



Neural activity reveals perceptual grouping in working memory



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ABSTRACT

There is extensive evidence that the contralateral delay activity (CDA), a scalp recorded event-related brain potential, provides a reliable index of the number of objects held in visual working memory. Here we present evidence that the CDA not only indexes visual object working memory, but also the number of locations held in spatial working memory. In addition, we demonstrate that the CDA can be predictably modulated by the type of encoding strategy employed. When individual locations were held in working memory, the pattern of CDA modulation mimicked previous findings for visual object working memory. Specifically, CDA amplitude increased monotonically until working memory capacity was reached. However, when participants were instructed to group individual locations to form a constellation, the CDA was prolonged and reached an asymptote at two locations. This result provides neural evidence for the formation of a unitary representation of multiple spatial locations.

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1. Introduction

The contralateral delay activity (CDA) is an electrophysiological measure that indexes the contents of visual working memory (Vogel and Machizawa, 2004; Awh et al., 2007). In a CDA task, visual stimuli are presented to both hemifields, which in turn equalizes perceptual activation across hemispheres. The key to this task is that observers are pre-cued to encode information from only one of the hemifields (this varies from trial-to-trial). The stimuli are then removed from the screen, and observers are required to maintain the information in working memory during a delay period of up to several seconds before performing a same-different judgment. The CDA is a difference score that is calculated by subtracting ipsilateral from contralateral EEG delay period activity relative to the encoded side of the visual field. As the number of objects required to be held in visual working memory increases, so does the CDA difference amplitude, and as an individual's working memory capacity plateaus, so does the CDA (Vogel and Machizawa, 2004).

Up to now, the CDA has only been measured during visual-object working memory tasks – tasks that require observers to remember the visual identity of several objects. The first question we wish to answer is whether a visual-spatial working memory task – a task that requires the memorization of spatial locations – can also elicit a CDA. Visual-object working memory tasks engage ventral stream processing,

whereas visual-spatial working memory tasks engage the dorsal-parietal stream (Courtney et al., 1996; Smith et al., 1995) so it is unclear whether a spatial task would elicit a CDA.¹ In addition, although visual working memory has a limited-capacity, the number of items that can be effectively held in working memory can be increased by using mnemonics such as chunking (Yantis, 1992). That implies that if observers successfully encode several locations as a single unit (e.g. chunked into a constellation), then the amplitude of the CDA should be markedly different compared to when those same items are encoded as individual locations. This notion is supported by work showing that a reduction in the CDA indexes the ability to group several objects to form a single representation, provided strong Gestalt grouping principles are present (Gao et al., 2011a,b; Luria and Vogel, 2014; Peterson et al., 2015). More recent work suggests that reflexive Gestalt grouping can be overridden with more complex stimuli (Balaban and Luria, 2016). In addition, Balaban and Luria found that the prior history of stimulus feature conjunctions influences grouping. Thus, it appears that stimulus properties and top-down factors can influence the ability to form unitary representations of multiple objects.

To investigate whether encoding strategies for spatial locations can influence the CDA, we instructed participants either to encode locations individually or to group them to form a unitary representation. We reasoned that grouping spatial locations would require an executive

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¹ We note, however, that source localization (Becke et al., 2015; Robitaille et al., 2009) and neuroimaging (Todd and Marios, 2004; Xu and Chun, 2006) studies support a neural origin of the CDA that includes parietal areas, suggesting that this component might also index visual-spatial working memory.

process that would only be employed when the stimulus array consisted of more than a single spatial location. Thus, we predicted that, when using a chunking strategy, CDA amplitude would increase when encoding two spatial locations, but would not further increase for larger set sizes. In contrast, when participants were instructed to encode spatial locations individually, we predicted that the CDA amplitude would increase monotonically as a function of set size, as has previously been observed for visual object working memory tasks (Vogel and Machizawa, 2004; Awh et al., 2007). In addition, if these strategies (individual locations vs. grouping) recruit different neural structures, then we might find qualitative differences in the CDA (Peterson et al., 2015).

2. Method

2.1. Participants

Thirty-four healthy participants (five males) from the undergraduate student population of George Mason University completed the study in exchange for course credit. Participants were randomly assigned to one of two instructional conditions (see below for details regarding the experimental groups). Sample sizes were based on those used in previous research ($n = 12$, Vogel and Machizawa, 2004). Six participants were later removed from analyses due to poor behavioral performance (performance equivalent to chance) or due to insufficient trial counts for computing reliable ERPs (<60 trials per condition). This left fifteen participants in the spatial instruction group and thirteen participants in the constellation instruction group. Participants were between 18 and 31 years of age ($M = 20.67$ years, $SD = 3.53$ years), had normal or corrected-to-normal vision, and were not taking any medication that affected the central nervous system. Informed consent was obtained prior to the beginning of the experiment, and all procedures were approved by the Institutional Review Board at George Mason University.

2.2. Stimuli

Stimuli were presented on an LG Flatron monitor with a vertical refresh rate of 75 Hz and a horizontal refresh rate of 83 kHz. Modified MATLAB scripts from Vogel and Machizawa (2004) were used to present stimuli and record participants' responses. Each of the bilaterally presented stimulus arrays consisted of one to four locations of colored squares randomly drawn from a list of eight colors (red, blue, green, yellow, magenta, violet, black, and white). The color of the squares did not differ between the memory array and the test array. The stimulus arrays were identical to those described in McCollough et al. (2007); the arrays subtended $4^\circ \times 7.3^\circ$ and were centered 3° to the left or right of a continuously presented central fixation cross on a gray background. Each square subtended $0.49^\circ \times 0.49^\circ$.

At the beginning of each trial, a small, triangular directional cue, was presented for 200 ms above the center fixation-circle; 1200 ms following cue presentation, the memory array was displayed for 150 ms. Following the memory array, there was a 1150 ms retention interval during which only the fixation circle was present. A test array was

then presented for an unlimited amount of time until the participants responded with a two-button choice to indicate if the test array was the same or different from the memory array (see Fig. 1). The inter trial interval (ITI) was set at 500 ms. Participants were given breaks in between each block to avoid fatigue. The length of breaks was unlimited; participants were instructed to take as long of a break as needed and then to press the space bar to proceed to the next block.

2.3. Procedure

The task was a spatial change detection task, modeled after Vogel and Machizawa's color change detection task (Vogel and Machizawa, 2004). Participants were cued to remember the locations of colored squares comprising one (memory array) of the two bilaterally presented arrays while fixating on a cross in the center of the screen; the number of locations to be remembered ranged from one to four. On half of the trials, a single square from the memory array was moved to a randomly selected new location. The hemifield in which a location change occurred was equiprobable. Participants pressed the "z" key with their left index finger to indicate if the memory array and test array were the same and the "/" key with their right index finger to indicate if the memory array and test array were different. Half of the participants received instructions to form a constellation of the spatial locations (e.g. imagine lines between locations to form a shape) to aid encoding of the spatial locations; the remaining half were instructed to remember the individual locations of the colored squares. Participants performed 15 blocks with 12 trials of each set size per block (48 trials in each block), resulting in 180 trials of each set size (total of 720 trials in entire task). In between each block, participants were able to briefly rest before moving on to the next block. All participants completed a practice block prior to recording EEG to become familiar with the task.

2.4. EEG data acquisition and analysis

EEG data was acquired using a NuAmps amplifier and SCAN 4.3 recording software (Compumedics Neuroscan, NC) at a sampling frequency of 500 Hz. A 40-channel electrode cap was used (with the standard 10–20 electrode locations) with the left mastoid electrode serving as the on-line reference. The data were re-referenced to the average of the left and right mastoid electrodes offline. Data were collected from all 34 in-cap electrodes. Eye movements were monitored using electrodes placed on the outer canthus of each eye as well as from electrodes placed above and below the left eye. The impedances of the electrodes were maintained below 5 k Ω . EEG data were filtered online with a high pass filter of 0.10 Hz and a 30 Hz low pass filter was applied offline. Data were epoched from 150 ms before the memory array onset to 1000 millisecond post-stimulus presentation.

Epochs were initially rejected on the basis of drift, extreme voltage, and high frequency noise using the EEGLAB functions 'pop_rejtrend', 'pop_eegthresh', and 'pop_rejspec', respectively. Epochs with a drift of 75 μV or greater (and r^2 of 0.8 or greater), values $\geq \pm 1000 \mu\text{V}$ or

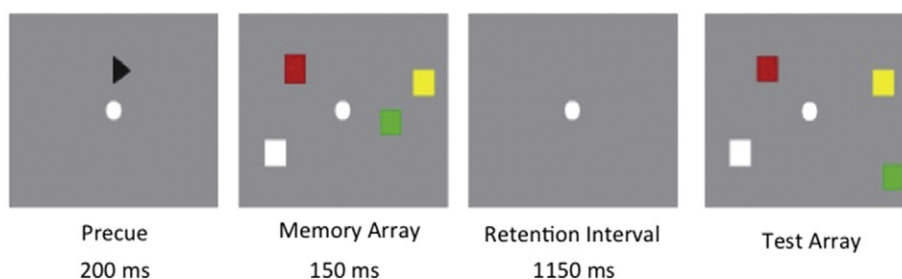


Fig. 1. Example stimuli (not to scale). Participants were cued to remember the locations of the colored squares in the memory array followed by a retention interval. After the retention interval, a test array appeared where the participant responded to the array.

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