990) and smaller for new items that need to be stored on top of a large existing working memory load (McEvoy, Smith, & Gevins, 1998). In line with this, in dual-task paradigms, the performance on the primary task has been found to be negatively correlated with the LPC amplitude for the secondary task (Paller, McCarthy, & Wood, 1988; Kramer, Wickens, & Donchin, 1985; Isreal, Chesney, Wickens, & Donchin, 1980). Consequently, we used the LPC as an index of the effort invested in maintaining the attentional template. We predicted that more effort would be invested in the template in anticipation of an effortful search task than for a pop-out search task.

Furthermore, using a nonlateralized ERP component as an index of working memory maintenance provided a test for an important alternative explanation of the CDA decline with target repetition. The CDA is a lateralized component; a decline in CDA amplitude could be caused by a decline in working memory maintenance, but also by a decrease in the laterality of the working memory representation. Repeated encounter, on varying sides, with the same object might lead to a more “centrally” maintained working memory representation rather than a handoff to a long-term memory representation and, thus, to a decrease in laterality. If this would be the case, then the decline in the CDA would be accompanied by a sustained LPC at midline electrodes, showing that working memory effort for maintenance stays intact.

Both the CDA and the LPC are indexes related to working memory maintenance. However, based on the aforementioned literature, we claim that the CDA is a marker for the number of maintained visual-spatial working memory representations and that the decrease in the CDA reflects handoff of representations from visual

working memory to other stores. The LPC, on the other hand, indexes the effort invested in maintaining these working memory representations, and a decrease in the LPC thus reflects less working memory effort. This decrease might either be the result of a handoff from visual working memory or of devoting less effort for maintaining a representation that is still in working memory—in this case because the search task is anticipated to be easier.

METHODS

Participants

Fourteen and 23 healthy volunteers participated in Experiment 1 and Experiment 2, respectively, for course credit or monetary compensation. Seven participants in total were excluded because of excessive noise in their EEG recordings or to ocular artifacts, leaving 12 participants in Experiment 1 (ages 20–28 years, nine women) and 18 in Experiment 2 (ages 18–36 years, 12 women). The study was conducted in accordance with the Declaration of Helsinki and was approved by the faculty's ethical committee. Written informed consent was obtained. Because of a technical problem, one participant in Experiment 1 completed 1736 experimental trials rather than 1792, and one participant in Experiment 2 completed 800 experimental trials rather than 840; both were included in the analyses.

Stimuli

Viewing distance was 75 cm. Figure 1 shows an example trial. The background color was gray (58.18 Cd/m^2). The fixation cross, visible throughout the trial, was a black plus sign (0.23° of line length, 0.05° line thickness). In the cue array, a cue and a visually balancing noncue were presented 1.17° to the left and right of the fixation. In Experiment 1, they were both Landolt squares ($0.7^\circ \times 0.7^\circ$, line thickness 0.1°) with a gap on one side (top, bottom, left, or right, 0.68°); one was presented in red (25.70 Cd/m^2), and the other was in green (47.64 Cd/m^2). In Experiment 2, they were Landolt Cs, that is, circles (diameter 0.69° , line thickness 0.08°) with a gap of 0.22° on one side of eight possible orientations (top, bottom, left, right, or 45° of rotation off these main directions); again, one presented in red and the other in green.

The visual search display contained either 6 or 12 items, presented equidistantly on an imaginary circle with a radius of 2.9° . In Experiment 1, the items were Landolt squares. In the distinct target search task, there was one red item and one green item, and the rest was black; the target shape could only appear in the cue color. In the nondistinct target search task, items were all the same color as the cue, that is, either red or green. The search display in Experiment 2 consisted of just one Landolt C among circles in distinct target search task (in target

absent trials, the single Landolt C had a gap direction that was at least 90° off compared with that of the cue), and in nondistinct target task, all items were Landolt Cs presented in black.

Design and Procedure

Each trial began with the fixation cross for a randomly jittered duration of 800–1200 msec in Experiment 1 and 1200–1600 msec in Experiment 2. Then, the target cue and the nontarget item were presented for 100 msec. For each participant, the target color was constant over the course of the experiments (counterbalanced). In a retention interval of 900 msec, only the fixation cross was presented. The search display was then presented till response. Auditory feedback on accuracy was provided. The intertrial interval was jittered between 1000 and 1400 msec in Experiment 1 and between 1200 and 1600 msec in Experiment 2. During the intertrial interval, a word indicated whether the upcoming cue would be the same as the previous trial (OLD) or whether it would be a new one (NEW), following Carlisle et al. (2011). The last 100 msec of the intertrial interval consisted of only the fixation cross, without the labels OLD or NEW.

The task was to maintain fixation until the search display was presented and then to indicate, as fast as possible without risking accuracy, whether the target was present or absent. In Experiment 1, in case of a target repetition, that is, when the word “OLD” was presented, participants were asked to verify the target cue in their memory by attending to the cue although they remembered it from the previous trial. This instruction was not given in Experiment 2.

Both experiments employed a factorial design with 2 task types (distinct; nondistinct), $\times 2$ set sizes (6; 12), $\times 2$ target presence (present; absent), and an additional factor of target repetitions (1, 3, 6, or 7 trials in Experiment 1 and 2 or 6 trials in Experiment 2). Set size and target presence were randomly mixed within blocks, with equal numbers for each level. The length and number of target repetition runs were chosen to yield a relatively equal distribution of trials per repetition that was still unpredictable for participants; per block, there were four runs of 1, 3, and 7 repetitions and two runs of 6 repetitions in Experiment 1. In Experiment 2, there were five runs of both 2 and 6 repetitions per block. In Experiment 1, each participant performed each task type in a separate session (order counterbalanced) on two separate days (0–6 days in between, 3.5 days in average).

Before each session, participants completed a practice block of 20–24 trials. In Experiment 2, there was a practice block with 6 trials in each task type, 12 trials in total. If accuracy was below 75%, they completed another practice block (1.12 blocks on average, with a maximum of 2 blocks in Experiment 1; in Experiment 2, all participants performed above criterion in the very first target block). In both experiments, before each block, there were also

five practice trials to familiarize with the particular task type and target color (no particular accuracy requirement this time). The experimental trials consisted of 16 blocks ($\times 2$ sessions) of 56 trials in Experiment 1 and 22 blocks of 40 trials in Experiment 2, with a short break between blocks, during which participants were shown their cumulative average accuracy and RTs.

Data Analyses

Degrees of freedom were corrected for sphericity violations using Greenhouse–Geisser epsilon (Jennings & Wood, 1976). Post-ANOVA analyses of multiple comparisons were performed with Student–Newman–Keuls (SNK) tests. Effect of repetition was treated as a linear contrast (Rosenthal & Rosnow, 1985), but the results of the standard omnibus tests were the same (in terms of reaching significance). The RT analyses and all ERP analyses included trials with correct responses only.

Behavioral Analyses

Data were trimmed in two steps. First, trials with a search response faster than 150 msec and slower than 8000 msec were rejected ($<0.1\%$ of all trials for both Experiments 1 and 2), and subsequently those with a search RT of 2.5 standard deviation above or below the mean per condition were excluded. This two-step trimming led to rejection of 2.6% and 2.1% of all trials in Experiments 1 and 2. Further behavioral analyses were performed on target-present trials only. Accuracy and RTs were entered in two repeated-measures ANOVAs with the factors Task Type, Set Size, and Target Repetition (results from the Accuracy ANOVAs will not be presented but were similar to those from the RT ANOVAs).

ERP Recording and Analysis

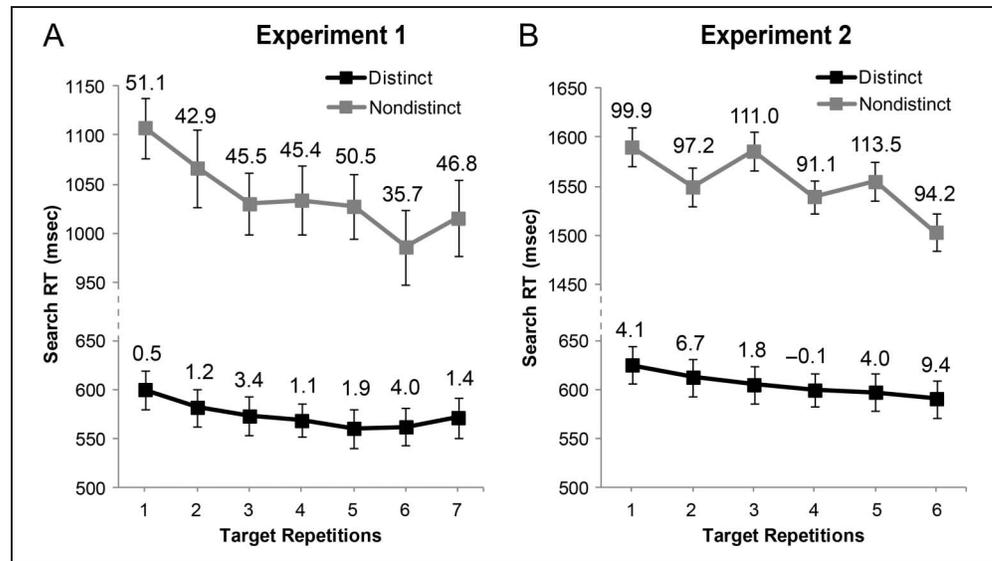
EEG and EOG were recorded from 70 sintered $-AG/AgCl$ electrodes positioned at 64 standard International 10/20 System sites and six external locations mentioned below, using the Biosemi ActiveTwo system (Biosemi, Amsterdam, the Netherlands). The ground of ActiveTwo system consists of a feedback loop between the active common mode sense electrode and the passive driven right leg electrode that “form a feedback loop, which drives the average potential of the subject (the Common Mode voltage) as close as possible to the ADC reference voltage in the AD-box (the ADC reference can be considered as the amplifier ‘zero’).” As a result, no impedance measurements or gain adjustments are needed with the ActiveTwo system (www.biosemi.com). The vertical EOG (VEOG) was recorded from electrodes located 2 cm above and below the right eye, and the horizontal EOG (HEOG) was recorded from electrodes 1 cm lateral to the external canthi. The VEOG was used in the detection of blink artifacts, and the HEOG was used in the detection of horizontal eye movement

artifacts. Electrophysiological signals were digitized at 512 Hz. ERP analyses were conducted using a combination of Matlab (Mathworks, Natick, MA), the EEGLAB toolbox (Delorme & Makeig, 2004), and ERPLAB toolbox (www.erpinfo.org).

All ERPs were computed with respect to a 200-msec prestimulus baseline period and were re-referenced off-line to the average of left and right mastoids. The data were filtered with an IIR Butterworth filter with a band-pass of 0.01–40 Hz. Trials with incorrect behavioral responses or with ocular artifacts or large voltage shifts were excluded. Blinks and horizontal eye movements during 200 msec prestimulus till 1000 msec poststimulus interval were identified with a step function that detects whether there is a sudden change in the voltage that exceeds a particular threshold (step-like artifact detection function in ERPLAB toolbox: `pop_artstep`). The threshold was 60 μV in bipolar VEOG for blinks. The rejection of horizontal eye movements was performed in two steps. First, the single-trial waveforms were inspected to determine an optimum threshold for each participant that rejects a high proportion of the trials with artifacts while keeping a relatively low proportion of artifact-free trials (Woodman & Luck, 2003). In the second step, the individuals with a residual HEOG activity greater than 3.2 μV (i.e., residual eye movements greater than 0.2° , propagated voltage greater than 0.3 μV at posterior sites; see Lins, Picton, Berg, & Scherg, 1993a, 1993b) were excluded from the analyses, which was the ground for exclusion for two participants in Experiment 1 and four participants in Experiment 2. For participants with more than 10% of trials containing blinks (two participants in Experiment 1 and one in Experiment 2), an independent component analysis was performed (Makeig, Bell, Jung, & Sejnowski, 1996), and blink artifacts were corrected by removing blink-related independent components. However, the trials at which the blinks occurred during cue presentation were excluded from analyses. To detect nonocular artifacts, a function similar to that applied to EOG channels to detect ocular artifacts was applied to the EEG channels (i.e., the moving window peak-to-peak threshold function in ERPLAB toolbox: `pop_artmwppt`), this time with a threshold of 100 μV . Individuals were excluded from analyses if, after all the artifact rejections, the remaining number of trials per bin was lower than 65 trials. This has led to the rejection of one additional participant in Experiment 2. For the participants that were involved in the analyses, on average 11.5% and 11.4% of all trials were rejected by artifact detection functions mentioned above for Experiments 1 and 2, respectively.

The CDA and N2pc were calculated as the difference waves between electrode sites contralateral versus ipsilateral to the location of the target cue. On the basis of previous studies, the N2pc was measured at P7/8, PO7/8, and O1/2 between 225 and 300 msec (for reviews, see Luck, 2012; Sawaki & Luck, 2010) and the CDA at P5/6,

Figure 2. Mean search RT and search efficiency (in msec per item, given as the number above each data point) in (A) Experiment 1 and (B) Experiment 2 for the distinct target task (black) and nondistinct target task (gray) trials for each repetition. Target repetitions are given on the x axis. The error bars represent SEMs for normalized data, that is, corrected for between-subject variance (Cousineau, 2005).



P7/8, PO7/8, and O1/2 between 300 and 900 msec after the onset of the cue (McCollough et al., 2007). For the lateralized components, that is, the N2pc and CDA, we entered the data into an ANOVA with the within-subject factors of Hemisphere (right; left), Contralaterality with respect to the target cue (ipsilateral; contralateral), Electrode Pair (mentioned above), Task Type (distinct; nondistinct), and Target Repetition (1; 2&3; 4&5; 6&7 trials in Experiment 1 and 1; 2; 3&4; 5&6 trials in Experiment 2). As the later repetitions occurred progressively less often, for the analyses they were binned into pairs to improve signal-to-noise ratio. Only the effects that involve contralaterality will be reported. ANOVAs for non-lateral components, that is, the P3b, LPC, and P170, had as factors Electrode Site (Fz; Cz; Pz), Task Type, and Target Repetition. Because the time course of the P170, P3b, and LPC components are highly dependent on task demands (Polich, 2012; Kenemans, Kok, & Smulders, 1993), we defined them post hoc on the basis of their observed peak latencies at critical electrodes suggested in the literature; for both experiments, 150–200 msec for the P170 and 475–700 msec for the LPC after the onset of the cue. For the P3b, the intervals were 300–400 msec in Experiment 1 and 330–430 in Experiment 2.

EXPERIMENT 1

Behavior

Figure 2 shows the average search RT and search efficiency for each target repetition and task type. Search RT was lower for the distinct target task than for the nondistinct target task, $F(1, 11) = 243.70, p < .001, \eta_p^2 = .96$, and lower for set size 6 than for set size 12, $F(1, 11) = 124.36, p < .001, \eta_p^2 = .92$. RTs decreased with increasing target repetition, $F(1, 11) = 11.36, p = .006, \eta_p^2 = .51$. There was a marginal Task Type \times Repetition interaction, $F(1, 11) = 4.27, p = .063, \eta_p^2 = .28$: As can

be seen in Figure 2, repetition was relatively more beneficial in the nondistinct target task. Furthermore, the Task Type \times Set Size interaction was significant, $F(1, 11) = 140.98, p < .001, \eta_p^2 = .93$; set size had a substantial effect in the nondistinct target condition, although it had no effect in the distinct target condition. There was no Set Size \times Repetition interaction, $F(1, 11) = 0.14, p = .72, \eta_p^2 = .01$, nor was the three-way interaction between Set Size, Repetition, and Task Type significant, $F(1, 11) = 0.72, p = .42, \eta_p^2 = .06$. The accuracy pattern followed that of the RTs except there was no effect of repetition. Accuracy values are shown in Table 1.

Electrophysiology

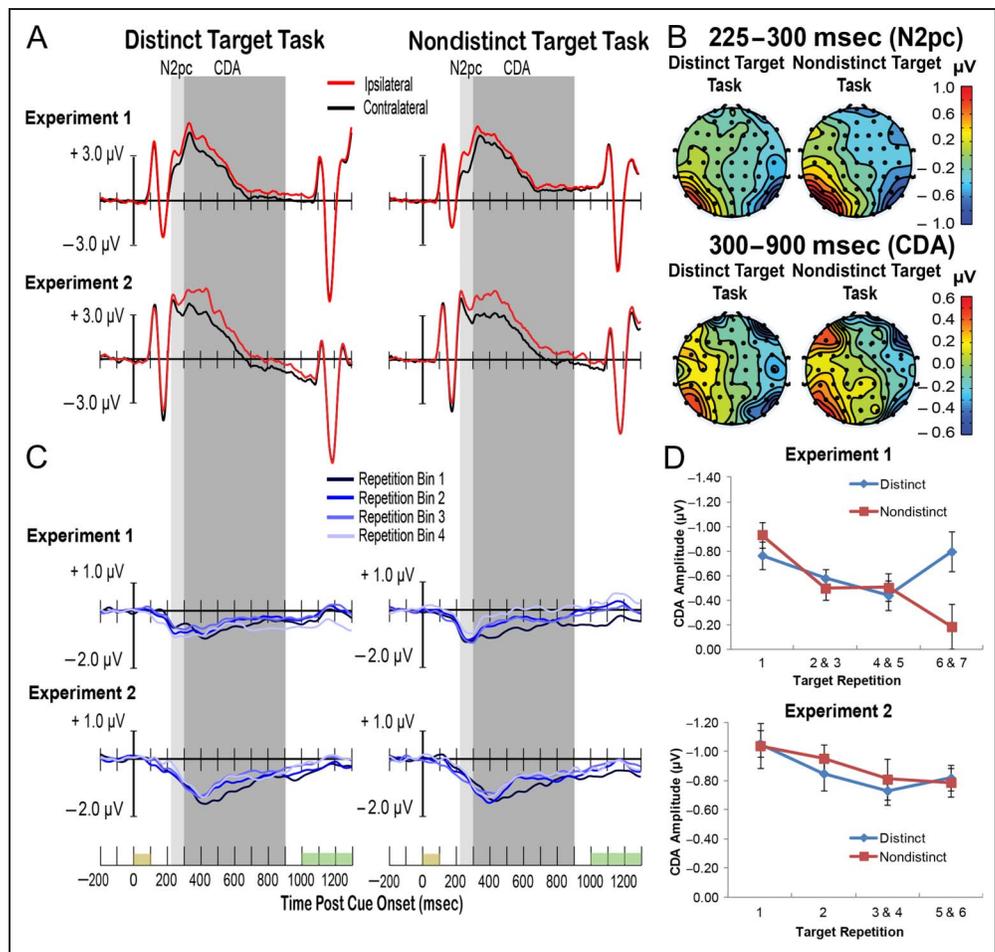
CDA

Figure 3 shows the CDA waveforms averaged across the electrode pairs used in analyses (P5/6, P7/8, PO7/8, and O1/2). The main effect of Contralaterality was significant, $F(1, 11) = 21.13, p = .001, \eta_p^2 = .66$, indicating that a CDA was triggered by the onset of the cue. This CDA decreased in amplitude with target repetition, as indicated by a significant Contralaterality \times Repetition interaction, $F(1, 11) = 7.77, p = .018, \eta_p^2 = .41$. SNK tests showed that the CDA for Repetition 1 was greater than

Table 1. The Mean Accuracies for Both Experiments across Set Sizes and Task Types

Set Size	Percent Correct (%)			
	Experiment 1		Experiment 2	
	6	12	6	12
Distinct target	94.5	95.2	97.0	96.9
Nondistinct target	87.6	81.6	87.7	80.2

Figure 3. (A) The grand-averaged waveforms at the average of PO7/8, P7/8, P5/6, and O1/2 electrode pairs, contralateral (black) and ipsilateral (red) to the location of the cue. Plotted separately are distinct target trials (left) and nondistinct target trials (right). (B) The scalp distribution of the N2pc and the CDA, in Experiment 1, averaged over their measurement windows, calculated as the voltage distribution in trials in which the cue was presented on the left subtracted from the ones in which it was presented on the right, divided by two. (C) The grand-averaged contralateral minus ipsilateral difference wave, computed from mean amplitude at PO7/8, P7/8, P5/6, and O1/2 electrodes, and low-pass filtered at 5 Hz for visualization purposes, plotted across target repetitions and task types. The shades of blue, from darkest to lightest, stand for Repetition 1, Repetitions 2&3, Repetitions 4&5, and Repetitions 6&7 in Experiment 1 (top), and Repetition 1, Repetitions 2, Repetitions 3&4, and Repetitions 5&6 in Experiment 2 (bottom). The light gray and dark gray rectangular regions represent the time window at which N2pc and CDA was calculated, respectively. The shadings on the timeline indicate the duration of the cue display (yellow) and the search display (green). Note that positive is plotted upward. (D) The grand-averaged CDA amplitude in both experiments as a function of target repetitions. The error bars represent *SEMs* for normalized data, that is, corrected for between-subject variance (Cousineau, 2005).



all the other repetitions, which were not significantly different from each other. The CDA amplitude was equal for both task types, as the Task Type \times Contralaterality interaction was not significant, $F(1, 11) = 2.87, p = .12, \eta_p^2 = .21$. Importantly, the rate of decrease of the CDA for both task types was the same, as suggested by the lack of a Task type \times Contralaterality \times Repetition interaction, $F(1, 11) = 0.24, p = .64, \eta_p^2 = .02$.

The Contralaterality \times Electrode Pair interaction was significant, $F(3, 33) = 4.76, p = .007, \eta_p^2 = .30$. SNK tests on CDA (contra- minus ipsilateral waves) showed that the CDA amplitude at P7/8 ($M = -0.85, SD = 0.79 \mu V$) and PO7/8 ($M = -0.79, SD = 0.67 \mu V$) was greater than at O1/2 ($M = -0.36, SD = 0.37 \mu V$), whereas the CDA at P5/6 ($M = -0.57, SD = 0.48 \mu V$) was not significantly different from other electrode pairs.

N2pc

Figure 3 also shows N2pc waveforms, which precede those of the CDA. There was a main effect of Contra-

laterality, $F(1, 11) = 41.46, p < .001, \eta_p^2 = .79$, indicating the presence of a N2pc. The magnitude of the N2pc did not change across target repetitions, as evidenced by the lack of a Contralaterality \times Repetition interaction, $F(1, 11) = 0.20, p = .890, \eta_p^2 = .01$. There was a Task Type \times Contralaterality interaction, $F(1, 11) = 10.71, p = .007, \eta_p^2 = .49$: The N2pc was larger for the nondistinct target task ($M = -1.57, SD = 0.70 \mu V$) than for the distinct target task ($M = -1.17, SD = 0.83 \mu V$). There was also a Contralaterality \times Electrode interaction, $F(2, 22) = 13.05, p < .001, \eta_p^2 = .54$. SNK tests showed that N2pc amplitude was greater at P7/8 ($M = -1.71, SD = 0.82 \mu V$) and PO7/8 ($M = -1.58, SD = 1.07 \mu V$) than at O1/2 ($M = -0.80, SD = 0.61 \mu V$). No other interaction was significant (all $F_s < 1.61, p_s > .22$).

P3b and LPC

Figure 4A, C shows the ERP plots from Fz, Cz, and Pz electrodes for the P3b and LPC time windows and concomitant scalp topographies. For the P3b, there was a marginal

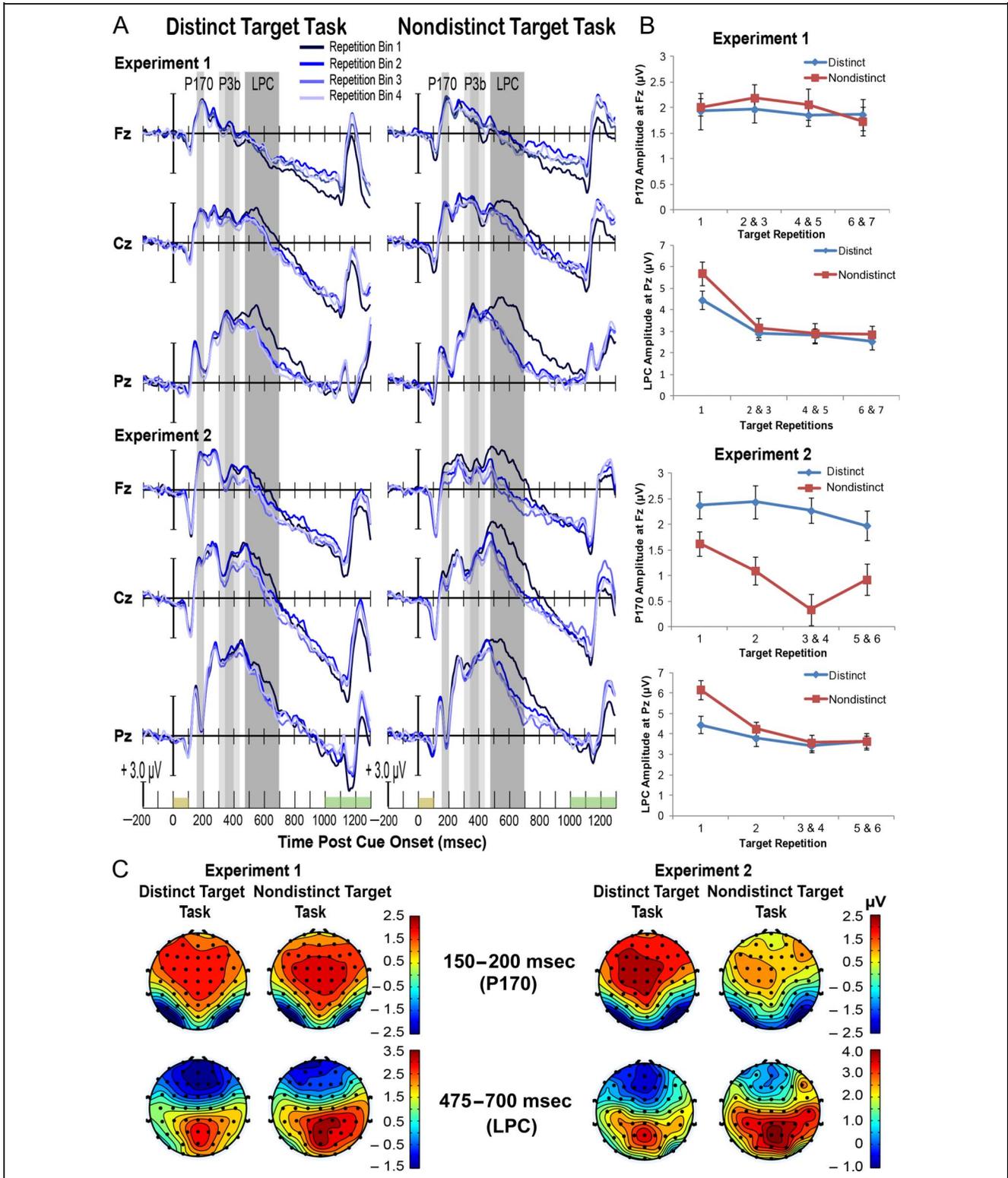


Figure 4. (A) The grand-averaged waveforms at the electrodes Fz, Cz, and Pz for distinct target trials (left) and nondistinct target trials (right). The shades of blue, from darkest to lightest, stand for Repetition 1, Repetitions 2&3, Repetitions 4&5, and Repetitions 6&7 in Experiment 1 (top) and Repetition 1, Repetition 2, Repetitions 3&4, and Repetitions 5&6 in Experiment 2 (bottom). The gray rectangular regions represent the time window at which the P170 (150–200 msec), the P3b (300–400 msec in Experiment 1 and 330–430 msec in Experiment 2), and the LPC (475–700 msec) was calculated. The shadings on the timeline indicate the duration of the cue display (yellow) and the search display (green). (B) The grand-averaged P170 amplitude at Fz and grand-averaged LPC amplitude at Pz as a function of repetitions, separately for distinct and nondistinct target trials in Experiment 1 (top) and in Experiment 2 (bottom). The error bars represent *SEMs* for normalized data, that is, corrected for between-subject variance (Cousineau, 2005). (C) The scalp topography of P170 (150–200 msec, top) and LPC (475–700 msec, bottom) separately for distinct target and nondistinct target trials in Experiment 1 (left) and in Experiment 2 (right).

main effect of Task Type, $F(1, 11) = 3.63, p = .083, \eta_p^2 = .25$, with a larger P3b in the nondistinct target task. There was no effect of repetition, $F(1, 11) = 1.61, p = .231, \eta_p^2 = .13$, suggesting that overall P3b amplitude did not decrease with repetitions. There was a main effect of electrode, $F(2, 22) = 10.09, p = .006, \eta_p^2 = .48$. P3b amplitude at Pz ($M = 4.68, SD = 4.26 \mu V$) was greater than at Cz ($M = 2.40, SD = 3.18 \mu V$) and Fz ($M = 0.79, SD = 2.42 \mu V$). The Task Type \times Electrode interaction was significant, $F(2, 22) = 4.52, p = .009, \eta_p^2 = .41$. Post hoc SNK tests indicated that the nondistinct target task created a larger P3b than distinct target task at Cz, but not at Fz or Pz. No other interaction reached significance ($F_s > 1.86, p_s < .199$).

For the LPC, there was an effect of Target Repetition, $F(1, 11) = 11.11, p = .007, \eta_p^2 = .50$. Like the CDA, the LPC amplitude decreased with target repetition. In contrast to the CDA, the main effect of Task Type was now also significant, $F(1, 11) = 5.39, p = .040, \eta_p^2 = .33$; the LPC amplitude was greater in the nondistinct target task than in the distinct target task. There was a main effect of Electrode, $F(2, 22) = 64.68, p < .001, \eta_p^2 = .86$. Positivity at Pz ($M = 3.42, SD = 1.23 \mu V$) was greater than Cz ($M = 1.78, SD = 1.35 \mu V$), and they were both greater than Fz ($M = -0.88, SD = 1.06 \mu V$). An Electrode \times Repetition interaction, $F(1, 11) = 4.66, p = .054, \eta_p^2 = .30$, suggested that the decrease in the LPC amplitude with target repetition was different across electrodes. Post hoc analyses indicated that the effect of Target Repetition was present at Pz and Cz, but not at Fz. As can be seen in Figure 4C, LPC at Pz (the electrode where its amplitude was largest) in the first repetition was greater than the other repetitions, as confirmed by SNK post hoc tests, replicating the CDA pattern. Neither the Electrode \times Task Type interaction, $F(2, 22) = 2.27, p = .15, \eta_p^2 = .17$, nor the Task Type \times Repetition interaction, $F(1, 11) = 2.23, p = .16, \eta_p^2 = .17$, nor the three-way Electrode \times Task Type \times Repetition interaction, $F(1, 11) = 0.30, p = .59, \eta_p^2 = .03$, was significant.

P170

Figure 4A also shows the time window at which the P170 was calculated. The P170 magnitude did not differ across target repetition, $F(1, 11) = 0.80, p = .390, \eta_p^2 = .07$, nor for task type, $F(1, 11) = 0.50, p = .493, \eta_p^2 = .04$. There was a main effect of Electrode, $F(2, 22) = 3.96, p = .055, \eta_p^2 = .27$. SNK tests revealed that the P170 was greater at Fz ($M = 1.95, SD = 2.56 \mu V$) and Cz ($M = 2.26, SD = 2.79 \mu V$) compared with the Pz ($M = 1.65, SD = 2.65 \mu V$). No interaction was significant ($F_s < 0.61, p_s > .48$).

Discussion

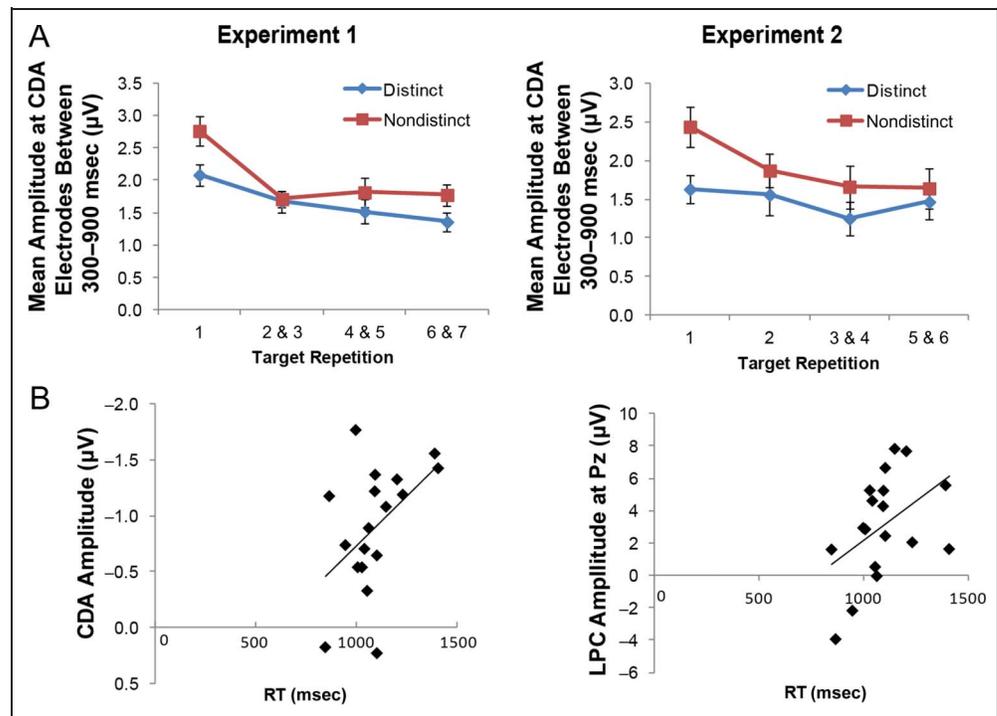
Experiment 1 tested the effects of search difficulty on the processing, maintenance, and learning of attentional templates. As expected, search was efficient in the distinct target task (search slope of zero) and not in the

nondistinct target task (search slope of ± 45 msec per element). ERPs measured to the onset of the cue showed that (1) CDA and LPC amplitudes decreased with target repetition, whereas the P170, P3b and N2pc did not. For both the CDA and the LPC, the rate of decrease was equal in distinct and nondistinct target search tasks. (2) N2pc, P3b, and LPC amplitudes were greater when the anticipated task was more difficult, that is, in the nondistinct compared with the distinct target search task, but not for the CDA nor the FSP. Contrary to our hypothesis, the former finding indicates that the learning rate of attentional templates is independent of the search difficulty; with target repetition, an attentional template is transferred from working memory to long-term memory at the same rate in efficient and effortful search tasks. At a behavioral level, this transfer was accompanied by a reduction in RT, but not by a reduction in search slope. In other words, search efficiency is not affected by whether an attentional template is maintained in long-term memory or in working memory, at least not for the range of up to seven target instances as measured here.

Anticipated task difficulty affected the mean amplitudes of the LPC and N2pc components. The LPC has been suggested to reflect the effort of working memory processing (Polich, 2012; Kok, 2001; Kusak et al., 2000; García-Larrea & Cézanne-Bert, 1998; McEvoy et al., 1998; Ruchkin et al., 1990; Paller et al., 1988; Kramer et al., 1985; Isreal et al., 1980). Therefore, we suggest that the larger LPC before the difficult task shows that maintenance of the attentional template in working memory is performed with a greater effort under difficult search conditions. This effect was not there in the CDA, suggesting that it is not sensitive to task difficulty. Although the CDA and LPC are computed at different electrodes (those at which each is largest), it is not necessarily the case that the difference between CDA and LPC reflects different processing in different brain regions. In fact, when we computed mean amplitude across CDA electrodes (without subtracting contra- and ipsilateral waves, but averaging across all electrodes), both in the LPC time interval and the original time interval of the CDA, we found a similar sensitivity to task difficulty as in the LPC (see Figure 5A). This suggests that it is the lateral nature of the CDA, not its scalp position, that underlies its differences with the LPC. Because the effect of task difficulty on N2pc was not replicated in the next experiment, we will defer its discussion to Experiment 2.

Finally, and contrary to Woodman et al. (2013), here the P170 amplitude did not decline with target repetition. One possibility is that the implicit learning of the various gap directions that the target cue could have was rapidly saturated, leaving little room for the P170 to be affected further by streaks of repetition. Note that we only used four gap directions, and saturation may have been faster than in Woodman et al. (2013), where eight gap directions were used. In Experiment 2, we therefore used eight gap directions.

Figure 5. (A) Mean amplitude at the electrodes at which the CDA was calculated, that is, averaging amplitude at electrodes PO7, PO8, P7, P8, P5, P6, O1, and O2, whether or not they are ipsi- and contralateral to the cue, in the interval between 300 and 900 msec postcue (the CDA interval), across target repetitions in Experiment 1 (left) and in Experiment 2 (right). The error bars represent *SEMs* for normalized data, that is, corrected for between-subject variance (Cousineau, 2005). (B) The relationship between individual participant's behavioral RT and the CDA amplitude (left) and the LPC amplitude (right) in Experiment 2.



Another change we made in Experiment 2 was to take out color in the search displays. Note that, in Experiment 1, the easy and difficult search not only differed in difficulty but also in the use of color to define the target. More specifically, in Experiment 1, the search display in the distinct target task contained one red, one green, and several black items, whereas it contained only target-colored items in the nondistinct target task. Priming, a form of implicit learning, has been suggested to be dependent on not only the features of the target but also on those of the distractors. For example, priming was found to be greater when there is a salient distractor, as in the distinct target task in Experiment 1 of this study, than when there is none (Meeter & Olivers, 2006). Furthermore, the fact that distractors shared the target color in the nondistinct target task might motivate participants to drop the color value of the cue in that task in order not to be guided to distractors. This manipulation of the cue representation could lead to an extra working memory effort that underlies the larger LPC in the nondistinct target task. Consequently, any difference in CDA or LPC across task types and target repetitions could be caused by differences in maintaining the color information rather than by search difficulty.¹ To allay these concerns, in Experiment 2 the search displays contained only black stimuli, and all targets were defined by shape (see Figure 1).

EXPERIMENT 2

Behavior

Figure 2 shows the average search RT for each target repetition and task type. Search RT was lower for the dis-

tinct target task than for the nondistinct target task, $F(1, 17) = 397.68, p < .001, \eta_p^2 = .96$, and lower for set size 6 than for set size 12, $F(1, 17) = 802.45, p < .001, \eta_p^2 = .92$. RTs decreased with increasing target repetition, $F(1, 17) = 3.99, p = .062, \eta_p^2 = .19$. Furthermore, the Task Type \times Set Size interaction was significant, $F(1, 17) = 582.36, p < .001, \eta_p^2 = .97$. Set size had a substantial effect in the nondistinct target condition, whereas it had no effect in the distinct target condition. There was no Set Size \times Repetition interaction, $F(1, 17) = 0.03, p = .85, \eta_p^2 = .01$, nor was the three-way interaction between Set Size, Repetition, and Task Type significant, $F(1, 17) = 0.03, p = .86, \eta_p^2 = .01$. The accuracy pattern (Table 1) followed that of the RTs except there was no effect of Repetition.

Electrophysiology

CDA

Figure 3 shows the CDA waveforms averaged across the electrode pairs used in analyses (P5/6, P7/8, PO7/8, and O1/2). The main effect of Contralaterality was significant, $F(1, 17) = 46.59, p < .001, \eta_p^2 = .73$, indicating that a CDA was triggered by the onset of the cue. This CDA decreased in magnitude with target repetition, as shown by a significant Contralaterality \times Repetition interaction, $F(1, 17) = 6.96, p = .017, \eta_p^2 = .29$. As in Experiment 1, there was no Task Type \times Contralaterality interaction, $F(1, 17) = 0.09, p = .76, \eta_p^2 = .01$, and no Task Type \times Contralaterality \times Repetition interaction, $F(1, 17) = 0.15, p = .904, \eta_p^2 = .01$, suggesting that the CDA was the same for the two task types. The Contralaterality \times Electrode

interaction was significant, $F(3, 51) = 14.34, p < .001, \eta_p^2 = .46$. SNK tests on CDA (contra- minus ipsilateral waves) showed that the CDA at PO7/8 ($M = -1.18, SD = 0.77 \mu V$) and P7/8 ($M = -1.04, SD = 0.49 \mu V$) was greater than at P5/6 ($M = -0.73, SD = 0.65 \mu V$) and O1/2 ($M = -0.53, SD = 0.51 \mu V$).

N2pc

Figure 3 also shows N2pc waveforms. There was a main effect of Contralaterality, $F(1, 17) = 18.22, p = .001, \eta_p^2 = .52$, indicating the existence of a N2pc. The magnitude of the N2pc did not change across target repetitions, as evidenced by the lack of a Contralaterality \times Repetition interaction, $F(1, 17) = 1.90, p = .19, \eta_p^2 = .10$. The N2pc was equal in the two tasks, as shown by the lack of Task Type \times Contralaterality interaction, $F(1, 17) = 0.01, p = .947, \eta_p^2 = .01$. There was a Contralaterality \times Electrode interaction, $F(2, 34) = 7.23, p = .002, \eta_p^2 = .30$. SNK tests on difference waves showed that N2pc amplitude was greater at P7/8 ($M = -0.73, SD = 0.63 \mu V$) and PO7/8 ($M = -0.81, SD = 0.87 \mu V$) than at O1/2 ($M = -0.42, SD = 0.58 \mu V$). There was a four-way interaction of Task Type \times Repetition \times Hemisphere \times Contralaterality, $F(1, 17) = 11.25, p = .004, \eta_p^2 = .39$, which was not further investigated. No other effect or interaction was significant (all $F_s < 1.61, p_s > .17$).

P3b and LPC

Figure 4A, C shows the ERP plots from Fz, Cz, and Pz electrodes for the P3b and LPC time windows and concomitant scalp topography for the LPC. There was a main effect of Electrode on P3b, $F(2, 34) = 34.22, p < .001, \eta_p^2 = .67$. P3b amplitude at Pz ($M = 5.87, SD = 2.64 \mu V$) was greater than at Cz ($M = 2.58, SD = 2.46 \mu V$), and they were both greater than at Fz ($M = 1.11, SD = 2.45 \mu V$). There was no main effect of Task Type on P3b amplitude, $F(1, 17) = 0.19, p = .893, \eta_p^2 = .01$, but a main effect of Repetition, $F(1, 17) = 4.35, p = .052, \eta_p^2 = .20$, and an Electrode \times Repetition interaction, $F(1, 17) = 5.49, p = .032, \eta_p^2 = .24$. Post hoc analyses showed that the effect of repetition was significant at Fz and Cz, but not at Pz. The Task Type \times Electrode interaction was significant, $F(2, 34) = 3.36, p = .047, \eta_p^2 = .16$, but the SNK tests on the difference values between nondistinct and distinct tasks for P3b did not yield any significant differences for none of the electrodes. No other interaction reached significance ($F_s > 0.86, p_s < .67$).

For the LPC, there was a main effect of Electrode, $F(2, 34) = 32.77, p < .001, \eta_p^2 = .66$. Positivity at Pz ($M = 4.08, SD = 3.32 \mu V$) was greater than Cz ($M = 1.91, SD = 3.32 \mu V$), and they were both greater than Fz ($M = 0.02, SD = 2.27 \mu V$). There was a main effect of Target Repetition, $F(1, 17) = 27.89, p < .001, \eta_p^2 = .62$; the LPC amplitude decreased across repetitions. There was a Marginal Electrode \times Repetition interaction, $F(1, 23) =$

$3.23, p = .090, \eta_p^2 = .16$, suggesting that the decrease in the LPC amplitude with target repetition was different across electrodes. Post hoc analyses indicated that the effect of Target Repetition was nonetheless present at each electrode. Neither the main effect of Task Type was significant, $F(1, 17) = 3.02, p = .100, \eta_p^2 = .15$, nor the Electrode \times Task Type interaction, $F(2, 34) = 1.44, p = .250, \eta_p^2 = .08$, suggesting that LPC amplitude, at all electrodes, was equal in the distinct and nondistinct target search tasks. However, there was a significant Task Type \times Repetition interaction, $F(1, 17) = 7.75, p = .013, \eta_p^2 = .31$. As can be seen in Figure 4B, the LPC difference between Distinct and Nondistinct Target Tasks was present at the first repetition but not in further repetitions, as confirmed by SNK tests on the LPC difference between nondistinct and distinct tasks across repetitions. The Electrode \times Task Type \times Repetition interaction was not significant, $F(1, 17) = 0.76, p = .396, \eta_p^2 = .04$.

P170

Figure 4A shows waveforms at which the P170 was calculated. There was no effect of electrode, $F(2, 34) = 1.25, p = .299, \eta_p^2 = .07$. There was a main effect of Task Type, $F(1, 17) = 17.68, p = .001, \eta_p^2 = .51$. As seen in Figure 4B, the P170 amplitude was greater in the distinct target task relative to nondistinct target task. There was again no effect of Repetition, $F(1, 17) = 1.96, p = .180, \eta_p^2 = .10$. However, there was a significant Electrode \times Repetition interaction, $F(1, 17) = 4.38, p = .052, \eta_p^2 = .21$. Post hoc tests showed that P170 decreased with repetition at Fz, but not at Cz and Pz. Neither the Task Type \times Repetition interaction nor the Electrode \times Task Type \times Repetition interaction was significant, $F(1, 17) = 0.51, p = .485, \eta_p^2 = .03$ and $F(1, 17) = 0.74, p = .403, \eta_p^2 = .04$, respectively.

Correlations between Measures of Behavior and ERPs

For both experiments, we investigated whether the ERP measures of working memory correlated with behavioral responses. We partialled out the CDA in LPC-behavioral correlations and vice versa. In Experiment 2, as seen in Figure 5B, individual mean LPC and mean CDA amplitude were positively correlated with overall RT, with partial correlations of, respectively, $r(15) = .454, p = .067$ (bivariate: $r = .415$), and $r(15) = .505, p = .039$ (bivariate: $r = .474$); participants with smaller CDAs or LPCs were faster in their responses. These correlations were not significant in Experiment 1, probably because of the smaller set size. Note that both the RT and ERP values were calculated from trials with correct behavioral responses only.

Discussion

The results of Experiment 2 largely replicated those of Experiment 1. Search was fast and more efficient (search

slope of zero) in the distinct target task and slower and effortful (search slope of ± 100 msec) in the nondistinct target task. Again, RT decreased with target repetitions, but the search efficiency did not. For ERPs, both the CDA and the LPC decreased with target repetitions, the former to an equal extent for both search types. And again, the LPC, but not the CDA, was sensitive to search difficulty, albeit this time only on the first target instance. Moreover, the overall CDA and LPC amplitudes were positively correlated with search RT. This finding is consistent with the theories of learning and automaticity (Logan, 1988) and suggests participants who rely less on the working memory (and presumably more on long-term memory) perform faster on a visual search task (Carlisle et al., 2011).

In contrast to Experiment 1, the P170 now decreased with repetition, suggesting that the number of cue alternatives (here gap directions) indeed plays a role. The main effect of repetition on P170 seems to be mainly driven by nondistinct target condition, although it was not strong enough to yield a significant Task Type \times Repetition interaction.

The N2pc results were not consistent with Experiment 1, as this time its amplitude was not sensitive to anticipated search difficulty. Given the lack of a replication of the N2pc sensitivity to search difficulty in Experiment 1 (which we also repeatedly failed to find in other, nonpublished experiments), we suspect that the N2pc effect in Experiment 1 was a false positive. Alternatively, stimulus complexity might have played a role, as the more complex stimuli of Experiment 2 might have required a strong attentional selection regardless of search difficulty.

GENERAL DISCUSSION

In two experiments, we investigated the effects of search task difficulty on selection, maintenance, and learning of the attentional template. Through our set size manipulation, we confirmed that search was efficient (i.e., search slope was zero) in a distinct target condition modeled after Carlisle et al. (2011), whereas it was much more effortful (resulting in a steeper search slope) in a nondistinct target condition. As predicted, we observed ERP components related to working memory maintenance in the delay period, at electrodes typically reported in the literature: the CDA, maximal at parietal-occipital electrodes (McCollough et al., 2007; Vogel & Machizawa, 2004), and the LPC, maximal at central-parietal regions, that is, Cz and Pz (Polich, 2012; Ruchkin et al., 1990). The most important findings are as follows:

1. The CDA decreased with target repetition, suggesting that the attentional template was learned after repeated search for the same target (Carlisle et al., 2011). Importantly, search difficulty did not affect the rate of decrease of the CDA. This goes against our hypothesis that more effortful search would require a working memory tem-

plate in a longer sequence of trials than would efficient search for distinct targets. The rate of learning an attentional template is independent of the search difficulty.

2. Another index of working memory maintenance, the LPC, also decreased with target repetition, providing additional support for the idea that, with target repetition, the template is learned.
3. The LPC, but not the CDA, was sensitive to anticipated search difficulty, as its amplitude was greater before the nondistinct target task relative to distinct target task. In the light of the literature suggesting that the LPC amplitude reflects the effort invested in working memory processing (Polich, 2012; Kok, 2001; Kusak et al., 2000; García-Larrea & Cézanne-Bert, 1998; McEvoy et al., 1998; Ruchkin et al., 1990; Paller et al., 1988; Kramer et al., 1985; Isreal et al., 1980), this result indicates that anticipating a difficult search results in a greater working memory effort in maintaining an attentional template.

We thus extend the Carlisle et al. (2011) findings by showing that the CDA decreases with target repetition at the same rate when effortful search is required and when participants can rely on efficient search with distinct targets. This finding indicates that the rate of learning an attentional template is independent of the search difficulty. The correlations between both LPC and CDA amplitudes and RT suggests that responses are faster (regardless of accuracy) for participants who perform a handoff of the template to long-term memory faster or to a greater extent.

Furthermore, we show that maintaining an attentional template in working memory is performed with a greater effort when a more difficult search task is anticipated. This effect was mainly evident on the first encounter for a particular cue, as revealed by greater LPC amplitude in the first repetition. Moreover, the LPC findings refute the idea that the decrease in the CDA merely reflects a reduction of lateralization—that is, a shift from lateralized to central memory representations rather than a decrease in maintenance of or effort invested in working memory representations. Because the LPC is measured at midline electrodes, a decrease in lateralization should not affect it. Yet, a decrease in LPC amplitude with repetition was observed, just like for the CDA.

The P3b has been suggested to be sensitive to the level of arousal (Kok, 2001), which may carry over into the LPC. Thus, the sensitivity of the LPC to anticipated task difficulty might be because of greater overall arousal levels. Another marker of arousal is an increased contingent negative variation (CNV) component (e.g., Tecce, 1972). Greater arousal would be evident as stronger negativity just before the onset of the search display. Although we did see a negative-going component, possibly a CNV, before the search display, this was not larger for nondistinct target task. Furthermore, considering that the task difficulty was constant throughout the blocks rather than

being determined by the presentation of the cue, we suggest it is not likely that a general arousal level would be time-locked to the onset of the cue. Thus, we suggest that the LPC effect in this study did not reflect differences in the general arousal level, but rather, the amount of effort deployed for maintenance of the attentional template in working memory.

Note that the CDA and the LPC have overlapping scalp distributions and time windows of measurement, but one is a lateralized component whereas the other is not. Computing nonlateralized activity at CDA electrodes in the CDA time window (and in the LPC time window), we observed a bilateral activity that is sensitive to search difficulty. One explanation would be that the LPC reflects the activity of a general frontoparietal network involved in attention and working memory functioning (Polich, 2007, 2012), and because this overall working memory activity may be common to both hemispheres, it could be subtracted out in the computation of a lateral component such as the CDA. This claim is consistent with our interpretation of the two components; the CDA being a marker for the number of maintained visual working memory representations, whereas the LPC being a marker of the amount of effort invested to maintain these representations.

Finally, although the decrease in the CDA and the LPC suggest diminished working memory maintenance and effort, respectively, the evidence for a transfer to more implicit memories is rather mixed. Woodman et al. (2013) have recently proposed that a decline in the P170 amplitude provides evidence for transfer to long-term memory on the basis of a study on priming by Voss et al. (2010). We failed to find such a decline in Experiment 1 but did find it in Experiment 2. One explanation might be in the number of alternative targets (i.e., gap directions). Because the number of target alternatives was larger in Experiment 2 than it was in Experiment 1, a quick saturation of learning may have occurred in Experiment 1, whereas learning in Experiment 2 might have been more gradual, leading to a P170 decline. However, the decrease in CDA and LPC amplitude with repetition would argue against such a lack of learning in Experiment 1. Therefore, we suggest another explanation for the inconsistent P170 results. What has been referred to as the P170 by Woodman et al. (2013) and Voss et al. (2010) bears close resemblance to what has been called the FSP (frontal selection positivity) or also anterior P2(a) in previous work on selective attention (Potts, 2004; Baas, Kenemans, & Mangun, 2002; Potts & Tucker, 2001; Kenemans et al., 1993). In those studies, the FSP has been shown to be responsive to the selection of task-relevant visual features, rather than their maintenance. If the FSP and P170 are two labels for the same component, then the decrease in P170 amplitude might be an outcome of the feature selection becoming easier or less relevant when the target is already stored in long-term memory. Note that with the increase in gap number in Experiment 2, the size of the gaps also became smaller (from 68° to 22°, the latter being equal to Woodman

et al., 2013). This might have made the task-relevant feature initially harder to select than in Experiment 1, but at the same time created more room for the FSP/P170 to decline with repetition, as selection became easier. In short, in the light of the literature and results of this study, we suggest that the decrease of the P170 across target repetition is because of a decline in the frequency or effort of selecting the task-relevant feature. Therefore, it is not indexing long-term memory consolidation, but rather it is a consequence of such a consolidation.

Conclusion

With repeated targets, participants relied progressively less on a target template stored in working memory, as indicated by a decrease of CDA and LPC amplitudes. Importantly, this shift was independent of whether search was efficient or effortful. However, the anticipation of effortful, as opposed to efficient search, did result in increased working memory effort for maintaining the template in working memory, as reflected by a larger LPC. Our results suggest that the functional importance of attentional templates does not affect their rate of long-term memory learning, but only the amount of working memory effort for their maintenance.

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Note

1. We thank Nancy Carlisle for raising this alternative explanation.

REFERENCES

- Baas, J., Kenemans, J. L., & Mangun, G. R. (2002). Selective attention to spatial frequency: An ERP and source localization analysis. *Clinical Neurophysiology*, *113*, 1840.
- Bundesen, C., Habekost, T., & Kyllingsbæk, S. (2005). A neural theory of visual attention: Bridging cognition and neurophysiology. *Psychological Review*, *112*, 291–328.
- Carlisle, N. B., Arita, J. T., Pardo, D., & Woodman, G. F. (2011). Attentional templates in visual working memory. *Journal of Neuroscience*, *31*, 9315–9322.
- Chelazzi, L., Duncan, J., Miller, E. K., & Desimone, R. (1998). Responses of neurons in inferior temporal cortex during memory-guided visual search. *Journal of Neurophysiology*, *80*, 2918–2940.
- Chelazzi, L., Miller, E. K., Duncan, J., & Desimone, R. (1993). A neural basis for visual search in inferior temporal cortex. *Nature*, *363*, 345–347.

- Cousineau, D. (2005). Confidence intervals in within-subject designs: A simpler solution to Loftus and Masson's method. *Tutorials in Quantitative Methods for Psychology*, *1*, 42–45.
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*, 9–21.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*, 193–222.
- Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review*, *96*, 433.
- Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalography and Clinical Neurophysiology*, *99*, 225–234.
- García-Larrea, L., & Cézanne-Bert, G. (1998). P3, positive slow wave and working memory load: A study on the functional correlates of slow wave activity. *Electroencephalography and Clinical Neurophysiology*, *108*, 260–273.
- Hickey, C., Di Lollo, V., & McDonald, J. J. (2009). Electrophysiological indices of target and distractor processing in visual search. *Journal of Cognitive Neuroscience*, *21*, 760–775.
- Ikkai, A., McCollough, A. W., & Vogel, E. K. (2010). Contralateral delay activity provides a neural measure of the number of representations in visual working memory. *Journal of Neurophysiology*, *103*, 1963–1968.
- Isreal, J. B., Chesney, G. L., Wickens, C. D., & Donchin, E. (1980). P300 and tracking difficulty: Evidence for multiple resources in dual-task performance. *Psychophysiology*, *17*, 259–273.
- Jennings, J. R., & Wood, C. C. (1976). The e-adjustment procedure for repeated-measures analyses of variance. *Psychophysiology*, *13*, 277–278.
- Kenemans, J., Kok, A., & Smulders, F. T. Y. (1993). Event-related potentials to conjunctions of spatial frequency and orientation as a function of stimulus parameters and response requirements. *Electroencephalography and Clinical Neurophysiology*, *88*, 51–63.
- Klaver, P., Talsma, D., Wijers, A. A., Heinze, H. J., & Mulder, G. (1999). An event-related brain potential correlate of visual short-term memory. *NeuroReport*, *10*, 2001.
- Kok, A. (2001). On the utility of P3 amplitude as a measure of processing capacity. *Psychophysiology*, *38*, 557–577.
- Kramer, A. F., Wickens, C. D., & Donchin, E. (1985). Processing of stimulus properties: Evidence for dual-task integrality. *Journal of Experimental Psychology: Human Perception and Performance*, *11*, 393.
- Kusak, G., Grune, K., Hagendorf, H., & Metz, A. M. (2000). Updating of working memory in a running memory task: An event-related potential study. *International Journal of Psychophysiology*, *39*, 51–65.
- Lins, O. G., Picton, T. W., Berg, P., & Scherg, M. (1993a). Ocular artifacts in EEG and event-related potentials I: Scalp topography. *Brain Topography*, *6*, 51–63.
- Lins, O. G., Picton, T. W., Berg, P., & Scherg, M. (1993b). Ocular artifacts in recording EEGs and event-related potentials II: Source dipoles and source components. *Brain Topography*, *6*, 65–78.
- Logan, G. D. (1988). Toward an instance theory of automatization. *Psychological Review*, *95*, 492–527.
- Luck, S. J. (2012). Electrophysiological correlates of the focusing of attention within complex visual scenes: N2pc and related ERP components. In S. J. Luck & E. S. Kappenman (Eds.), *The Oxford handbook of event-related potential components* (pp. 329–360). New York: Oxford University Press.
- Luck, S. J., & Hillyard, S. A. (1994). Spatial filtering during visual search: Evidence from human electrophysiology. *Journal of Experimental Psychology: Human Perception and Performance*, *20*, 1000.
- Makeig, S., Bell, A. J., Jung, T. P., & Sejnowski, T. J. (1996). Independent component analysis of electroencephalographic data. In D. S. Touretzky, M. C. Mozer, & M. E. Hasselmo (Eds.), *Advances in neural information processing systems* (pp. 145–151). Cambridge, MA: MIT Press.
- McCollough, A. W., Machizawa, M. G., & Vogel, E. K. (2007). Electrophysiological measures of maintaining representations in visual working memory. *Cortex*, *43*, 77–94.
- McEvoy, L. K., Smith, M. E., & Gevins, A. (1998). Dynamic cortical networks of verbal and spatial working memory: Effects of memory load and task practice. *Cerebral Cortex*, *8*, 563–574.
- Meeter, M., & Olivers, C. N. L. (2006). Intertrial priming stemming from ambiguity: A new account of priming in visual search. *Visual Cognition*, *13*, 1–28.
- Paller, K. A., McCarthy, G., & Wood, C. C. (1988). ERPs predictive of subsequent recall and recognition performance. *Biological Psychology*, *26*, 269–276.
- Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*, *118*, 2128–2148.
- Polich, J. (2012). Neuropsychology of P300. In S. J. Luck & E. S. Kappenman (Eds.), *Oxford handbook of ERP components* (pp. 159–188). New York: Oxford University Press.
- Potts, G. F. (2004). An ERP index of task relevance evaluation of visual stimuli. *Brain and Cognition*, *56*, 5–13.
- Potts, G. F., & Tucker, D. M. (2001). Frontal evaluation and posterior representation in target detection. *Cognitive Brain Research*, *11*, 147–156.
- Rosenthal, R., & Rosnow, R. (1985). *Contrast analysis: Focused comparisons in the analysis of variance*. Cambridge University Press.
- Ruchkin, D. S., Johnson, R., Canoune, H., & Ritter, W. (1990). Short-term memory storage and retention: An event-related brain potential study. *Electroencephalography and Clinical Neurophysiology*, *76*, 419–439.
- Sawaki, R., & Luck, S. J. (2010). Capture versus suppression of attention by salient singletons: Electrophysiological evidence for an automatic attend-to-me signal. *Attention, Perception and Psychophysics*, *72*, 1455–1470.
- Sutton, S., & Ruchkin, D. S. (2006). The late positive complex. *Annals of the New York Academy of Sciences*, *425*, 1–23.
- Tecce, J. J. (1972). Contingent negative variation (CNV) and psychophysical processes in man. *Psychological Bulletin*, *77*, 73.
- Theeuwes, J. (1991). Cross-dimensional perceptual selectivity. *Attention, Perception and Psychophysics*, *50*, 184–193.
- Theeuwes, J. (1992). Perceptual selectivity for color and form. *Perception & Psychophysics*, *51*, 599–606.
- Treisman, A., & Souther, J. (1985). Search asymmetry: A diagnostic for preattentive processing of separable features. *Journal of Experimental Psychology: General*, *114*, 285.
- Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature*, *428*, 748–751.
- Voss, J. L., Schendan, H. E., & Paller, K. A. (2010). Finding meaning in novel geometric shapes influences electrophysiological correlates of repetition and dissociates perceptual and conceptual priming. *NeuroImage*, *49*, 2879–2889.
- Wolfe, J. M., Cave, K. R., & Franzel, S. L. (1989). Guided search: An alternative to the feature integration model for visual search. *Journal of Experimental Psychology: Human Perception and Performance*, *15*, 419–433.
- Woodman, G. F., & Arita, J. T. (2011). Direct electrophysiological measurement of attentional templates in visual working memory. *Psychological Science*, *22*, 212–215.
- Woodman, G. F., Carlisle, N. B., & Reinhart, R. M. (2013). Where do we store the memory representations that guide attention? *Journal of Vision*, *13*, 1–7.
- Woodman, G. F., & Luck, S. J. (2003). Serial deployment of attention during visual search. *Journal of Experimental Psychology: Human Perception and Performance*, *29*, 121.