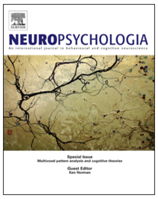
Neuropsychologia 56 (2014) 63–72

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia



The neurophysiological index of visual working memory maintenance is not due to load dependent eye movements

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ARTICLE INFO

Article history:
Received 4 November 2013
Received in revised form
12 December 2013
Accepted 15 December 2013
Available online 15 January 2014

Keywords:
Visual working memory
Eye movements
ERP
CDA

ABSTRACT

The Contralateral Delayed Activity (CDA) is slow negative potential found during a variety of tasks, providing an important measure of the representation of information in visual working memory. However, it is studied using stimulus arrays in which the to-be-remembered objects are shown in the periphery of the left or the right visual field. Our goal was to determine whether fixational eye movements in the direction of the memoranda might underlie the CDA. We found that subjects′ gaze was shifted toward the visual field of the memoranda during the retention interval, with its magnitude increasing with the set size. However, the CDA was clearly observed even when the subjects′ gaze shifts were absent. In addition, the magnitude of the subjects′ gaze shifts was unrelated to their visual working memory capacity measured with behavioral data, unlike the CDA. Finally, the onset latency of the set size dependent eye movements followed the onset of the set size dependent CDA. Thus, our findings clearly show that the CDA does not represent a simple inability to maintain fixation during visual working memory maintenance, but that this neural index of representation in working memory appears to induce eye movements toward the locations of the objects being remembered.

1. Introduction

The CDA is a slow wave of subjects′ event-related potentials (ERPs) that is found contralateral to the location in space that to-be-remembered objects are presented. This contralateral negativity increases in amplitude as the set size of the to-be-remembered array increases and stops increasing at each individual′s visual working memory capacity estimated behaviorally (Vogel & Machizawa, 2004). This sensitivity to visual working memory load and predictive relationship to an individual′s working memory capacity have made the CDA a vital tool with which to study the temporary storage of information in memory (Carlisle, Arita, Pardo, & Woodman, 2011; Kundu, Sutterer, Emrich, & Postle, 2013; Luria, Sessa, Gotler, Jolicoeur, & Dell′Acqua, 2010; Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005). However, it is important to determine whether this measure truly indexes memory-related activity and is not due to the simpler alternative explanation that it is a manifestation of eye movements. This alternative becomes particularly concerning because recent evidence indicates that even very small eye movements (e.g. microsaccades), that are difficult to exclude from the analyses of the EEG and ERP data, modulate electrophysiological responses measured over the back of the head (Dimigen, Valsecchi, Sommer, & Kliegl, 2009; Yuval-Greenberg, Tomer, Keren, Nelken, & Deouell, 2008).

If systematic gaze shifts occur with the memory load, then it could explain the characteristics of the CDA. Unilateral visual memory tasks are used to measure the CDA. Fig. 1 illustrates a unilateral visual memory task in which four objects are presented in the left and the right visual fields, but subjects are required to remember only the four object presented on the left, as indicated by the cue. Following the memory array is a retention interval in which nothing appears on the screen, and the subjects′ exhibit a contralateral negativity over the right posterior cortex that is sustained during the memory retention interval. However, the spatial cues used in this memory paradigm are known to elicit microsaccades to the relevant direction in previous studies of the deployment of covert attention (Engbert & Kliegl, 2003; Hafed & Clark, 2002; Yokoyama, Noguchi, & Kita, 2012). Moreover, previous work has shown that people make eye movements toward the locations of objects that they previously viewed, but are now holding in visual working memory (Williams, Pouget, Boucher, & Woodman, 2013), consistent with theories proposing that spatial attention is tightly coupled to visual working memory maintenance (Awh & Jonides, 2001). Therefore, if gaze is systematically

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http://dx.doi.org/10.1016/j.neuropsychologia.2013.12.028

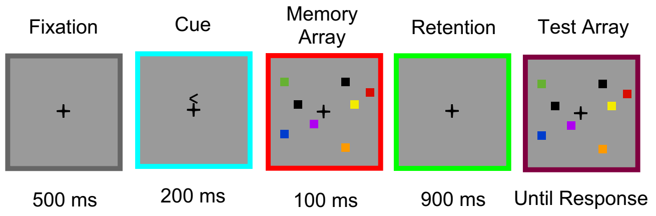

Fig. 1. Example stimulus sequence of the unilateral visual memory task. The boundary color of each square box of the stimulus (which is not shown during the experiment) matches the color of the timeline shown with the time course plots of the paper.

shifted to the visual field of memoranda, then the corneoretinal potential could be producing the more negative potential of the CDA at the contralateral occipitoparietal electrodes because the corneoretinal potential generates a dipole that is positive at the cornea and negative at the posterior retina (Plöchl, Ossandon, & Konig, 2012).

Here we tested the hypothesis that systematic shifts in gaze occur during the memory retention intervals and underlie the CDA in the paradigm used to measure it. We tested this hypothesis by concurrently recording subjects' ERPs and their eye movements using a high-resolution eye tracker. If this hypothesis is correct, then we should observe that gaze shifts are load dependent like the CDA. In addition, when systematic gaze shifts are absent (on average) from a set of trials, the CDA should be absent. Finally, the latency of these gaze shifts should occur simultaneously with the onset of the CDA. In contrast, if the CDA does measure the active maintenance of information in visual working memory independent of eye movement behavior, then we should see that the subjects' eye movements are dissociable from the CDA using these amplitude and latency relationships.

2. Materials and methods

2.1. Participants

Twenty-four adults with normal color vision, acuity, and no neurological history provided informed consent in advance of procedures approved by Vanderbilt University's Institutional Review Board. Subjects were compensated $10 per hour for their participation. Five subjects' data were excluded from the analysis. The exclusion criteria included problems in recording eye movements (one), excessive blinking (one), trouble in discriminating reddish colors (one), and averaged gaze shifts during the retention intervals greater than 0.5° of visual angle (two).

2.2. Apparatus

Observers were seated and their head was positioned 114 cm from a computer screen on a chinrest. Manual responses were made on a gamepad (Logitech Precision, Switzerland) during the memory task. All stimuli were presented on a gray background ($x=0.41$, $y=0.51$, 47.5 cd/m^2) using the Psychophysics Toolbox-3 (Brainard, 1997; Pelli, 1997) in conjunction with Matlab (Mathworks, MA, USA).

2.3. Stimuli and procedure

On all trials the to-be-remembered objects were colored squares. The size of each colored square was $0.9^\circ \times 0.9^\circ$ of visual angle. Each square was randomly assigned one of six possible colors (red, $x=0.548$, $y=0.334$, yellow, $x=0.420$, $y=0.503$, green, $x=0.278$, $y=0.614$, blue, $x=0.114$, $y=0.065$, cyan, $x=0.200$, $y=0.291$ and magenta, $x=0.291$, $y=0.146$).

The stimulus sequence from an example trial is shown in Fig. 1. Subjects completed two visual memory tasks in different blocks of trials. One was a whole-field change-detection task used to estimate visual working memory capacity (described below). The other was the typical unilateral change-detection task used to study the CDA (Vogel & Machizawa, 2004; Vogel et al., 2005).

In the unilateral change-detection task, each trial began with a red warning cross presented for 500 ms (to signal a new trial was about to begin) followed by a black fixation cross for 500 ms (both $0.6^\circ \times 0.6^\circ$). Then a cue was presented above fixation (1.2°) for 200 ms pointing to either the left ($<$) or the right ($>$). Next, we presented the memory array for 100 ms. Each array consisted of one, two, four or six colored squares presented on both sides of the fixation (e.g., see a set size 4 array in Fig. 1A). The colored squares were presented within an imaginary box ($6^\circ \times 12^\circ$) with the center displaced 4.7° to the left and right of fixation with a minimum inter-item distance of at least 2.4°. A 900 ms retention interval followed the memory array in which only the fixation was presented. Finally, the test array was presented until subjects responded. The test array was identical to the memory array (i.e., a *same trial*) or the color of a single item in the cued visual field was replaced with any one of the other colors (i.e., a *different trial*). Subjects had to press different buttons using their left or right index finger to report whether the test array was the same or different. The response mapping was counterbalanced across subjects for this same versus different judgment. Subjects completed 28 blocks of 32 trials, for a total of 896 trials. Subjects' eye position was checked and recalibrated at the end of any trial, when necessary, with a mandatory recalibration at the beginning of each 32-trial block.

To estimate subjects' working memory capacity, subjects performed a whole-field change-detection task in which the same stimulus sequence was used except for the following. Instead of the cue indicating either the left or the right visual field, a minus sign ($-$) was presented indicating that subjects had to remember the entire memory array. These memory arrays had either one, two, three or four items presented on both sides of the fixation cross resulting in set sizes of two, four, six or eight objects. These set sizes were randomly interleaved. Subjects completed 8 blocks and each block consisted of 48 trials, for a total of 384 trials. The whole-field change-detection task was performed either before or after the unilateral change-detection task with order counterbalanced across subjects.

2.4. Electrophysiological recording and analyses

We recorded the EEG with tin electrodes embedded in an elastic cap (Electro-Cap International, Eaton, OH, USA). The caps contained a subset of the International 10/20 System sites (Fz, Cz, Pz, F3, F4, C3, C4, P3, P4, PO3, PO4, T3, T4, T5, T6, O1 and O2) in addition to two non-standard sites (OL, placed halfway between O1 and T5; OR, placed halfway between O2 and T6). The electrodes were referenced online to the right mastoid, and re-referenced offline to the average of the right and left mastoids (Nunez, 2006). We recorded the horizontal electrooculogram (EOG) from two electrodes placed approximately 1 cm from the external canthus of each eye and an electrode placed approximately 3 cm above and below the left eye to measure the vertical EOG. Signals were amplified using an SA Instrumentation amplifier with a gain of 20,000 and a bandpass of 0.01–100 Hz. The amplified signals were digitized by a PC-compatible computer at a rate of 250 Hz and averaged offline. Individual trials contaminated with blinks, muscle noise, or amplifier saturation were rejected prior to averaging.

The ERP waveforms were timelocked to the onset of the memory array and baseline corrected to the interval -200 ms to 0 ms before the onset of the memory array. The CDA responses were obtained by subtracting the contralateral responses from the ipsilateral responses from the occipitoparietal electrodes (PO3/4, OL/R, T5/6) for each set size. Waveforms were low-pass filtered (a two-way least-squares finite-impulse-response filter with 0 Hz and 35 Hz for low and high end of the frequency band) for presentation in the figures only. The analyses were performed on the unfiltered mean voltages. For statistical analyses, the CDA amplitudes were obtained by averaging the traces of the temporal window between 500 ms and 1000 ms following the memory array onset.

2.5. Eye movement recording and analysis

The subjects' eye movements were recorded with an Eyelink 1000 (SR Research, Ontario, Canada) video-based eye tracker. For all subjects, the position of the left eye was recorded with a 1000 Hz sampling rate. To measure subjects' changes in their gaze position during the retention interval, the eye-tracker data were normalized such that they were timelocked to the onset of the memory array and baseline corrected to the interval between -200 ms and 0 ms before the onset of the memory array. Like the CDA, gaze shifts were then measured by averaging the eye traces from 500 ms to 1000 ms with respect to the memory array onset.

2.6. Microsaccades analysis

To detect microsaccades, we applied the algorithm developed by Engbert and Kliegl (2003) with following variations. Briefly, the velocity vector was created using a moving average over five data samples to suppress noise. For each trial, a threshold was set at the value that was 6 times the standard deviation by applying a median estimator for the time series of the horizontal and vertical eye positions, respectively. Because we only recorded the left eye for all subjects, we could not apply the last step that Engbert and Kliegl (2003) used in which they combined the time series of both eyes' positions to reduce erroneous detection of microsaccades. Instead, we eliminated erroneous detection if the peak velocity and saccade amplitude identified in the first step lasted less than 12 ms. In addition, we disregarded those movements occurring within a 50 ms refractory period following a gaze shift. We set this 50 ms refractory period based on the