Psychological Science
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Psychological Science published online 30 December 2010

DOI: 10.1177/0956797610395395

Short Report

Psychological Science
XX(X) 1–4

DOI: 10.1177/0956797610395395
http://pss.sagepub.com

Direct Electrophysiological Measurement of Attentional Templates in Visual Working Memory

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Received 6/16/10; Revision accepted 9/10/10

When parents look for their children on the playground, internal representations of these important targets must guide the search through the cluttered and chaotic scene. Several theories of attention propose that observers hold target representations (i.e., attentional templates) in visual working memory (VWM) to control perceptual attention (Bundesen, Habekost, & Kyllingsbaek, 2005; Desimone & Duncan, 1995). Although this is a foundational theoretical assumption, there is no direct electrophysiological evidence from humans supporting this proposal, and recordings from monkeys have yielded mixed results (Chelazzi, Miller, Duncan, & Desimone, 1993, 2001; Kusunoki, Sigala, Gaffan, & Duncan, 2009). This makes it difficult to rule out the classic hypothesis that visual search operates like a prepared reflex, unguided by VWM representations (Logan, 1978). In the present study, we tested the attentional-template hypothesis by recording event-related potentials (ERPs) from subjects while they searched for targets in complex scenes.

On each trial, subjects saw a target-cue array followed by a complex search array (see Fig. 1a). We focused our analyses on the ERPs following the cue to determine whether the contralateral-delay activity (CDA) was present. The CDA is a relative negativity at parietal, occipital, and temporal electrodes that are contralateral with respect to the location of a stimulus that is stored in VWM, typically during a delay interval. Specifically, the CDA indexes the maintenance of representations in VWM (e.g., Vogel & Machizawa, 2004), thus providing an ideal tool for testing the hypothesis that people maintain attentional templates in VWM during search. That is, unlike imaging studies demonstrating how brain areas modulate under different task demands (e.g., Soto, Humphreys, & Rotshtein, 2007), our experiment used the CDA component to definitely determine whether the same VWM mechanisms relied on in explicit-memory tasks are engaged in maintaining attentional templates. If templates are maintained in VWM, then a cue-elicited CDA should continue until search is performed. Furthermore, if the cue-elicited CDA directly measures the attentional template, then CDA amplitude measured prior to the search task should predict subsequent performance.

Method

Participants

Fifteen volunteers (18–35 years of age, neurologically normal with normal color vision and acuity) provided informed consent.

Stimuli

The stimuli were viewed on a gray background (54.3 cd/m^2) with a black fixation cross (< 0.01 cd/m^2, 0.4° × 0.4° of visual angle). The two cue stimuli were Landolt squares (0.7° × 0.7°, 0.1° line thickness, 0.5° gap) that were presented 2.2° to the left and right of center; one was green (x = .281, y = .593; 45.3 cd/m^2) and the other red (x = .612, y = .333; 15.1 cd/m^2). The visual search arrays contained 12 black Landolt squares (< 0.01 cd/m^2, centered 4.4° from fixation), each with a gap on the left, right, top, or bottom.

Procedure

Figure 1a illustrates the timing of events during each trial. Two cues, one of which identified the search target, were presented before a brief delay that was followed by the search array. The task-relevant cue was indicated by its color, and the color identifying the task-relevant cue (red or green) alternated across blocks to prevent physical stimulus confounds (Woodman, 2010). A target containing a gap on the same side as the cued shape was presented on 50% of trials. The target shape (gap at the top, bottom, left, or right), the location of the relevant cue (left or right), target presence (present or absent), and the target location were randomized across trials. Participants responded to each search array as quickly and accurately as possible on a handheld game pad, using the index finger of

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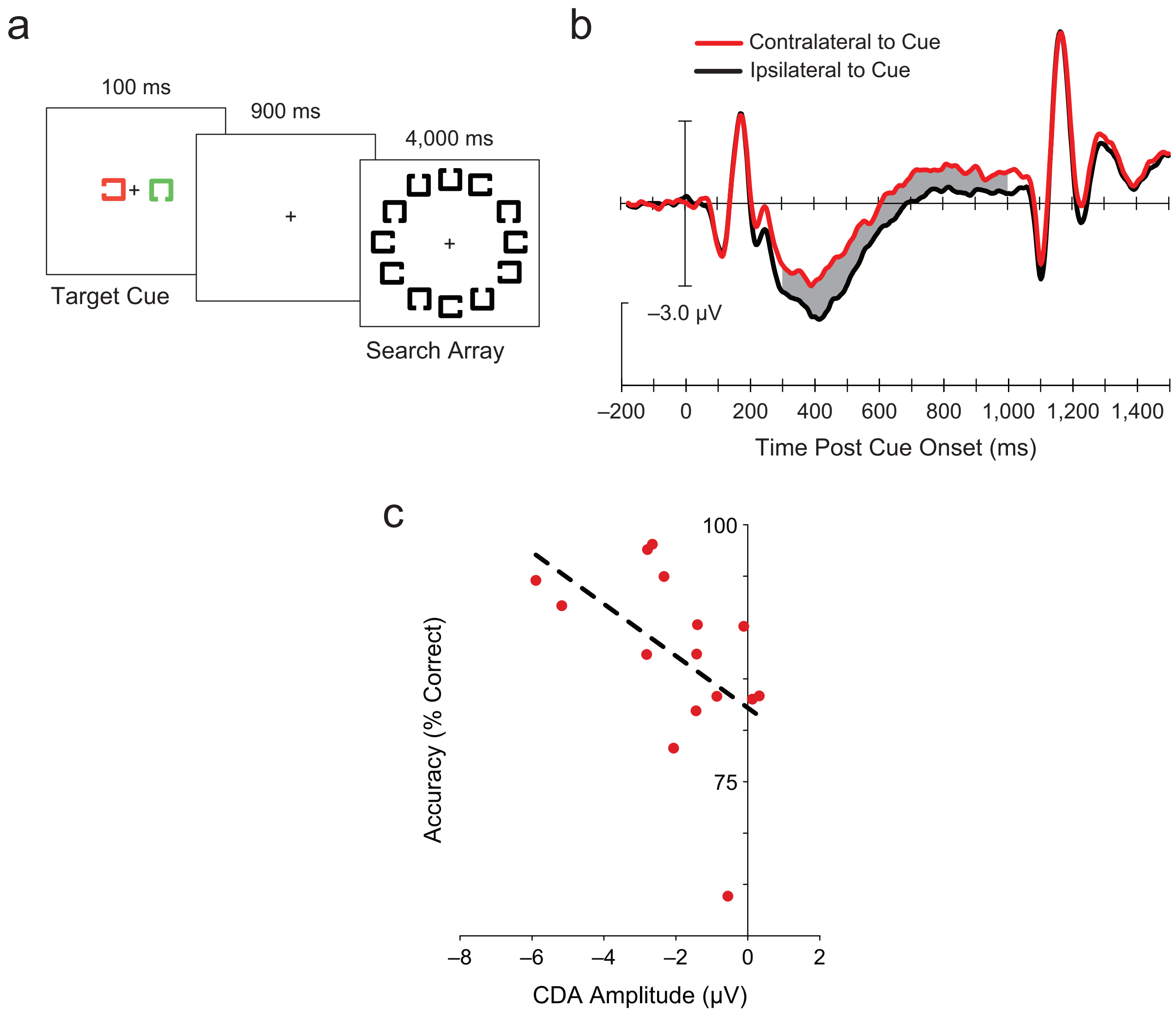

Fig. 1. Experimental stimuli, event-related potential (ERP) findings, and the relationship between the ERPs and behavior. On each trial (a), a target cue consisting of two colored Landolt squares (one that identified the search target and one that was task irrelevant) was presented before a delay and then a search array consisting of 12 black Landolt squares. The cue that was task relevant was color-coded. The graph in (b) shows grand-average waveforms from electrodes T5 and T6, where the contralateral-delay activity (CDA) was maximal, according to whether the electrode was contralateral or ipsilateral to the location of the cue. The gray region shows the measurement window (300–1,000 ms post cue onset) in which the significant CDA was measured. The graph in (c) shows visual search accuracy as a function of CDA amplitude following the cue. Note that a more negative voltage indicates a larger CDA. Each point represents the data from an individual subject, and the dashed line represents the linear regression.

their right hand to indicate that the target was present and the middle finger of their right hand to indicate that the target was absent. Twenty-four practice trials preceded four blocks of 192 experimental trials.

ERP recording and analysis

We recorded the electroencephalogram and electrooculogram using standard procedures (Woodman & Luck, 2003; Woodman & Vogel, 2008). A two-step method for artifact and subject rejection (Woodman & Luck, 2003) excluded 16.8% of trials per subject and prompted the replacement of 3 subjects. The CDA was measured 300 to 1,000 ms after cue onset (Vogel & Machizawa, 2004). Mean ERP amplitudes were entered into an analysis of variance with the factors of contralaterality (electrode sites ipsilateral or contralateral to the cue), hemisphere (left- or right-hemisphere electrode), target presence (present or absent), and electrode site (PO3/4, O1/2, OL/R, or T5/6). All p values were Greenhouse-Geisser corrected (Jennings & Wood, 1976). Given the absence of significant effects of cue color, the data were collapsed across that variable.

Results

Behavior

Subjects were more accurate on target-absent than on target-present trials (92.2% vs. 79.3% correct, respectively), $F(1, 14) = 6.68$, $\eta^2 = 0.21$, $p < .001$. This finding suggests that performance was limited by an inability to maintain the target representation on a subset of trials. When responses were correct, reaction times (RTs) were faster on target-present than on target-absent trials (1,300 ms vs. 1,965 ms, respectively), $F(1, 14) = 108.69$, $\eta^2 = 0.63$, $p < .001$.

ERPs

Figure 1b shows the cue-elicited waveforms. The observed amplitude difference between electrodes contralateral versus ipsilateral to the target cue resulted in significant effects of contralaterality, $F(1, 14) = 14.67$, $\eta^2 = 0.002$, $p < .01$, and electrode site, $F(3, 42) = 7.27$, $\eta^2 = 0.04$, $p < .001$, as well as a Contralaterality × Electrode Site interaction, $F(3, 42) = 15.85$, $\eta^2 = 0.13$, $p < .0001$, due to the expected CDA scalp distribution with a temporal-parietal maximum. No other main effects or interactions were significant (ps > .25).

The difficulty of the search task created a range of behavioral performance that allowed us to determine whether the amplitude of the cue-elicited CDA predicted how well search was performed. As Figure 1c shows, subjects with larger cue-elicited CDAs also performed the search task more accurately ($r^2 = .26$, $p < .05$). The relationship between CDA amplitude and RT was not significant ($r^2 = .07$ $p > .20$). The latter finding is not surprising given that search RTs are influenced by the speed of attentional shifts and categorization, as well as thresholds for deciding target absence (Bundesen, 1990; Chun & Wolfe, 1996). The fact that search accuracy was predicted by the cue-elicited CDA supports our conclusion that by using ERPs, we directly measured the VWM representations that drove the attention-demanding search process.

Conclusions

We have shown that VWM representations guide attention when observers perform tasks in which the target switches from moment to moment, a typical situation in the real world (e.g., searching for one's son in the pool and then one's daughter near the swings). Our findings validate a critical assumption of several prominent theories of attention (e.g., Bundesen et al., 2005; Desimone & Duncan, 1995). Seemingly contradictory findings from monkey neurophysiological studies (Chelazzi et al., 2001; Kusunoki et al., 2009) and human behavioral studies (Woodman & Luck, 2007; Woodman, Vogel, & Luck, 2001) had raised doubt about the attentional-template hypothesis. However, these previous studies most likely minimized the contribution of VWM by using a small, well-learned set of stimuli (Kusunoki et al., 2009; Woodman, Luck, & Schall, 2007).

Our findings also have implications for determining the locus of cognitive impairments in clinical disorders. Specifically, an inability to represent attentional templates in VWM could be mistaken for attention deficits during tasks requiring strong top-down control (Gold, Fuller, Robinson, Braun, & Luck, 2007; Zubin, 1975). The technique used in this experiment may provide a way to define specific subtypes within a variety of clinical diagnoses that are characterized by attentional abnormalities and in which VWM malfunctions masquerade as attention deficits (Hill, Harris, Herbener, Pavuluri, & Sweeney, 2008; Walshaw, Alloy, & Sabb, 2010).

Acknowledgments

Deborah Pardo aided in data collection.

Declaration of Conflicting Interests

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

Funding

G.F.W. is supported by the National Eye Institute and National Science Foundation.

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