Toppan Best-set Premedia Limited	
Journal Code: PSYP	Proofreader: Mony
Article No: PSYP12217	Delivery date: 25 Mar 2014
Page Extent: 5	

Psychophysiology, •• (2014), ••–••. Wiley Periodicals, Inc. Printed in the USA.

DOI: 10.1111/psyp.12217

BRIEF REPORT

Visual working memory gives up attentional control early in learning: Ruling out interhemispheric cancellation

ROBERT M. G. REINHART,[a] NANCY B. CARLISLE,[b] AND GEOFFREY F. WOODMAN[a]

[a]Department of Psychology, Center for Cognitive and Integrative Neuroscience, Vanderbilt Vision Research Center, Vanderbilt University, Nashville, Tennessee, USA
[b]Center for Mind and Brain, University of California, Davis, Davis, California, USA

Abstract

Current research suggests that we can watch visual working memory surrender the control of attention early in the process of learning to search for a specific object. This inference is based on the observation that the contralateral delay activity (CDA) rapidly decreases in amplitude across trials when subjects search for the same target object. Here, we tested the alternative explanation that the role of visual working memory does not actually decline across learning, but instead lateralized representations accumulate in both hemispheres across trials and wash out the lateralized CDA. We show that the decline in CDA amplitude occurred even when the target objects were consistently lateralized to a single visual hemifield. Our findings demonstrate that reductions in the amplitude of the CDA during learning are not simply due to the dilution of the CDA from interhemispheric cancellation.

Descriptors: Attention, Visual working memory, Learning, Event-related potentials, Contralateral delay activity

The idea that we transition from relying on working memory to relying on long-term memory representations as we become fluent at a task is central to theories of learning and automaticity (Anderson, 1982, 2000; Logan, 1988, 2002; Rickard, 1997). Recent empirical work has shown that a component of subjects' event-related potentials (ERPs) called the contralateral delay activity (CDA) can be used to directly examine the transfer of representations controlling attention (i.e., attentional templates) from working memory to long-term memory during learning (Carlisle, Arita, Pardo, & Woodman, 2011; Gunseli, Olivers, & Meeter, in press; Reinhart & Woodman, 2013; Woodman, Carlisle, & Reinhart, 2013). The CDA is a slow-wave negativity observed over posterior electrodes sites contralateral to the position of a remembered object that persists over a memory retention interval (McCollough, Machizawa, & Vogel, 2007; Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005; Vogel, Woodman, & Luck, 2005; Woodman & Vogel, 2008). Using a cued visual search task in which a new target object is cued and then searched for across a run of consecutive trials, Carlisle et al. (2011) found a systematic decrease in CDA amplitude as subjects searched for the same target object. This CDA decrease was interpreted as evidence for the transfer of attentional templates from visual working memory to long-term memory during learning, particularly given its trial-to-trial relationship with behavior following the power law of learning (Newell & Rosenbloom, 1981). The present study tests a critical alternative explanation for these observations.

Following the publication of Carlisle and colleagues (2011), the result that the CDA declines as subjects learn to look for a specific object has been replicated (Gunseli et al., in press; Reinhart & Woodman, 2013). However, an alternative explanation for this electrophysiological effect has not been ruled out. A key experimental design feature shared among these studies is that the target object presented in the cue and search arrays randomly alternated between left and right visual hemifields within a run of same-target trials. The lateral presentation of stimuli is necessary for the measurement of the CDA component, allowing for the subtraction of contralateral and ipsilateral activity relative to object location in the visual field. However, the alternating nature of stimulus presentation over time could lead to the observed decrease in CDA amplitude for reasons unrelated to learning.

In this alternative explanation, each representation indexed by the CDA remains active across trials, with some passive decay over time. For example, if a target appears in the right visual field on trial n, this would produce a more negative voltage over the posterior left hemisphere relative to the right hemisphere. If a target appears in the left visual field on trial $n + 1$, this would produce another CDA but with the opposite voltage distribution across the scalp. The lateralized memory representations built on top of one another across trials n and $n + 1$ would sum resulting in their partially canceling each other out. Over several trials, the alternating nature of target presentation may cause a decline in CDA

This work was supported by grants from the National Institutes of Health (R01-EY019882, P30-EY008126, T32-EY007135, and P30-HD015052) and National Science Foundation (BCS-0957072). We thank Julianna Ianni and Laura McClenahan for help with data collection, and Tom Palmeri for a useful question.

Address correspondence to: Geoffrey F. Woodman, PMB 407817, 2301 Vanderbilt Place, Vanderbilt University, Nashville, TN 37240-7817, USA. E-mail: geoffrey.f.woodman@vanderbilt.edu

amplitude due to this hemispheric washout. Under the hemispheric washout hypothesis, the observed decrease in CDA amplitude as subjects search for the same target across trials does not reflect visual working memory surrendering attentional control to long-term memory, but instead this CDA decline is due to the endurance of previously encoded memory representations (M. Eimer, personal communication, November 19, 2010). Thus, the hypothesis assumes the trial-context recurrence of no-longer-relevant activity, similar to the idea of task-set inertia (Allport, Styles, & Hsieh, 1994) and object-specific inertia (Waszak, Hommel, & Allport, 2003), referring to when a task-relevant object from the previous trial is carried over to the next trial in which it is task irrelevant.

In the present study, we tested the hemispheric washout account of the observed CDA reductions as subjects search for the same target objects across trials. Experiment 1 was identical to the cued visual search task employed in Carlisle et al. (2011) with the exception that the target in the cue array was consistently lateralized within each run of same-target trials (see Figure 1A). In an even stronger test of the hemispheric washout hypothesis, Experiment 2 restricted both the cue and search target to the same visual hemifield within each run of same-target trials (see Figure 1E).

If the previously observed CDA decline is due to a hemispheric washout of lateralized brain activity, then the CDA would increase with accumulating representations presented within the same hemifield when subjects are unilaterally cued to search for the same target, and will be unrelated to the speeding of search reaction times (RTs). Alternatively, if the CDA is a valid marker of visual working memory surrendering attentional control during learning, then the CDA should rapidly decrease as subjects continue to search for the same target, despite the unilateral presentation of the cue (Experiment 1) or the unilateral presentation of the cue and search target (Experiment 2). This CDA decrease should also mirror the decrease in the search RT function that occurs with learning as instances of performing the same task accumulate (e.g., Logan, 1988, 2002).

Method

Subjects

Different groups of 15 paid subjects participated in Experiments 1 and 2. All subjects provided informed consent prior to procedures approved by the Vanderbilt Institutional Review Board. The participants (18–35 years of age, 53% women) had normal color vision, normal or corrected-to-normal visual acuity, and no history of neurological problems.

Stimuli and Procedures

The stimuli were identical to those of Experiment 3 in Carlisle et al. (2011). Each trial began with a fixation cross for 1,200–1,600 ms (randomly jittered using a rectangular distribution). Then, the cue stimuli were presented for 100 ms, followed by a 1,000-ms interval in which the screen was blank other than the fixation cross. Finally, the search array was presented for 2,000 ms, followed by an intertrial interval of 1,200–1,600 ms. The possible target in the visual search array (i.e., the red item when the possible target was red) matched the shape of the task-relevant cue on half of all trials (i.e., target present) and did not match on the other half (i.e., target absent) randomized across trials. Across trials, the target cue remained the same throughout each run of 3, 5, or 7 trials (the length of the run was randomly selected). Figure 1A shows an example of a run with three target repetitions.

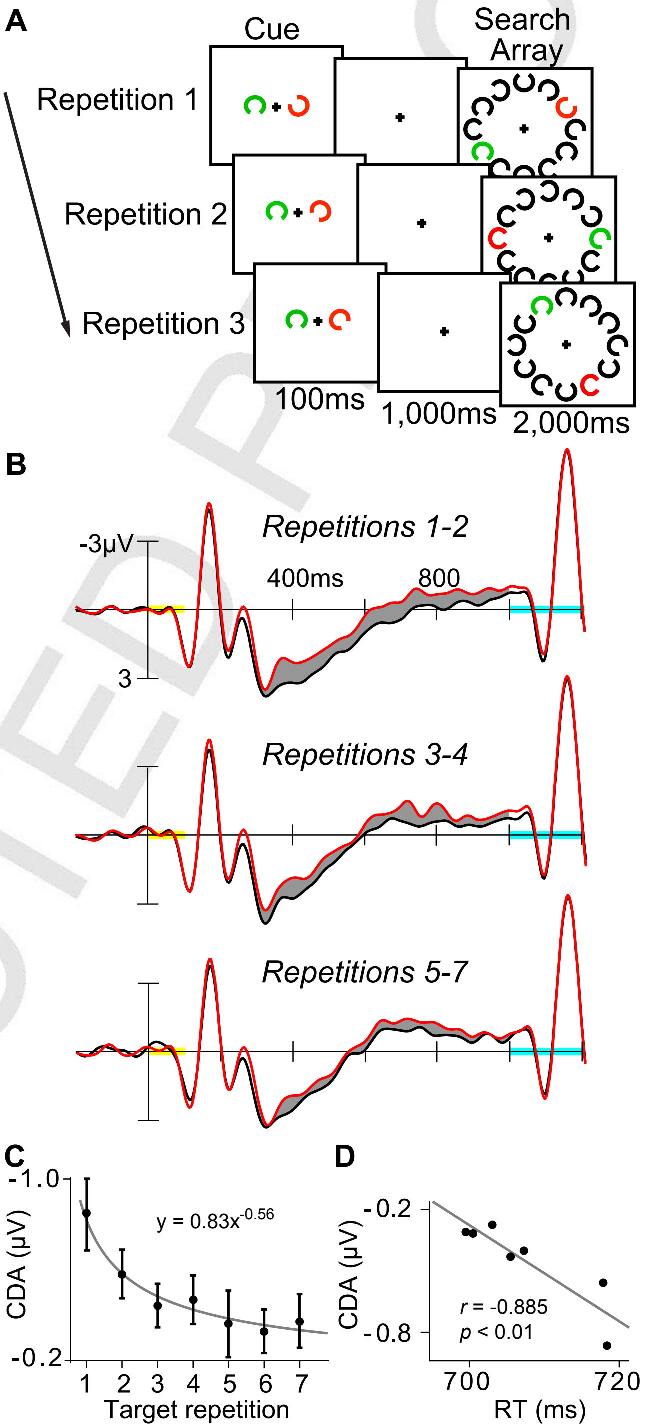

Figure 1. The design and results of Experiment 1. A: The task-relevant cue (red or green Landolt-C) signaled the shape of the target in the upcoming search array. The location of the cue was confined to either the left or right visual hemifield across runs of 3, 5, or 7 same-target trials. Central fixation was maintained for the trial duration. B: Grand-average event-related potential (ERP) waveforms from posterolateral electrodes contralateral (red) and ipsilateral (black) to the cue location across target repetitions. For display purposes, the measurement window of the contralateral delay activity (CDA) is shaded in gray. Duration of the cue (yellow) and search array (cyan) is color coded. C: Mean CDA amplitude for each consecutive target repetition with power-function fit and ± 1 SEM errors bars. D: Scatter plot of the relationship between mean CDA amplitude and mean search RT for each target repetition.

In Experiment 1, the target object cue remained in the same location for each run of trials. However, the location of the target in the search array was randomly selected across trials. On each new run of trials, the target cue changed to a different orientation, and the side of target cue presentation was randomly chosen. In Experiment 2, the target object cue and the possible target object in the search array were both restricted to the same hemifield within a run of same-target trials, with this lateralization randomly changing between same-target runs. Figure 2A shows an example of a run with three target repetitions. Subjects were all required to respond to the search array by pressing one button on a handheld gamepad to indicate target presence and a different button to indicate target absence, using the thumb of their right hand, giving equal importance to speed and accuracy. Each subject performed two blocks of 360 trials, with 30-s breaks approximately every 65 trials with the constraint that breaks would not interrupt a run of trials.

The electroencephalogram (EEG) recording was identical to the methods used in Carlisle et al. (2011). The EEG was recorded (250 Hz sampling, 0.01–100 Hz band-pass filter) using an SA Instrumentation Amplifier with tin electrodes arrayed according to the International 10–20 system (Fz, Cz, Pz, F3/F4, C3/C4, P3/P4, PO3/PO4, T3/T4, T5/T6, O1/O2), including two nonstandard sites (OL, midway between O1 and T5; and OR, midway between O2 and T6), embedded in an elastic cap (Electrocap International). We acknowledge that the 0.01 Hz high-pass filter on the amplifier could be a shortcoming of our approach if the endurance of CDAs in a run of trials manifests as a DC shift in signal. Signals were referenced online to the right mastoid electrode and rereferenced offline to the average of the left and the right mastoids (Nunez & Srinivasan, 2006). Bipolar electrodes at the outer canthi of each eye and electrodes above and below the left orbit monitored horizontal and vertical eye positions, respectively. Trials accompanied by incorrect behavioral responses or ocular or myogenic artifacts were excluded from the averages, resulting in the rejection of an average of 18.2% of trials per subject. We used a two-step ocular artifact rejection method (Woodman & Luck, 2003) that required us to replace three subjects in Experiment 1 and two subjects in Experiment 2 due to excessive eye movements.

Data Analysis

The CDA was measured across PO3/4, O1/2, OL/R, and T5/6 as the difference in mean amplitude between the electrodes contralateral versus ipsilateral to the cue, 300–1,000 ms following cue onset, consistent with previous CDA experiments (Carlisle et al., 2011; Vogel & Machizawa, 2004; Vogel et al., 2005). Greenhouse-Geisser epsilon correction was applied to the degrees of freedom (Jennings & Wood, 1976).

Results

Experiment 1

The behavioral results of Experiment 1 replicated those of Carlisle et al. (2011). Search RTs became shorter as subjects searched for the same target across a run of trials, evidenced by a main effect of target repetition on search RT, $F(6,84) = 2.64$, $p < .05$. Search accuracy was high (mean ± *SD*, 95.2 ± 0.04% correct) and did not differ across target repetitions ($p > .54$) or between target present and absent trials ($p > .40$). In sum, subjects became faster at searching for the target as it repeated across trials.

Figure 1B shows the ERP waveforms from Experiment 1 relative to the location of the task-relevant cue. Despite the consistently lateralized presentation of task-relevant cues, we observed a rapid decline in CDA amplitude. To increase signal-to-noise and the stability of our measures, we binned the data using two or three consecutive trials consistent with Carlisle et al. (2011). Mean CDA amplitude systematically decreased across repetition bins after a change in target identity (trials 1–2: mean −0.71 µV; trials 3–4: mean −0.41 µV; trials 5–7: mean −0.30 µV).

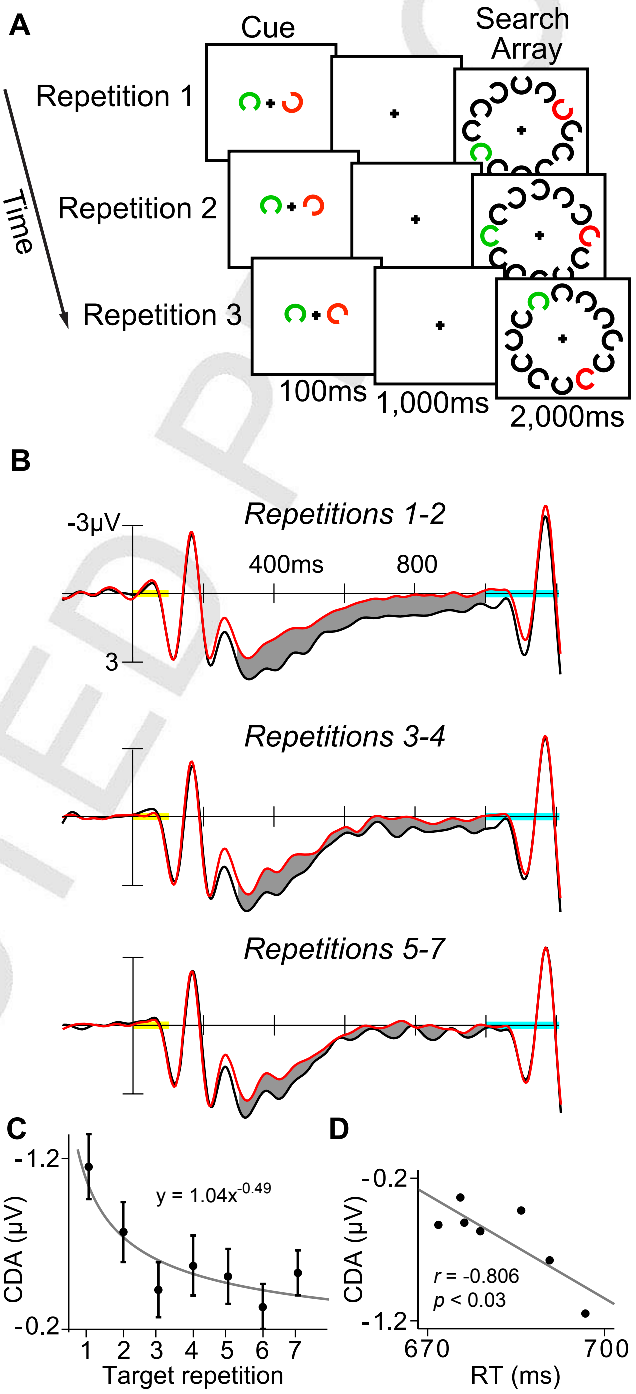

Figure 2. The design and results of Experiment 2. A: The task in Experiment 2 was identical to that of Experiment 1 except that both the cue and search target were confined to the same visual hemifield. B–D: Event-related potential and behavioral data are plotted as in Figure 1B–D.

The CDA data were entered into an analysis of variance (ANOVA) with the following within-subjects factors: contralaterality (ipsilateral vs. contralateral to the task-relevant cue) and repetition bin (1–2 vs. 3–4 vs. 5–7 consecutive trials since a change in target identity). This resulted in a significant Contralaterality × Repetition Bin interaction, $F(2,28) = 7.21$, $p < .01$. There were also main effects of contralaterality, $F(1,14) = 19.49$, $p < .01$, and repetition bin, $F(2,28) = 3.88$, $p < .05$. Because we did not see the CDA increase or even remain unchanged across trials, our findings are inconsistent with the hemispheric washout hypothesis, but consistent with the reductions in CDA being due to visual working memory giving up attentional control as subjects learn.

To rule out the possibility that the CDA decrease was due to subjects' waning attention to the task-relevant cue, we measured the N2pc, a posterior negative potential contralateral to where in the visual field attention is focused (Luck, Fan, & Hillyard, 1993; Luck & Hillyard, 1990; Woodman & Luck, 2003). If subjects stopped attending to the cue, we should see smaller N2pc amplitudes across repetition bins. Using the same ANOVA as above with the exception of the N2pc measurement window (200–300 ms postcue onset), we found a main effect of contralaterality, $F(1,14) = 4.89$, $p < .05$, indicating that subjects deployed attention to the task-relevant cue. Critically, there was no Repetition Bin × Contralaterality interaction, $F(2,28) = 0.10$, $p > .87$, indicating that the decline in CDA was not due to subjects coming to ignore the cue across the runs of trials.

To further examine the relationship between CDA amplitude and target repetition, we measured the CDA trial by trial. Figure 1C shows that we observed a sharp decline in CDA amplitude within a run. Planned comparisons showed that CDA amplitude significantly deviated from zero at target repetitions 1, 2, 3, and 4, *F*s > 7.75, *p*s < .01; but not repetitions 5, 6, and 7, $F(1,14) = 2.27$, $p > .14$; $F(1,14) = 3.69$, $p > .07$; and $F(1,14) = 3.45$, $p > .07$, respectively. Moreover, the slope of this CDA amplitude decline fit a power function ($R^2 = 0.93$, $p < .01$) as expected if the power law of learning (Newell & Rosenbloom, 1981) governs the reduction of the CDA across target repetitions. Figure 1D shows that this drop in CDA amplitude was highly correlated with mean search RT, as expected if changes in CDA amplitude are intertwined with the learning that underlies this improvement in behavior.

Experiment 2

In Experiment 2, we further tested the hemispheric washout hypothesis. As shown in Figure 2A, not only did we restrict task-relevant cues to a single visual hemifield, but we also restricted the task-relevant item in the search array to the same visual hemifield within each run of same-target trials. This experimental design addresses the possibility that the lateralized item in the search array elicits a CDA of its own, resulting in hemispheric washout across trials. If the CDA decline observed in previous studies using alternating search target locations was due to sustained CDAs accumulating in different hemispheres, then the CDA amplitude in Experiment 2 should increase across trials of searching for the same object in the same hemisphere. However, if the CDA declines in amplitude even with all task-relevant stimuli lateralized to one hemifield, then this would strongly support the view that the CDA amplitude reductions are due to visual working memory giving up its role in controlling attention as subjects continue to search for the same targets.

Despite the consistent lateralization of all task-relevant stimuli, the behavioral and electrophysiological results of Experiment 2 showed the same pattern observed in Experiment 1. The speeding of search RTs across target repetitions was confirmed statistically by a main effect of repetition on search RT, $F(6,84) = 3.81$, $p < .01$. Search accuracy was near ceiling (mean ± *SD*, 94.6 ± 0.04% correct) and did not differ across target repetitions ($p > .54$) or between target present and absent trials ($p > .47$).

As shown in Figure 2B, despite the consistently lateralized presentation of both task-relevant cues and search targets within the same-target runs of trials, the CDA rapidly declined across repetition bins (trials 1–2: mean –0.96 μV; trials 3–4: mean –0.50 μV; trials 5–7: mean –0.45 μV). This was evidenced by the critical Contralaterality × Repetition Bin interaction, $F(2,28) = 6.08$, $p < .01$, and main effects of contralaterality, $F(1,14) = 43.47$, $p < .01$, and repetition bin, $F(2,28) = 4.01$, $p < .05$. The subjects continued to attend to the target cues across the runs as evidenced by the N2pc remaining unchanged across target repetitions (contralaterality main effect, $F(1,14) = 12.82$, $p < .01$, Repetition Bin × Contralaterality interaction, $F(2,28) = 0.64$, $p > .50$. As Figure 2C illustrates, by examining CDA amplitude across individual target repetitions, we found that the slope of the CDA decrease could be effectively modeled using a power function ($R^2 = 0.70$, $p < .02$). Finally, Figure 2D shows the strong negative correlation we found between mean CDA amplitude and mean search RT.

Discussion

Here, we rule out a competing hypothesis regarding the behavior of the CDA previously used to index the role of visual working memory in controlling attention. We show that the systematic decrease in CDA amplitude as subjects search for the same object cannot be attributed to CDAs accumulating in each hemisphere and washing out the contralateral versus ipsilateral difference that we use to measure the CDA. By lateralizing the task-relevant cue and search target within each run of trials, the possibility for hemispheric washout was eliminated, yet the CDA showed the same systematic decrease and was highly related to the behavioral manifestation of learning (i.e., speeding of RT).

These results add to a growing literature on the neurophysiological basis of attentional templates in visual working memory, a fundamental assumption in theories of attention (e.g., Bundesen, Habekost, & Kyllingsbaek, 2005; Desimone & Duncan, 1995; Duncan & Humphreys, 1989). Initial evidence for template-like activity came from monkey single-unit studies (e.g., Chelazzi, Duncan, Miller, & Desimone, 1998; Chelazzi, Miller, Duncan, & Desimone, 1993; Desimone, 1996). For example, the baseline firing rate of feature-selective neurons in posterior visual areas were found to be continually elevated when an object was currently the target of a visual search task (Chelazzi et al., 1993, 1998), but this was not clearly observed in all areas of the ventral visual stream (Chelazzi, Miller, Duncan, & Desimone, 2001). Converging support from humans indicates that the CDA may provide an equally important neural instantiation of attentional templates at the level of noninvasive, whole-brain electrophysiology (Carlisle et al., 2011; Woodman & Arita, 2011), mirroring the neuronal effects observed intracranially in monkeys.

The RT speeding observed in the current study is explained by learning theories as due to an increasing reliance on the relatively fast and automatic long-term memory system for controlling attention and the reduced reliance of the more cognitively demanding visual working memory system (Anderson, 1982, 2000; Logan, 1988, 2002; Rickard, 1997). For example, instance theory holds that attentional templates from both memory stores race in parallel toward a threshold, with RT benefits resulting from long-term memory processes more frequently winning the race to categorize the task-relevant objects in the environment (Logan, 1988, 2002). Our results are consistent with this view but, more broadly, validate the CDA as a general tool for examining the role of working memory representations in the automaticity of visual search.

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(Received September 4, 2013; Accepted January 25, 2014)