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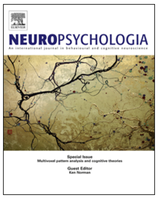

Is a search template an ordinary working memory? Comparing electrophysiological markers of working memory maintenance for visual search and recognition

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ABSTRACT

Visual search requires the maintenance of a search template in visual working memory in order to guide attention towards the target. This raises the question whether a search template is essentially the same as a visual working memory representation used in tasks that do not require attentional guidance, or whether it is a qualitatively different representation. Two experiments tested this by comparing electrophysiological markers of visual working memory maintenance between simple recognition and search tasks. For both experiments, responses were less rapid and less accurate in search task than in simple recognition. Nevertheless, the contralateral delay activity (CDA), an index of quantity and quality of visual working memory representations, was equal across tasks. On the other hand, the late positive complex (LPC), which is sensitive to the effort invested in visual working memory maintenance, was greater for the search task than the recognition task. Additionally, when the same target cue was repeated across trials (Experiment 2), the amplitude of visual working memory markers (both CDA and LPC) decreased, demonstrating learning of the target at an equal rate for both tasks. Our results suggest that a search template is qualitatively the same as a representation used for simple recognition, but greater effort is invested in its maintenance.

1. Introduction

A large part of everyday life is spent searching for visual objects that are relevant to our current goals, for example, when we are looking for a pen to write with, or the ripest fruit in the bowl. Visual search requires a memory representation of the target object, referred to as the search template (or the attentional template, Desimone & Duncan, 1995; Duncan & Humphreys, 1989). Specifically, search templates have been suggested to be maintained in visual working memory (VWM; Desimone & Duncan, 1995). Evidence for this claim comes from electrophysiological and neurophysiological studies on humans and monkeys. In these studies, a cue indicated the target object to search for in a subsequent search display. There was a brief blank interval between the cue and the search displays. During this interval, single-cell recordings in monkeys demonstrated sustained elevated firing in inferior temporal cortex, a high-level visual processing area (Chelazzi, Duncan, Miller, & Desimone, 1998; Chelazzi, Miller, Duncan, & Desimone, 1993). In humans, electroencephalogram (EEG) recordings have demonstrated the presence of the contralateral delay activity (CDA) during a similar interval (Carlisle, Arita, Pardo, & Woodman, 2011; Gunseli, Olivers, & Meeter, 2014; Reinhart, Carlisle, & Woodman, 2014; Woodman & Arita, 2011), which has been suggested to be an index of VWM maintenance (Klaver, Talsma, Wijers, Heinze, & Mulder, 1999; McCollough, Machizawa, & Vogel, 2007; Vogel & Machizawa, 2004).

There is thus accumulating evidence demonstrating that search templates are maintained in VWM. However, it is unclear whether the neural activity required for maintaining a search template differs than a representation maintained for simple recognition. In visual search, the search template serves to guide attention to the right object in a visual scene containing competing information, and serves to aid in selecting the target over distractors (Rao, Zelinsky, Hayhoe, & Ballard, 2002). These processes are not needed in simple VWM recognition tasks, as participants need typically only to compare the single probe object to the VWM representation of the previously presented cue (especially when memory load is one, Hyun, Woodman, Vogel, Hollingworth, & Luck, 2009; Rensink, 2002). We hypothesized that the additional functions of a search template may entail differences in the neural activity required for its maintenance. To test this hypothesis, we compared visual search to a simple recognition task, and measured event-related potential (ERP) components that provide an electrophysiological index of VWM maintenance of the cue representation.

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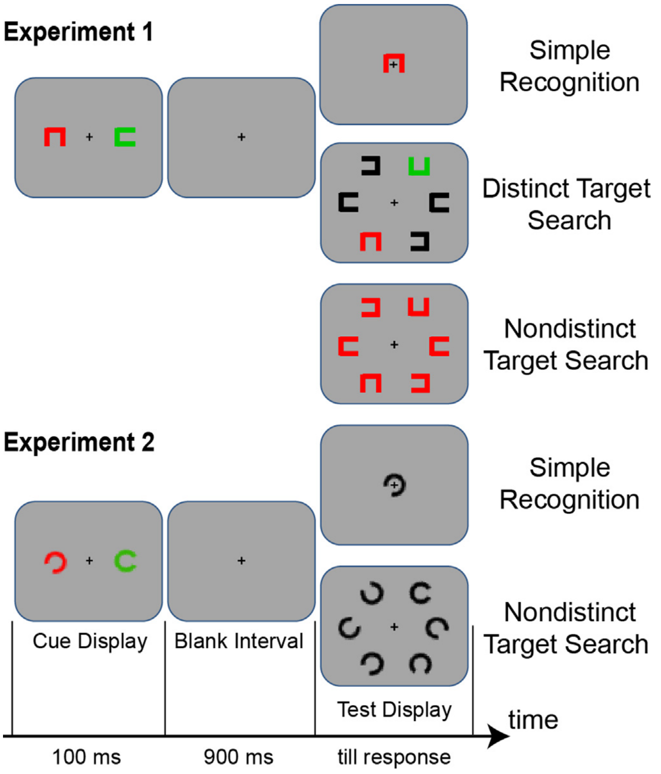

Fig. 1. Experimental procedure. The search target was defined by color (red in this example). The cue display contained two Landolt Cs; the target and a hemispherically balancing non-target, that were differentiated by their color. In the test display of the simple recognition task, there was a single Landolt C at the center. In distinct target search task, the test display had a single Landolt C with the target color, leading to an efficient search. In the nondistinct target search task, the colors of the Landolt Cs were all the same leading to an effortful search. In all test displays the correct response is "present" since they contain the target. Note that, for illustrative purposes, the sizes and colors of Landolt Cs, and the set size of the search tasks are different than the real experiments. In the real experiments set size was nine. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Fig. 1 illustrates the tasks used in the present experiments. Each trial started with the presentation of a cue display, to which the ERPs were measured. After a blank retention interval, the test display was presented. In Experiment 1, we compared a difficult search task, an easier search task, and a simple recognition task. In the search tasks the target had to be found among distractors. This either had to be done on the basis of form, which was inefficient (Gunseli et al., 2014), or on the basis of color, which made the search easy and efficient (Duncan & Humphreys, 1989; Theeuwes, 1991, 1992; Treisman & Souther, 1985). In the third, 'simple recognition' task, the display contained only a single Landolt C at the center of the screen that had to be compared to the cue. Thus, there was no need for search in this task.

We focused on two ERP components that have been found to reflect neural activity involved in VWM maintenance. The first component, the CDA, is a well-studied component of VWM maintenance. Its amplitude was observed to be greater for bigger memory set sizes (Vogel & Machizawa, 2004), and for maintaining representations that are more complex (Luria, Sessa, Gotler, Jolicœur, & Dell'Acqua, 2010; Luria & Vogel, 2011; Woodman & Vogel, 2008) or more precise (Machizawa, Goh, & Driver, 2012). These results suggest that the CDA is sensitive to both the quantity and the quality of VWM representations. Moreover, the CDA appears to be sensitive to the amount of attention that is required for the task at hand, as an ongoing multiple object tracking task has been observed to generate a larger CDA than a simple recognition task (Drew, Horowitz, Wolfe, & Vogel, 2011). It can be argued though that this study compared a memory to an attention task, rather than two memory tasks (as was also suggested by different scalp distributions, Dell'Acqua, Sessa, Toffanin, Luria, & Jolicœur, 2010). In the present study, we compared different memory tasks: There was always a single object to maintain and the task requirements differed only after the retention interval during which CDA was measured. To our knowledge, no study has investigated whether maintaining the same object, but with a different function in the upcoming task, leads to differences in the quality of a VWM representation, as indexed by the CDA.

The second ERP component of interest was the late positive complex (LPC). This sustained positive component at central-parietal electrode sites has been also referred to as the *positive slow wave*. In some studies a *sustained P3b* also comprised the LPC (Kok, 2001), but other studies have provided clear evidence for a distinction between a phasic P3b response and a later sustained LPC response (Kok, van de Vijver, & Bouma, 1985; Kusak, Grune, Hagendorf, & Metz, 2000; Ruchkin & Sutton, 1983; Sutton & Ruchkin, 2006). We too have previously dissociated the P3b and LPC, as we found the latter, but not the former, to be sensitive to the difficulty of the upcoming search task (Gunseli et al., 2014). The LPC has been found to be sensitive to memory load (García-Larrea & Cézanne-Bert, 1998; Kusak et al., 2000; Ruchkin, Johnson, Canoune, & Ritter, 1990), and also to the amount of WM processing (Kok, 2001; Polich, 2012). Consistent with this, it is smaller for maintaining new items in addition to an already high existing WM load (McEvoy, Smith, & Gevins, 1998). Similarly, in dual-task paradigms, performance on the primary task is negatively correlated with LPC amplitude for the secondary task (Isreal, Chesney, Wickens, & Donchin, 1980; Kramer, Wickens, & Donchin, 1985; Paller, McCarthy, & Wood, 1988). In the light of these studies, we analyzed the LPC separately from the P3b, and used the LPC as an index of the effort invested in maintaining a VWM representation.

We reasoned that a CDA difference between search and simple recognition tasks would indicate that search templates are stored in a qualitatively different way than VWM representations that are not used for attentional guidance. On the other hand, if the CDA differs also between search tasks, then this effect might be due to differences in task difficulty rather than task type (i.e. search vs. recognition). Moreover, if more effort is invested for maintaining a search template than for a representation used for a simple recognition task, the LPC amplitude should be greater in search tasks. Also, the functional role of search templates could result in the activation of different brain regions for their maintenance relative to other VWM representations (see Drew et al., 2011). In that case, the scalp distribution of the CDA and/or the LPC could be different across task types. In addition, in Experiment 2, we compared the rate of learning of representations across search and simple recognition tasks. The decrease in CDA and LPC amplitudes across repetitions of the same target in a visual search task has been taken as evidence for learning of search templates, i.e. the handoff of target representations from VWM presumably to long-term memory (Carlisle et al., 2011; Gunseli et al., 2014; Reinhart et al., 2014; Reinhart & Woodman, 2013). This learning has also been observed for VWM representations that are used for a simple recognition task (Reinhart & Woodman, 2013, Experiment 3). In the present study, we compared to learning rate between visual search and recognition tasks in order to investigate whether repeatedly searching for the same target would lead to a different rate of learning than repeatedly maintaining a representation for simple recognition.

2. Materials and methods

2.1. Participants

Thirty-eight healthy volunteers participated in the experiments for course credit or monetary compensation, 21 in Experiment 1 and 17 in Experiment 2. Six participants in total were excluded; four due to excessive noise in their EEG recordings (see Section 3), two to some electrodes having no signal during the recording, leaving 16 participants for each experiment (age 18–30 years, 10 female, for Experiment 1; and age 19–29 years, 10 female, for Experiment 2) of whom the data was analyzed. 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.

2.2. Stimuli

Viewing distance was 75 cm. Fig. 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). A trial started with a cue array, consisting of a cue and a visually balancing non-cue, presented 1.17° to the left and right of fixation. In Experiment 1, they were both Landolt squares (0.7° × 0.7°, 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), the other in green (47.64 Cd/m^2). Target cue color was fixed for half a session (see Section 2.3). In Experiment 2 they were Landolt Cs, i.e. 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. Experiment 2 involved a larger stimulus set so that learning could be better studied. Visual search arrays consisted of nine Landolt Squares in Experiment 1, and Landolt Cs in Experiment 2, presented equidistantly on an imaginary circle with a radius of 3.0°. For the sake of simplicity, further in the text, all stimuli will be referred to as Landolt Cs. In Experiment 1, in the *distinct target (easy) search task* there was one red and one green Landolt C and the rest was black, and the target shape could only appear in the target color, while in the *nondistinct target (difficult) search task* Landolt Cs were all in the same color as the cue, i.e. either red or green. In the *simple recognition task* there was only a single Landolt C presented at the center of the screen, which had the same color as the cue. In Experiment 2, the Landolt Cs in the test display were black regardless of the task type.

2.3. Design and procedure

Each trial began with the fixation cross for a randomly jittered duration of 800–1200 ms in Experiment 1, and 1200–1600 ms in Experiment 2. Next, the target cue and the non-target item were presented for 100 ms. The target color was switched from red to green or vice versa at the half of the experiment (the order counterbalanced across participants). During the retention interval of 900 ms only the fixation cross was presented. Then the test display was presented until response. Auditory feedback on accuracy was provided. The inter-trial interval was jittered between 1200 and 1600 ms. In Experiment 2, during the inter-trial 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) and Gunseli et al. (2014). The whole inter-trial interval in Experiment 1, and its last 100 ms in Experiment 2, consisted of the fixation cross. The task was to maintain fixation until the test display was presented and then to indicate, as fast as possible without risking accuracy, whether the target was present or absent. Participants were informed that, at the test display of the distinct target search task, only the Landolt C with the target color could have the target gap.

Experiment 1 employed a factorial design with three task types (simple recognition; distinct target search; nondistinct target search), × 2 target presence (present; absent), Experiment 2 with 2 task types (simple recognition; nondistinct target search), × 3 target repetitions (1, 4, or 5 trials), × 2 target presence (present; absent). Target presence varied equally and randomly across trials for each block. In Experiment 1, the gap direction of the cue was randomly selected in each trial. In Experiment 2, where the gap directions were sometimes repeated across trials, 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.

At the beginning of each experiment, there was an initial practice block of 5 trials per task type (15 trials in Experiment 1 and 10 trials in Experiment 2). If accuracy was below 75%, participants completed another practice block (Experiment 1: 1.22 blocks on average, with a maximum of 2 blocks; Experiment 2: 1.35 blocks on average, with a maximum of 3 blocks). Furthermore, before each block, there were 5 practice trials to get used to the particular task type and target color (no particular accuracy requirement this time). There were 12 blocks of 56 experimental trials in Experiment 1, and 20 blocks of 44 experimental trials in Experiment 2, with a short break between blocks in which participants were shown their cumulative average accuracy and response times.

3. Data analyses

Where necessary, *p*-values were adjusted based on the Greenhouse–Geisser epsilon correction on degrees of freedom for sphericity violations (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). The RT analyses and all ERP analyses included trials with correct behavioral responses only.

3.1. Behavioral analyses

Data were trimmed in two steps. First, trials with a search response faster than 150 ms and slower than 8000 ms were rejected ($<0.1\%$ of all trials for both Experiment 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 2.3% of all trials in Experiment 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 (for both experiments) and target repetition (for Experiment 2 only).

3.2. ERP recording and analysis

The electroencephalogram (EEG) and electro-oculogram (EOG) were recorded from 70 sintered—AG/AgCl electrodes positioned at 64 standard International 10/20 System sites and 6 external locations mentioned below, using the Biosemi ActiveTwo system (Biosemi, Amsterdam, the Netherlands). 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 (Lopez-Calderon & Luck, 2014).

All ERPs were computed with respect to a 200 ms pre-stimulus baseline period and were re-referenced offline to the average of left and right mastoids. The data was filtered with an IIR Butterworth filter with a bandpass of 0.01–40 Hz. Trials with incorrect behavioral responses or with ocular artifacts or large voltage shifts were excluded. The artifact detection was performed on the standard methods of our lab (see Gunseli et al., 2014), using the artifact detection functions of the ERPLAB toolbox. 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 rejected 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. Individuals were excluded from analyses if, after all the artifact rejections, the remaining number of trials per bin was lower than 80 trials. This led to the rejection of 1 additional participant in Experiment 1, and the 1 and only rejected participant in Experiment 2. For the participants that were involved in the analyses, on average 13.6%, and 12.7% of all trials were rejected by artifact detection functions mentioned above for Experiments 1 and 2 respectively.

The CDA was calculated as the difference waves between electrode sites contralateral versus ipsilateral to the location of the target cue. Based on previous studies, the CDA was measured at P5/6, P7/8, PO7/8, and O1/2 between 300 and 900 ms after the onset of the cue (McCollough et al., 2007). We entered the CDA data into an ANOVA with the within-subjects factors of hemisphere (right; left), contralaterality with respect to the target cue (ipsilateral; contralateral), electrode pair (mentioned above), task type (simple recognition; distinct target search—for Experiment 2 only; nondistinct target search) and for Experiment 2, target repetition (1; 2 and 3; 4 and 5 trials). As the later repetitions occurred progressively less often, for the analyses they were binned into pairs in order to improve signal-to-noise ratio. Only the effects that involve contralaterality were reported. The LPC was calculated between 475 and 700 ms after the onset of the cue (see Gunseli et al., 2014) and was entered into an ANOVA with the within-subjects factors of electrode site (Fz; Cz; Pz), task type, and target repetition. We have also analyzed the P3b, as the peak around 300 ms following the onset of the cue (Gunseli et al., 2014; Kusak et al., 2000; Ruchkin & Sutton, 1983; Sutton & Ruchkin, 2006), averaged between 330 and 430 ms in Experiment 1, and 275–375 ms in Experiment 2, based on the timing of observed average waveform peaks.

Since the interpretation of the null effect of task type on the CDA was critical to our conclusion that a search template is not different from a VWM representation used for simple recognition task, as a post-hoc approach, we calculated Bayes Factors for repeated measures ANOVA, in order to quantify the likelihood of the null hypothesis over the alternative hypothesis, in which r was set a priori to 1.0 (Rouder, Speckman, Sun, Morey, & Iverson, 2009).

4. Experiment 1. Maintenance of VWM representations across search and recognition tasks

4.1. Results

4.1.1. Behavior

Fig. 2 shows the average search RT and error rate for each task type. The main effect of task type on RT was significant, $F(2,30)=223.33$, $p<0.001$, $\eta_p^2=0.94$. Follow-up SNK tests indicated that RT was lowest in the simple recognition task, higher in the distinct target search task, and highest in the nondistinct target search task. The error rate pattern was similar to that of the RT. The main effect of task type on error rate was significant, $F(2,30)=47.85$, $p<0.001$, $\eta_p^2=0.76$. Follow-up SNK tests showed that participants were more accurate on simple recognition trials and distinct target search trials than on nondistinct target search trials, whereas the former two were no different from each other.

4.1.2. Electrophysiology

Fig. 3 shows the CDA waveforms averaged across the electrode pairs used in analyses (P5/6, P7/8, PO7/8 and O1/2). There was a main effect of contralaterality, $F(1,15)=17.35$, $p=0.001$, $\eta_p^2=0.54$, indicating that a CDA was triggered by the onset of the cue. There was no evidence that the CDA amplitude was different across task types, as the task type × contralaterality interaction was not significant, $F(2,30)=0.74$, $p=0.481$, $\eta_p^2=0.05$. There was a contralaterality × electrode pair interaction, $F(3,45)=5.43$, $p=0.008$, $\eta_p^2=0.27$; follow-up SNK tests on the CDA (contra-minus ipsilateral waves) showed that the CDA amplitude at P7/8 ($M=-0.89$, $SD=0.63$ µV) was greater than the CDA at P5/6 ($M=-0.56$, $SD=0.68$ µV) and at O1/2 ($M=-0.51$, $SD=0.56$ µV), and the CDA at PO7/8 ($M=-0.84$, $SD=0.97$ µV) was greater than the CDA at O1/2 (McCollough et al., 2007). No other interaction involving contralaterality was significant (all $Fs<2.75$, $ps>0.105$). Consistent with the ANOVA, the Bayes Factor analysis indicated that the null hypothesis (no difference in CDA between task types) was 9.9 times more likely to be true than the alternative hypothesis (a CDA difference between task types), JZS Bayes Factor (null \alternative)=9.9 (Rouder et al., 2009).

Fig. 3 also shows the grand average LPC waveforms calculated at Cz and Pz, the electrodes where its amplitude was largest (see below). Overall, the main effect of task type was significant, $F(2,30)=5.72$, $p=0.008$, $\eta_p^2=0.28$. Follow-up SNK tests indicated that, as seen in Fig. 3b, the LPC amplitude in both nondistinct target search task and distinct target search task was greater than in simple recognition task. There was a main effect of electrode, $F(2,30)=11.69$, $p=.001$, $\eta_p^2=0.44$. SNK tests yielded that the LPC at Pz ($M=1.17$, $SD=2.56$ µV) and at Cz ($M=0.27$, $SD=2.43$ µV) were not different than each other and both were greater than at Fz ($M=-1.20$, $SD=2.00$ µV). There was an electrode × task type interaction, $F(4,60)=2.64$, $p=0.069$, $\eta_p^2=0.15$. Separate repeated measures ANOVA tests at each electrode demonstrated that the effect of task type was present at Pz, $F(2,30)=10.39$, $p<0.001$, $\eta_p^2=0.41$, and Cz, $F(2,30)=4.54$, $p=.024$, $\eta_p^2=0.12$, but not at Fz, $F(2,30)=1.90$, $p=0.168$, $\eta_p^2=0.11$ (see Fig. 3d).

There was a main effect of electrode on P3b amplitude, $F(2,30)=28.70$, $p<0.001$, $\eta_p^2=0.65$. There was no significant effect of task type, $F(2,30)=2.17$, $p=0.132$, $\eta_p^2=0.13$. SNK tests yielded that the P3b was greatest at Pz ($M=5.35$, $SD=3.81$ µV), smaller at Cz ($M=3.17$, $SD=3.04$ µV), and smallest at Fz ($M=1.42$, $SD=1.77$ µV). The electrode × task type interaction was significant, $F(4,60)=6.00$, $p=0.003$, $\eta_p^2=0.29$. Separate ANOVAs at each electrode showed that the effect of task type was significant only at Pz, $F(2,30)=4.79$, $p=0.022$, $\eta_p^2=0.24$, but not at Fz or Cz ($Fs<1.72$, $ps>0.19$).

The relationship between an individual's ERP amplitudes and behavioral performance was investigated computing Spearman's rank-order correlations, which is less sensitive to outliers than Pearson's product-moment correlations, since one participant had an RT more than 2.5 SD above the group average. As seen in Fig. 4a, for the simple recognition task, the mean LPC amplitude calculated at Cz and Pz, the electrodes where its amplitude was largest, correlated with mean RT, $r_s(16)=0.574$, $p=0.020$. The other correlations were not significant ($ps>0.202$).

4.2. Discussion

Experiment 1 tested the effects of task type on the maintenance of VWM representations. More specifically, it compared, between a simple recognition task and two search tasks (of different difficulty), the amplitudes and scalp distributions of the CDA and the LPC components for maintaining a VWM representation. The simple recognition task, which did not involve a visual search, was performed more rapidly than both visual search tasks, and the distinct target search task was performed more rapidly and accurately than the nondistinct target search task. These results suggest that, as expected, performance was easiest at the simple recognition task and hardest at the nondistinct search task.

In terms of ERPs, the LPC was greater in both search tasks compared to the simple recognition task. This effect was strongest at the electrodes at which the LPC itself was strongest (Pz and Cz), suggesting that the distribution of the LPC over electrodes did not change, only its amplitude. These results indicate that anticipating a search task, compared to a simple recognition task, leads to greater working memory effort invested in maintaining the task-relevant-VWM-representation. Recently, Gunseli et al. (2014) observed a greater LPC for maintaining a search template when the upcoming search task was more difficult, although in this Experiment 1, the LPCs were statistically indistinguishable between search tasks. Consequently, we propose that the amount of effort invested for maintenance depends on the relative differences in the difficulty that a participant experiences across tasks, rather than reflecting a function-specific difference between search and recognition. Furthermore, for the simple recognition task, participants with smaller LPCs were faster suggesting that

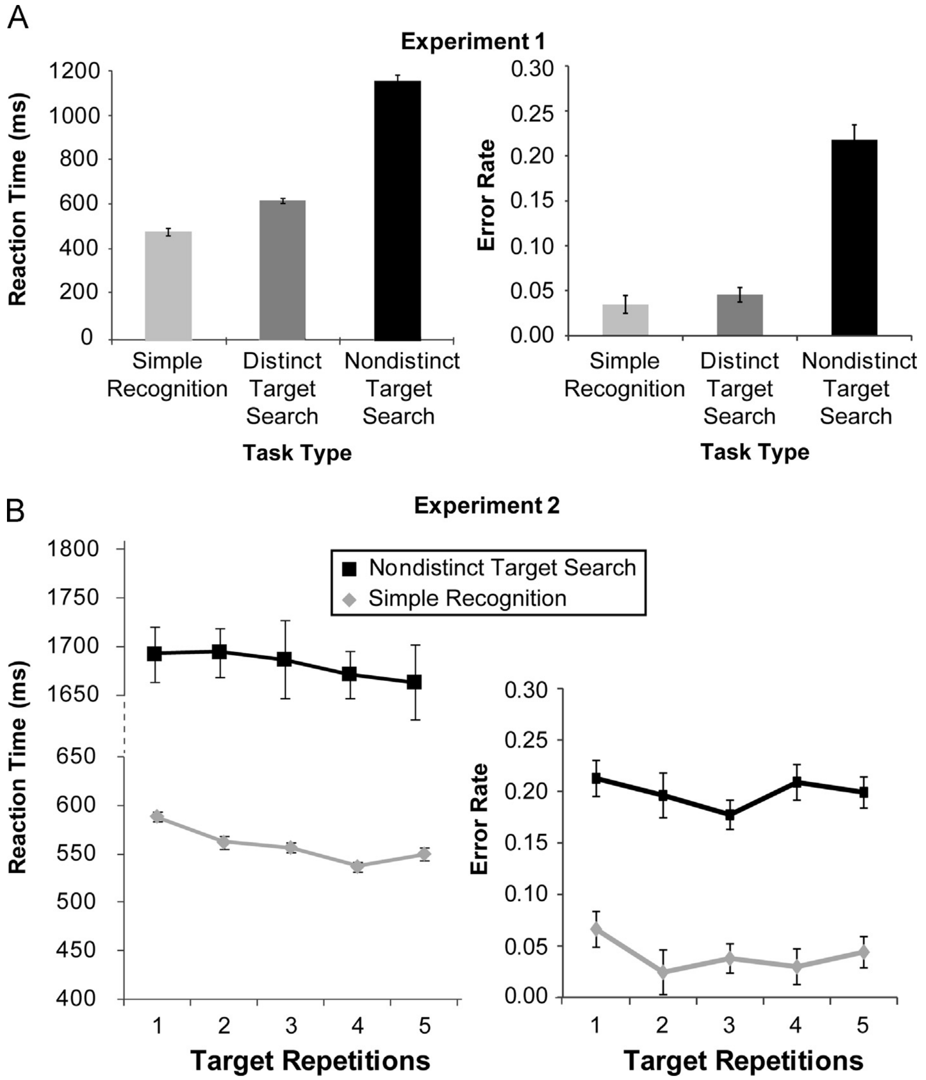

Fig. 2. Behavioral results. Mean reaction time (RT, left panel) and error rate (right panel) in the nondistinct target search task (black), distinct target search task (dark gray), and simple recognition task (light gray) trials for (a) Experiment 1 and (b) Experiment 2, where for the latter, target repetitions are given on the *x*-axis. The error bars represent standard errors of the mean for normalized data, i.e. corrected for between-subjects variance (Cousineau, 2005).

individuals who invest less effort in WM maintenance are able to perform the relevant task faster (Gunseli et al., 2014). The P3b followed a similar pattern to LPC as its amplitude was sensitive to task type, although this effect was significant only at Pz.

Neither the scalp distribution of the CDA nor its amplitude was sensitive to the task type. These results are also in line with Gunseli et al. (2014), who observed equal CDAs for maintaining a VWM representation for search tasks of different difficulty, and extends it further by demonstrating that the CDA amplitude is also independent of whether the representation is used for search or simple recognition. Therefore, we conclude that, in terms of these ERP markers, search templates are qualitatively the same as VWM representations used for recognition, although greater effort is invested for their maintenance. In Experiment 2, we investigated whether differences in the upcoming function (e.g. search vs. no-search) of a representation would affect its rate of learning when it is repeatedly presented across trials.

5. Experiment 2. Learning of VWM representations across search and recognition tasks

Previous research has shown that repeated search for the same target leads to learning—that is, a handoff from VWM to presumably long-term memory, as evidenced by a decrease in CDA amplitude (Carlisle et al., 2011; Gunseli et al., 2014). A similar learning has been observed for representations that are used in a simple recognition task (Reinhart & Woodman, 2013). Experiment 2 tested whether the rate of learning is different between these two tasks that require the representation for different functions. To decrease the likelihood of saturation of learning across trials, in Experiment 2, we increased the cue set size by using Landolt C's with eight possible gap directions rather than four as in Experiment 1. Furthermore, to eliminate possible color-based priming from the test displays to the cue display on the subsequent trial, the test displays contained only black Landolt C's.

5.1. Results

5.1.1. Behavior

Fig. 2b shows the average search RT and error rate for each task type and target repetition in Experiment 2. The main effect of task type on RT was significant, $F(1,15)=201.66$, $p<0.001$, $\eta_p^2=0.93$. RT was lower in simple recognition task, than in the nondistinct target search task. Neither the main effect of repetition, $F(1,15)=3.04$, $p=0.102$, $\eta_p^2=0.17$, nor the task type × repetition interaction was significant, $F(4,60)=0.12$, $p=0.974$, $\eta_p^2=0.01$. The error rate pattern was similar to that of the RT. Participants were more

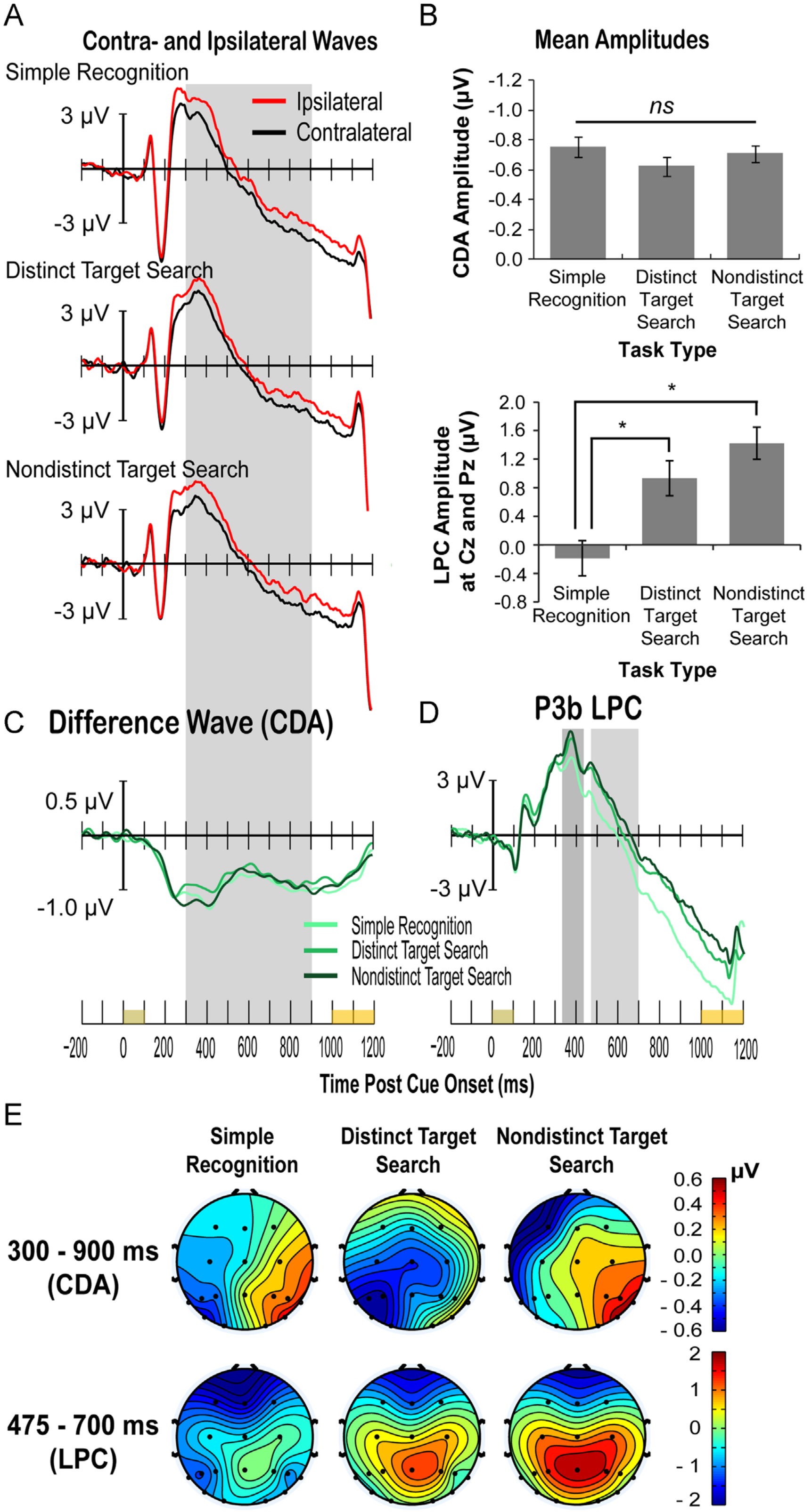

Fig. 3. ERP results from Experiment 1. (a) The grand average waveforms at the average of PO7/8, P7/8, P5/6, and O1/2 electrodes, contralateral (black) and ipsilateral (red) to the location of the cue, plotted separately for each task type. The shadings on the timeline indicate the duration of the cue display (dark yellow) and the search display (light yellow). Note that positive is plotted upwards. (b) Plots of grand average CDA and LPC amplitudes given separately for each task type. The error bars represent standard errors of the mean for normalized data, i.e. corrected for between-subjects variance (Cousineau, 2005). (c) The grand average waveform of CDA across task types that are shown in shades of green. The CDA was computed as contralateral minus ipsilateral difference wave, between 300 and 900 ms (marked with the gray rectangular region), from mean amplitude at PO7/8, P7/8, P5/6, and O1/2 electrodes, and low-pass filtered at 5 Hz for visualization purposes. (d) The grand average waveform of P3b (300–400 ms) and LPC (475–700 ms), averaged across Cz and Pz, the electrodes where the LPC amplitude was largest, given separately across target repetitions shown in shades of blue. (d) The scalp distribution of the CDA (top panel), averaged over 300–900 ms, calculated as the voltage distribution in trials in which the cue was presented on the right subtracted from the ones in which it was presented on the left, and divided by two. And the scalp distribution of the LPC (bottom panel) calculated as the mean voltage distribution across 475–700 ms.

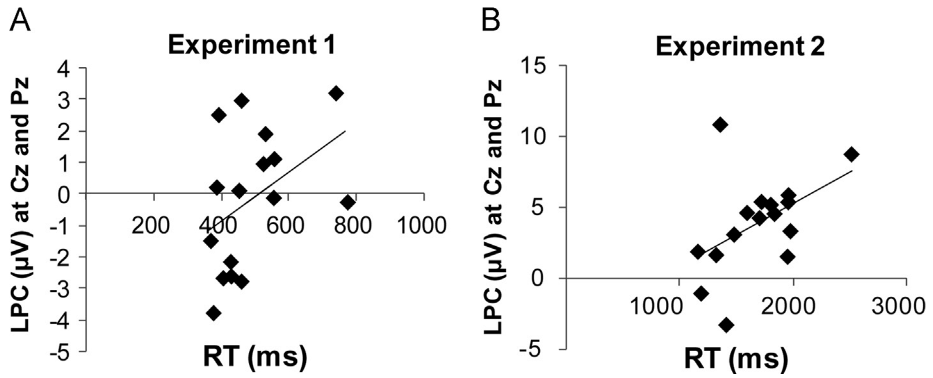

Fig. 4. ERP—behavior correlations. The relationship between individual participant's RT and the LPC amplitude (a) in Experiment 1 for the simple recognition task, and (d) in Experiment 2 for the nondistinct target search task.

accurate on simple recognition trials compared to nondistinct target search trials, $F(1,15)=105.27$, $p<0.001$, $\eta_p^2=0.88$. Neither the main effect of repetition, $F(1,15)=0.88$, $p=0.364$, $\eta_p^2=0.06$, nor the task type × repetition interaction was significant, $F(4,60)=0.86$, $p=0.494$, $\eta_p^2=0.05$.

5.1.2. Electrophysiology

Fig. 5 shows the CDA waveforms averaged across the electrode pairs used in the analyses (P5/6, P7/8, PO7/8 and O1/2). The main effect of contralaterality was significant, $F(1,15)=36.65$, $p<0.001$, $\eta_p^2=0.71$, indicating that a CDA was triggered by the onset of the cue. This CDA decreased in amplitude with target repetition, as indicated by a contralaterality × repetition interaction, $F(1,15)=4.73$, $p=0.046$, $\eta_p^2=0.24$. The CDA amplitude was again not different for both task types, as there was no task type × contralaterality interaction, $F(1,15)=2.50$, $p=0.135$, $\eta_p^2=0.14$. Importantly, no difference was found in the overall rate of decrease of the CDA across task types, as suggested by the lack of a task type × contralaterality × repetition interaction, $F(1,11)=0.22$, $p=0.643$, $\eta_p^2=0.02$. The contralaterality × electrode pair interaction was significant, $F(3,45)=4.31$, $p=0.009$, $\eta_p^2=0.23$. SNK tests on CDA (contra- minus ipsilateral waves) showed that the CDA amplitude at PO7/8 ($M=-0.93$, $SD=0.72$ μV), P7/8 ($M=-0.85$, $SD=0.55$ μV), and P5/6 ($M=-0.78$, $SD=0.48$ μV) were equal and all greater than at O1/2 ($M=-0.61$, $SD=0.51$ μV). No other interaction was significant (all $Fs<2.50$, $ps>0.135$). Consistent with the ANOVA, the Bayes Factor analysis indicated that the null hypothesis (no difference in CDA between task types) was 1.8 times more likely to be true than the alternative hypothesis (a CDA difference between task types), JZS Bayes Factor (null/alternative) = 1.8 (Rouder et al., 2009). For the contralaterality × task type × repetition, the null hypothesis (no difference in the rate of decrease in CDA across task types) was 3.4 times more likely than the alternative hypothesis (a difference in the rate of decrease in CDA across task types), JZS Bayes Factor (null/alternative) = 3.4 (Rouder et al., 2009).

Fig. 5 shows the LPC waves calculated at Cz and Pz. There was a main effect of electrode, $F(2,30)=5.82$, $p=.018$, $\eta_p^2=0.28$. SNK tests yielded that the LPC at Pz ($M=3.30$, $SD=2.87$ μV) and at Cz ($M=2.41$, $SD=3.13$ μV) were not different and were both greater than at Fz ($M=0.91$, $SD=3.09$ μV). There was an effect of target repetition, $F(1,15)=19.87$, $p<0.001$, $\eta_p^2=0.57$. 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, $F(1,15)=9.18$, $p=0.008$, $\eta_p^2=0.38$; the LPC amplitude was greater in nondistinct target task ($M=3.11$, $SD=3.12$ μV) than in simple recognition task ($M=1.30$, $SD=2.49$ μV). No interaction was significant (all $Fs<2.14$, $ps>0.14$).

Fig. 5 also shows the P3b waves calculated at Cz and Pz. There was a main effect of electrode on P3b amplitude, $F(1,15)=6.23$, $p=0.016$, $\eta_p^2=0.29$. SNK tests yielded that P3b at Pz ($M=5.83$, $SD=3.13$ μV) was greater than both at Cz ($M=4.27$, $SD=3.86$ μV) and at Fz ($M=3.43$, $SD=3.38$ μV), which were not significantly different than each other. The P3b was not sensitive to task type, $F(1,15)=0.85$, $p=0.775$, $\eta_p^2=0.01$. The electrode × task type was also not significant, $F(1,15)=0.40$, $p=0.961$, $\eta_p^2=0.01$. There was a main effect of repetition on P3b amplitude, $F(1,15)=4.76$, $p=.045$, $\eta_p^2=0.24$. The P3b amplitude decreased with target repetition. No other interaction was significant (all $Fs<2.44$, $ps>0.14$).

As seen in Fig. 4, and confirmed by Pearson's product–moment correlation, the mean LPC amplitude calculated at Cz and Pz (the electrodes where its amplitude was largest) marginally correlated with mean RT in nondistinct target search task, $r(16)=0.470$, $p=0.066$. No other correlation was significant ($ps>0.194$).

5.2. Discussion

Experiment 2 tested whether learning, as indicated by a decrease in VWM related components, occurs at a different rate for a search template in comparison to a VWM representation maintained for a simple recognition task. The CDA and LPC (and also the P3b) decreased at the same rate for each task, suggesting that the rate of learning, as well as the rate of decrease in the effort of maintenance, are equal for a VWM representation used for a search task and for a simple recognition task. The remaining results were consistent with Experiment 1; (1) responses were faster and more accurate in simple recognition compared to nondistinct target search task, (2) the LPC but not the CDA (nor the P3b), was sensitive to the task type, and (3) participants who invested less effort for maintaining the VWM representations, the 'efficient maintainers', performed faster, though only in the nondistinct search task.

6. General discussion

By investigating two ERP components related to WM maintenance, the present study tested whether maintenance and learning of a VWM representation change as a function of whether this representation is stored to be used for visual search or for simple recognition. The behavioral results of both experiments showed that the search tasks were more effortful (i.e. participants were less rapid and less accurate) than a simple recognition task. In terms of ERPs, for both experiments, the LPC was greater in the search tasks compared to the simple recognition task. However, its scalp distribution did not change. Moreover, neither did the scalp distribution of the CDA nor its amplitude change across tasks,

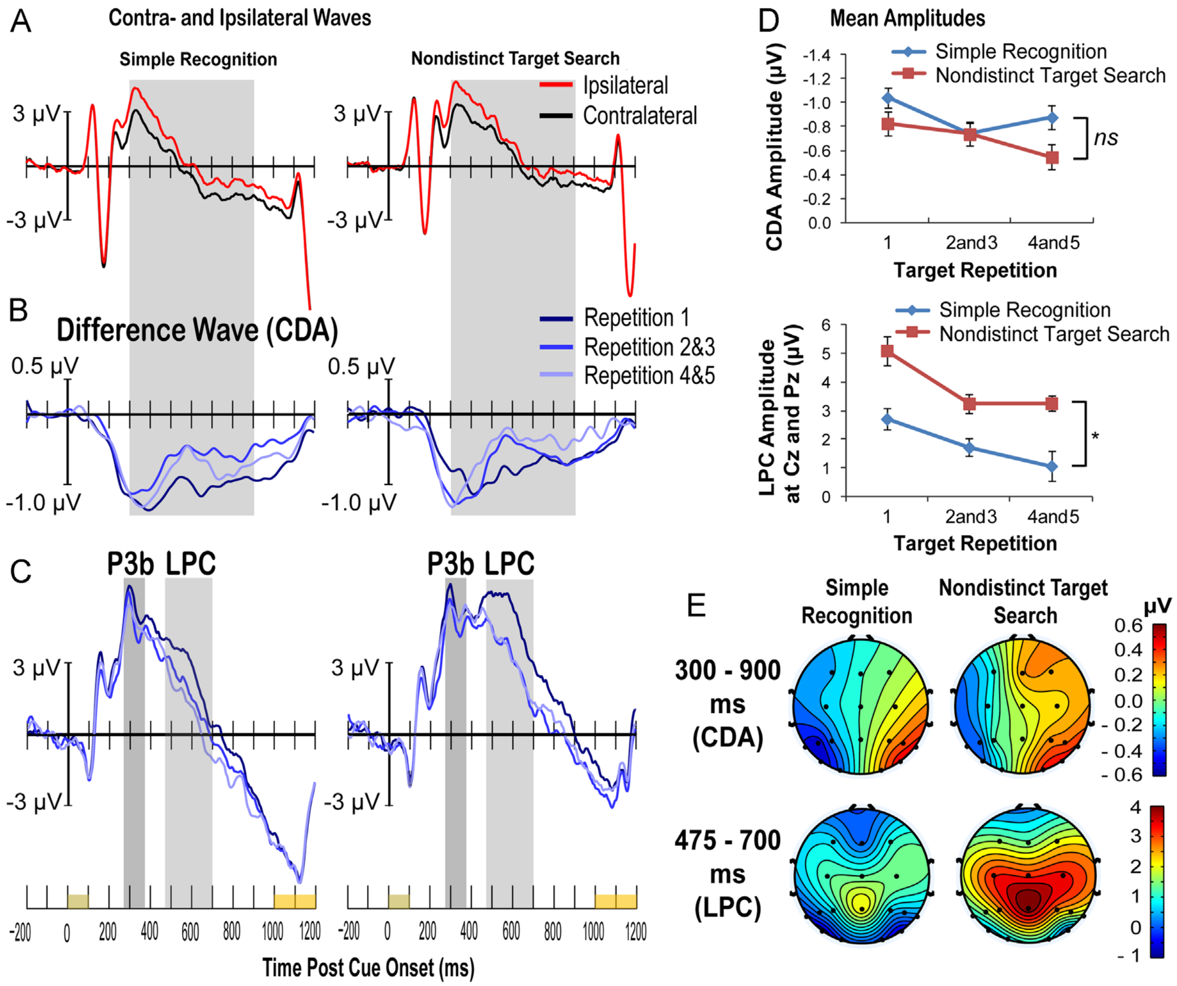

Fig. 5. ERP results from Experiment 2. (a) The grand average waveforms at the average of PO7/8, P7/8, P5/6, and O1/2 electrodes, contralateral (black) and ipsilateral (red) to the location of the cue, plotted separately for simple recognition task (left panel) and nondistinct target search task (right panel). The gray rectangular region represent the time window at which CDA was calculated (300–900 ms). The shadings on the timeline indicate the duration of the cue (dark yellow) and search display (light yellow). Note that positive is plotted upwards. (b) The grand average waveform of CDA, and (c) the grand average waveform of P3b (275–375 ms) and LPC (475–700 ms), averaged across Cz and Pz, the electrodes where the LPC amplitude was largest, given separately across target repetitions shown in shades of blue. (d) Plots of grand average CDA and LPC amplitudes given separately for each task type and target repetition (shown in the *x*-axis). The error bars represent standard errors of the mean for normalized data, i.e. corrected for between-subjects variance (Cousineau, 2005). (e) The scalp distribution of the CDA (top panel), and the LPC (bottom panel) calculated the same way as in Fig. 3 (Experiment 1).

suggesting that the quality of a VWM representation does not depend on the upcoming task type. These results are in line with findings from Gunseli et al. (2014) and provide support for the claims made there that anticipating a difficult task leads to a greater working memory effort, reflected in a larger LPC, but that the quality of the representation, indexed by the CDA, is not sensitive to this anticipated task difficulty. The present study extends these findings by demonstrating that the CDA is also insensitive to the upcoming task for which the maintained representation is going to be used.

The rate of learning across target repetitions, that is, a decrease in VWM involvement for maintaining a representation (as expressed by declining CDA and LPC amplitudes) was also equal for search and simple recognition tasks (Experiment 2). The learning of a VWM representation has been observed before separately for visual search (Carlisle et al., 2011; Gunseli et al., 2014; Reinhart et al., 2014; Reinhart & Woodman, 2013) and simple recognition tasks (Reinhart & Woodman, 2013). In the present study, we replicated these findings and additionally showed that the rate of learning is equal for a search template maintained for search and a VWM representation maintained for simple recognition. This result extends our previous findings of equal learning rates across search tasks of varying difficulty (Gunseli et al., 2014), and shows that the learning rate of a VWM representation is also independent of its functional role in the subsequent task.

Participants who invested less in maintaining a VWM representation (as indexed by smaller mean LPCs) performed faster in both tasks. This result is in line with results from Gunseli et al. (2014) that showed the same relationship for repeated search and extends it further to a simple recognition task. We propose that, since VWM has a limited capacity (Luck & Vogel, 1997; Vogel & Machizawa, 2004), if less VWM effort is invested in maintaining the cue, more resources can be devoted for performing the task itself. This, in turn, might lead to a faster performance. In line with this, previous research observed that participants who respond faster in a WM task has less BOLD activity in WM related brain regions (Rypma & D'Esposito, 2000), and that action video game players, who are known to have better quality VWM representations compared to non-gamers (Sungur & Boduroglu, 2012), have reduced activity in fronto-parietal network (Bavelier, Achtman, Mani, & Focker, 2012). Similarly, WM training, which leads to an increase in VWM capacity, has been observed to result in a reduced CDA amplitude, which was suggested to be due to improved efficiency in fronto-parietal network activation (Kundu, Sutterer, Emrich, & Postle, 2013). These results support the view that individuals who devote less effort for WM performance are actually the ones that are more efficient in performing this task. Moreover, it is noteworthy that the fronto-temporal network, which was suggested to underlie the improvement in WM efficiency in these studies, was also claimed to constitute the source of P3b/LPC formation (Polich, 2007; Polich, 2012). This would explain why the LPC amplitude was correlated with the behavioral performance in this and our previous study (Gunseli et al., 2014). The lack of a similar effect on the CDA can be attributed to fact that there was only a single object to remember, and thus it was not possible to make maintenance more efficient quantitatively (consistent with Kundu et al., 2013, who observed a training-related CDA decrase, only at set size 4). An alternative but not necessarily mutually exclusive explanation for the LPC-RT correlation is that, as the representations are learned over the course of the experiment, both their reactivation in VWM, and also their identification in the test display might become less effortful, leading to smaller LPC and RTs.

A distinction has been made between ‘privileged’ representations in VWM that are in the focus of attention and other representations within WM referred to as the region of direct-access (Oberauer, 2002), or activated long-term memory (Cowan, 1995, 1999). Indeed, focusing attention to a particular representation in VWM has been suggested to result in functional and neurological changes in its maintenance (Kuo, Stokes, & Nobre, 2012; LaRocque, Lewis-Peacock, Drysdale, Oberauer, & Postle, 2013; for a review, see LaRocque, Lewis-Peacock, & Postle, 2014; Lepsien & Nobre, 2007; Lewis-Peacock, Drysdale, Oberauer, & Postle, 2012; Nee & Jonides, 2013; Nelissen, Stokes, Nobre, & Rushworth, 2013; Öztekin, Davachi, & McElree, 2010). Similarly, VWM representations that guide visual attention, i.e. search templates, have also been suggested to be prioritized by means of focused attention within VWM, relative to ‘accessory WM items’ that must be maintained for a later test but are not required for performing in the upcoming search task (Olivers & Eimer, 2011; for a review, see Olivers, Peters, Houtkamp, & Roelfsema, 2011; Peters, Goebel, & Roelfsema, 2009; Peters, Roelfsema, & Goebel, 2012). In the present study, for all tasks, there was just a single representation to be maintained, which was presumably always in the focus of attention. Nevertheless, participants invested greater effort, as shown by a larger LPC, in maintaining this single representation when the upcoming task was anticipated to be more difficult. This result suggests that even within the focus of attention, which has been considered as a privileged unitary state of WM, representations can receive a graded amount of effort invested for their maintenance, depending on the difficulty of the upcoming task. Yet, it should be noted that our results do not, and cannot, argue against two states of WM, as we have not compared maintenance for currently relevant versus currently irrelevant (accessory) items.

The LPC, has been claimed index many different cognitive functions such as context update, arousal, or subjective visual awareness. We believe that, in the present procedure, the WM maintenance is the most plausible explanation that is also consistent with the literature. Another alternative explanation regarding the LPC sensitivity to upcoming task difficulty is the preparation for ignoring the distractors in the search task, which is more effortful in the nondistinct target search task.[1] However, if this was the case, then the individuals that are overall better prepared, in other words, the ones with larger LPCs, should have responded faster. Conversely, we observed the opposite pattern, that is, a positive correlation between the LPC and RT for the nondistinct target search task in Experiment 2, arguing against this alternative explanation.

In line with earlier claims, we observed both similarities and differences between the P3b and the LPC. The LPC amplitude was greatest at both Cz and Pz, whereas the P3b amplitude was largest at Pz. Moreover, the P3b was either weakly sensitive (Experiment 1) or not sensitive at all (Experiment 2) to task type (see also Gunseli et al., 2014, for a similar pattern), while the LPC was sensitive to task type in both experiments. On the other hand, P3b and the LPC were both sensitive to target repetitions (i.e. learning). The distinction between the P3b and the LPC is in line with the literature and suggests that, although they can have similarities, the P3b, defined as the narrow peak at central–parietal regions around 300 ms, does not always reflect the same cognitive processes as the LPC, which has a wider time range, a slightly different scalp topography, and can be sensitive to different experimental manipulations (Gunseli et al., 2014; Kusak et al., 2000; Ruchkin et al., 1990; Ruchkin & Sutton, 1983; Sutton & Ruchkin, 2006).

In summary, we found that the effort invested in maintaining a VWM representation, as indexed by the LPC amplitude, is proportional to the difficulty of the upcoming task. Greater effort is invested in maintaining a VWM representation when it will be used for visual search, than when it will be used for simple recognition. However, neither the scalp distribution of the LPC nor any aspect of the CDA was affected by task type. The rate of learning a VWM representation, as indexed by the decrease in CDA and LPC amplitudes, was also not dependent on the upcoming task. Our results demonstrate that the functional role of VWM representations does not qualitatively change the underlying neural activity—at least not the activity reflected by the CDA and LPC. This suggests that a search template is not a special category of VWM representations, when compared to a representation used for a simple recognition task. A role in visual search does, however, affect the amount of working memory effort invested in the template's maintenance.

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[1] We thank an anonymous reviewer for raising this alternative explanation.

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