Received: 11 May 2018 | Revised: 6 July 2018 | Accepted: 26 July 2018

DOI: 10.1111/psyp.13282

ORIGINAL ARTICLE

WILEY PSYCHOPHYSIOLOGY SPR

Contralateral delay activity tracks the storage of visually presented letters and words

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Funding information
National Eye Institute, Grant/Award Number: P30-EY08126, R01-EY019882 and R01-EY025275; National Institute of Mental Health, Grant/Award Number: R01-MH110378; National Institutes of Health, Grant/Award Number: R01-EY025275, R01-EY019882, R01-MH110378 and P30-EY08126

Abstract

Electrophysiological studies have demonstrated that the maintenance of items in visual working memory (VWM) is indexed by the contralateral delay activity (CDA), which increases in amplitude as the number of objects to remember increases, plateauing at VWM capacity. Previous work has primarily utilized simple visual items, such as colored squares or picture stimuli. Despite the frequent use of verbal stimuli in seminal investigations of visual attention and memory, it is unknown whether temporary storage of letters and words also elicit a typical load-sensitive CDA. Given their close associations with language and phonological codes, it is possible that participants store these stimuli phonologically, and not visually. Participants completed a standard visual change-detection task while their ERPs were recorded. Experiment 1 compared the CDA elicited by colored squares compared to uppercase consonants, and Experiment 2 compared the CDA elicited by words compared to colored bars. Behavioral accuracy of change detection decreased with increasing set size for colored squares, letters, and words. We found that a capacity-limited CDA was present for colored squares, letters, and word arrays, suggesting that the visual codes for letters and words were maintained in VWM, despite the potential for transfer to verbal working memory. These results suggest that, despite their verbal associations, letters and words elicit the electrophysiological marker of VWM encoding and storage.

KEYWORDS

contralateral delay activity, ERPs, verbal working memory, visual working memory

1 | INTRODUCTION

A given stimulus can often be coded in many ways. Written letters and words are a particularly good example of this. Becoming literate involves becoming fluent in automatically transforming these visual stimuli into acoustic and semantic codes (Booth, Perfetti, & MacWhinney, 1999; Humphreys, Evett, & Taylor, 1982; Tanenhaus, Flanigan, & Seidenberg, 1980). Indeed, dedicated areas of cortex appear to underlie the recognition of these special stimuli (McCandliss, Cohen, & Dehaene, 2003; Ossowski & Behrmann, 2015). Because of their dual identity, either visual or verbal codes might be stored in working memory when attempting to remember recently encountered letters and words. In the present study, we ask whether these linguistically meaningful stimuli elicit an electrophysiological component associated with the storage of visual information in working memory: the contralateral delay activity (CDA: Ikkai, McCollough, & Vogel, 2010; Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005; see Luria, Balaban, Awh, & Vogel, 2016, for a review).

The CDA is a sustained negativity recorded over occipital-parietal electrodes that is present when visual information has been encoded into visual working memory (VWM), also referred to as the sustained posterior contralateral negativity (Dell'Acqua, Sessa, Jolicœur, & Robitaille, 2006; Jolicœur, Sessa, Dell'Acqua, & Robitaille, 2006). It is typically maximal over lateral parieto-occipital electrodes (OL/OR or PO7/PO8) and begins approximately 300 ms after stimulus onset, typically sustaining through blank retention intervals. Its hallmark feature is its sensitivity to memory load; the amplitude of the CDA will increase with the number of to-be-remembered stimuli but does not increase further once the capacity of working memory is reached (Vogel & Machizawa, 2004). The CDA has been most often studied using colored stimuli (Vogel & Machizawa, 2004; Vogel et al., 2005), but oriented bars and gratings (Machizawa, Goh, & Driver, 2012; McCollough, Machizawa, & Vogel, 2007; Woodman & Vogel, 2008), simple shapes (Fukuda, Awh, & Vogel, 2010; Luria & Vogel, 2011a), moving targets (Drew & Vogel, 2008), and photographs of real-world objects (Brady, Störmer, & Alvarez, 2016; Galvez-Pol, Calvo-Merino, Capilla, & Forster, 2018; Schmidt, MacNamara, Proudfit, & Zelinsky, 2014; Xie & Zhang, 2018) have also been shown to elicit a load-dependent CDA. However, it is not clear whether the memorization of alphanumeric stimuli elicits a load-dependent CDA.

Alphanumeric stimuli, including words, have been used in countless seminal investigations of visual attention and memory. A short and far from exhaustive list of experiments using alphanumeric characters as stimuli are classics in cognitive psychology (Duncan & Humpreys, 1989; Eriksen & Eriksen, 1974; Eriksen & Hoffman, 1973; Lavie & Tsal, 1994; Neisser, 1964; Schneider & Shiffrin, 1977; Shiffrin & Schneider, 1977; Sperling, 1960; Sternberg, 1966; Treisman & Sato, 1990; Yantis & Jonides, 1990), and visually presented words fare no worse (Craik & Tulving, 1975; Meyer & Schvaneveldt, 1971; Peterson & Peterson, 1959; Stroop, 1935; Waugh & Norman, 1965; see Balota, Yap, & Cortese, 2006). Given their ubiquity as stimuli used to study a variety of mechanisms in cognitive psychology, it is reasonable to ask whether the CDA is sensitive to the encoding and storage of such stimuli.

The presence or absence of a load-dependent CDA for letters and words would provide information about how these stimuli are maintained in memory. On the one hand, one might expect that participants store visually presented letters and words phonologically, as is assumed in many experiments on verbal memory (Baddeley, 2003; Henson, Burgess, & Frith, 2000; Majerus et al., 2014). In this case, the CDA should not scale with set size as these items would not be stored in VWM. On the other hand, participants could instead opt to store arrays of verbal material in a visual format. Previous work has shown a CDA during visual search through arrays of letters (Emrich, Al-Aidroos, Pratt, & Ferber, 2009; Luria & Vogel, 2011b), and for to-be-reported targets (Jolicoeur et al., 2006; Jolicoeur, Brisson, & Robitaille, 2008; Wiegand et al., 2013). Regarding the use of VWM to store words, Predovan et al., 2009 (see also Prime, Dell'Acqua, Arguin, Gosselin, & Jolicoeur, 2011) found a CDA for sets of letters whose amplitude was smaller when the letter sets formed a word, which could mean that VWM stores chunked visual stimuli, but could also reflect a higher probability of phonological coding for words in place of VWM storage. By manipulating set size and comparing results to stimuli known to elicit visual storage, we aim to provide a strong test of the hypothesis that VWM participates in the temporary storage of alphanumeric and verbal stimuli. If arrays of verbal material are indeed stored in VWM, a load-sensitive CDA should be observed for verbal stimuli as well as more typical VWM stimuli (i.e., colored rectangles).

In the current study, we measured the amplitude of the CDA while subjects stored a well-studied stimulus in memory (highly discriminable colored squares; Vogel & Machizawa, 2004; Vogel et al., 2005) and while subjects remembered simple linguistic stimuli (i.e., uppercase letters in Experiment 1 and short words in Experiment 2). Given that the CDA appears to track the number of visual representations being maintained, the presence of a load-dependent CDA for linguistic materials would suggest common storage mechanisms for linguistic stimuli and visual stimuli during short retention intervals. On the other hand, if linguistic stimuli are automatically recoded and stored phonologically, then a load-dependent CDA will not arise, suggesting that storage of alphanumeric and verbal stimuli utilizes verbal working memory exclusively.

2 | EXPERIMENT 1

In Experiment 1, we directly compared the amplitude of the CDA for colored squares and uppercase consonants. If uppercase consonants are encoded and stored verbally, then we should not see a load-dependent CDA. However, if these stimuli are encoded and stored visually, then we would expect to see the CDA amplitude increase as more stimuli are stored in working memory, up until VWM capacity is reached.

2.1 | Method

2.1.1 | Participants

Twenty volunteers from the Vanderbilt community participated in exchange for financial compensation. All participants provided informed consent. Participants were recruited until a pre-established sample size of 12 participants remained after data-driven rejection criteria were applied (detailed below).

This resulted in the data of eight volunteers being excluded due to excessive eye movement and muscular artifacts. We chose 12 participants with approximately 200 trials per cell of the experimental design to be consistent with seminal studies of the CDA using colored squares as memoranda (McCollough, Machizawa, & Vogel, 2007; Vogel et al., 2005).

2.1.2 | Apparatus

The experiment was run in an electrically shielded, soundproof booth. Stimuli were presented on a CRT monitor contained in a Faraday cage, viewed from a distance of approximately 150 cm. Participants input their responses using a Logitech Precision gamepad (Carlisle, Artia, Pardo, & Woodman, 2011).

The EEG recordings were obtained with a 20-channel cap (Electro-Cap International, OH), embedded with tin electrodes that make contact with the skin through electrode gel. Two electrodes were placed at the outer canthi of each eye for recording horizontal eye movements. One tin electrode was placed approximately 2.5 cm below the right eyelid to measure blinks. All impedences were below 4 kΩ. During recording, the right mastoid electrode served as an online reference, and signals were rereferenced to the average of the right and left mastoids offline (Luck, 2005). Signals were amplified 20,000 times (SA Instrumentation Co., CA), with a high-pass filter of 0.01 Hz and a low-pass filter of 100 Hz and sampled at 250 Hz for digitization.

2.1.3 | Stimuli

Stimuli were presented using MATLAB and the Psychophysics Toolbox (Kleiner et al., 2007). Experimental trials consisted of four types of displays: a fixation display, a cue display, a memory sample display, and a memory test

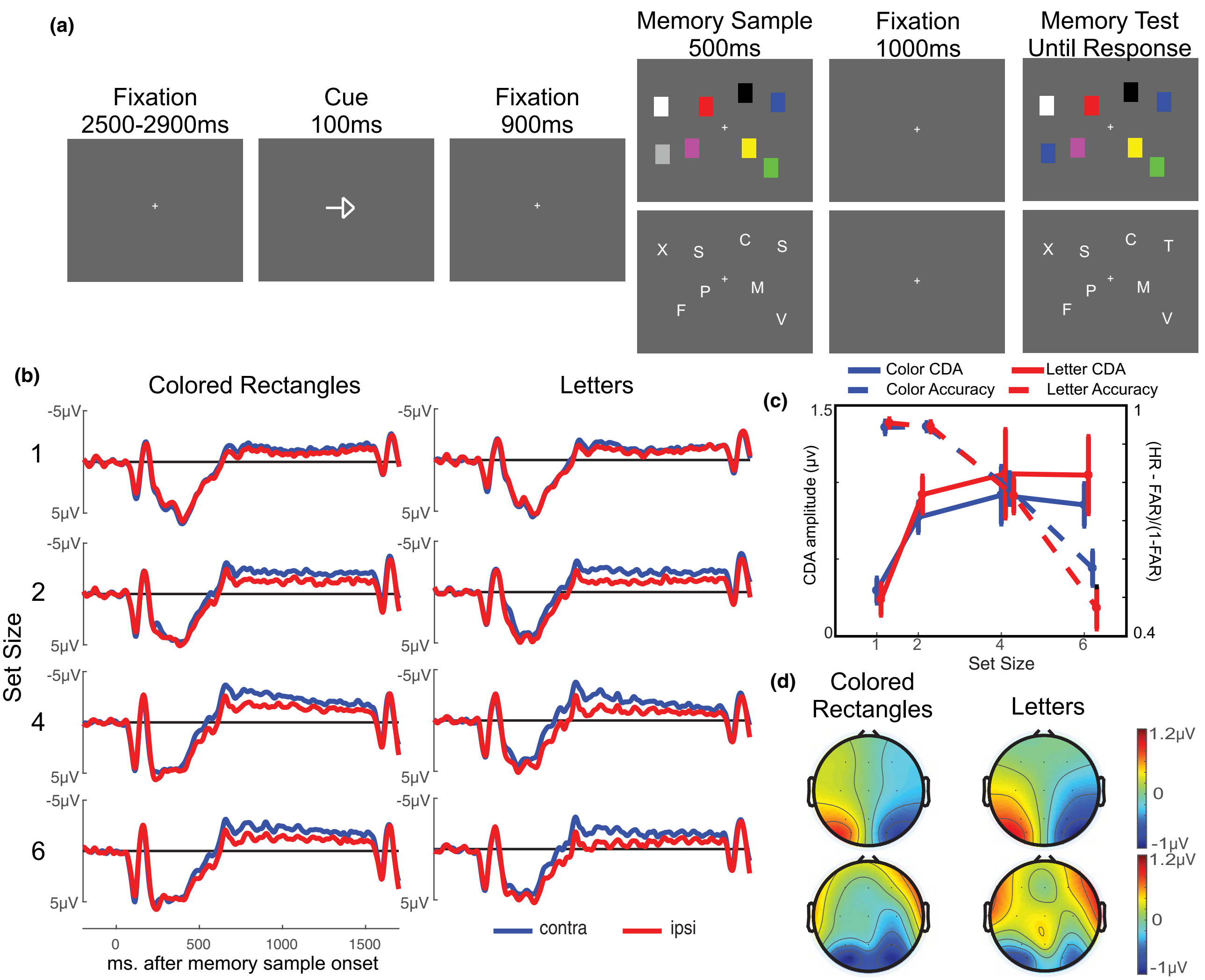

FIGURE 1 (a) Illustrative depiction of trial stimuli in Experiment 1. (b) Contralateral and ipsilateral waveforms, averaged over electrode pairs PO3/PO4, O1/O2, OL/OR, and T5/T6, separated by set size and stimulus type. (c) Mean CDA amplitudes and memory accuracy for each stimulus type and set size. (d) Topographical maps for each stimulus type for the CDA interval, 300–1,500 ms. Upper plots show contra–ipsi voltage distributions, and lower plots show scalp distributions irrespective of attended hemifield

display (see Figure 1a) on gray backgrounds (37 cd/m^2). The fixation display consisted of a white fixation cross (44 cd/m^2; 0.2°) in the center of the screen. The cue display consisted of a white arrow (44 cd/m^2; 0.8° wide and 0.4° tall) in the center of the screen facing either left or right. Memory sample displays comprised a fixation cross (44 cd/m^2; 0.2°) and bilateral sets of either 1, 2, 4, or 6 colored rectangles: red (7 = cd/m^2, $x = 0.58$, $y = 0.34$); green (27 = cd/m^2, $x = 0.27$, $y = 0.59$); blue (6 = cd/m^2, $x = 0.15$, $y = 0.08$); magenta (12 = cd/m^2, $x = 0.25$, $y = 0.14$); yellow (39 = cd/m^2, $x = 0.44$, $y = 0.51$); gray (11 = cd/m^2, $x = 0.26$, $y = 0.28$); white (44 = cd/m^2, $x = 0.26$, $y = 0.28$); or black (0.5 = cd/m^2, $x = 0.27$, $y = 0.31$), sampled without replacement; or 1, 2, 4, or 6 uppercase consonants printed in Arial font: *C, F, M, P, S, T, V,* or *X*, colored in white, 44 cd/m^2, sampled without replacement. Sizes of the two stimuli were equated by using the bounding box surrounding each letter as the possible sizes of colored rectangles (approx. 0.34° wide and 0.4° tall on average). Stimuli were randomly placed in the left or right hemifield by placing them along the circumference of one of three progressively eccentric imaginary circles (2°, 3.8°, 5.5° radius), centered on fixation, such that only three stimuli could be presented on a given circle's circumference. To ensure that all stimuli were placed away from the midline, stimuli appeared only within 60-degree arcs, centered on the horizontal midline (i.e., between two and four o'clock on the right of fixation, and between eight and ten o'clock on the left of fixation). To prevent any overlap, 10 degrees of radial jitter were added to stimulus placement between successive eccentricities. For a given memory sample display, all items were either colored rectangles or letters. Memory test displays were identical to memory sample displays, except that one item, on either the cued or uncued side, could change relative to the memory sample display on a given trial.

2.1.4 | Procedure

Participants completed 1,536 trials, over the course of four blocks. Within each block, participants completed runs of 50 trials, after which they were encouraged to take a short break. Both conditions (set size and stimulus type) were varied randomly from trial to trial. Trials all comprised the following events: an intertrial blank display for 2,200 ms, ±200 ms of jitter, a 500-ms fixation display, a 100-ms cue display, a 900-ms fixation display, a 500-ms memory sample display, a 1,000-ms fixation display, and a memory test display that persisted until a response was entered. Participants were instructed to maintain fixation throughout the trial and to restrict their blinks to the period between their responses and the onset of the arrow-cue on the next trial. Participants were to attend the stimuli in the hemifield indicated by the arrow cue on that trial and to report, upon the memory test display, whether any item in the attended hemifield had changed or none had. Responses were entered using the right hand, with a button for each of the two decisions (change, no change). No articulatory suppression was used, as this is known to discourage verbal coding (Logie, Della Sala, Wynn, & Baddeley, 2000).

2.1.5 | Data analysis

Voltages were baseline corrected by subtracting the mean of the 200 ms preceding each trial. Epochs with artifacts due to blinks, saccades, and amplifier saturation were rejected using a two-step method (Woodman & Luck, 2003). In the first step we rejected trials with artifacts, and in the second step we calculated the averaged horizontal electroculogram (HEOG) for left and right cue trials. If this averaged HEOG exceeded ±3 μV, then the subject was excluded from the analyses. Subjects for whom more than 33% of epochs contained artifacts were also rejected from further analysis. This led to the exclusion of eight participants, and on average 5.44% of trials ($SD = 5.79\%$) were excluded for those participants who were included.

Voltage values were rereferenced to the average of the left and right mastoids. ERPs were calculated for each condition and each participant, excluding epochs marked with artifacts, using MATLAB, and inferential statistics were calculated using JASP (JASP Team, 2018). Greenhouse-Geisser corrections were applied in all cases where the assumption of sphericity was violated. To identify an appropriate temporal window for calculating the CDA amplitude, we plotted the grand-averaged contralateral and ipsilateral ERPs time-locked to the memory sample display for electrodes OL/OR, where the CDA is typically maximal (Vogel et al., 2005), as recommended by Woodman (2010). These plots showed that the contralateral and ipsilateral difference extended until the memory test display offset, justifying a 350–1,500-ms window (see Figure 1b). To identify electrodes contributing to the CDA, we created topographical plots of the contra–ipsi difference wave amplitude in the identified time window. These plots showed that, while the CDA was indeed maximal at OL/OR, contralateral negativity was also present at surrounding electrodes O1/O2, PO3/PO4, and T5/T5 (see Figure 1d). Topographical ERP plots were generated using the *topoplot()* function from EEGLAB (Delorme & Makeig, 2004).

2.2 | Results and discussion

Memory performance was quantified using the method recommended by Rouder, Morey, Morey, and Cowan (2011): (hit rate −false alarm rate)/(1 − false alarm rate). Memory for both colored rectangles and letters was affected by set size, $F(1.20, 13.15) = 87.84$, $p < 0.001$, with memory for letters suffering slightly more than memory for colors as set size increased,

$F(1.49, 16.33) = 3.22$, $p = 0.078$; see Figure 1a. Taking the maximum k estimate from all set sizes for each participant, the average capacity for colored rectangles was 2.47, $SE = 0.14$, and 2.40 for letters, $SE = 0.13$, $t(11) = 0.67$, $p = 0.36$.

The CDA was computed as the mean voltage of the difference wave (ipsilateral − contralateral) between 350 and 1,500 ms following memory sample onset at electrode pairs PO3/PO4, O1/O2, OL/OR, and T5/T6 (see Figure 1b,c). A repeated measures analysis of variance (ANOVA) revealed two main effects: CDA amplitude increased with set size, $F(1.85, 20.38) = 9.37$, $p = 0.002$, and was larger at OL/OR and T5/T6, $F(1.94, 21.30) = 9.92$, $p < 0.001$. Critically, neither the main effect nor interactions involving the factor of stimulus type (colored squares vs. letters) were significant ($p > 0.26$). Given that both stimulus types elicited a load-dependent CDA, these data are consistent with the conclusion that letter stimuli are encoded and maintained using the same neural mechanisms as colored rectangles, that is, VWM.[1]

Although our sample is not ideal for correlational analyses, we examined the relationships between performance and CDA amplitudes between stimulus types. We did this because these measures should be related under the hypothesis that all stimulus types are similarly stored in memory. Average accuracy for colored rectangles was correlated with average letter accuracy, $r(10) = 0.55$, $p = 0.063$, and CDA amplitude was likewise correlated between stimulus types, $r(10) = 0.69$, $p = 0.001$. Thus, further support for the conclusion that both stimulus types were stored in VWM comes from significant correlations between performance and ERPs.

3 | EXPERIMENT 2

Experiment 1 showed that remembering visually presented letters over a short period appears to recruit similar neural mechanisms as colored rectangles, the canonical stimulus for VWM (Luck & Vogel, 1997; Zhang & Luck, 2008). In Experiment 2, we asked whether visually presented words would also elicit a capacity-limited CDA. We measured memory performance at smaller set sizes (1, 2, 3, 4) in this experiment to avoid any potential issues with crowding, given the larger area of space subtended by words.

3.1 | Method

3.1.1 | Participants

Sixteen participants from the same pool, none of whom participated in Experiment 1, volunteered for Experiment 2. All were paid for their participation and provided informed consent. Data from four subjects were excluded from analyses due to excessive artifacts using the two-step procedure described previously.

3.1.2 | Stimuli

Stimuli used in Experiment 2 were identical to those in Experiment 1 with the exception of the memory sample and memory test displays. Instead of being shown colored rectangles and letters, participants were shown either colored rectangles or three-letter words. The following words were used: BED, CUP, DOG, HAT, LEG, MAP, SUN, TOY. These words were chosen to fit the following criteria: different first letter, consonant-vowel-consonant structure, and high natural language frequency (Browne, Culligan, & Phillips, 2013). The colored rectangles condition was designed to visually equate the sizes of the colored stimuli with the words. The words and colored rectangles were both approximately $0.71° \times 0.25°$. Finally, participants were shown 1, 2, 3, or 4 stimuli bilaterally.

3.2 | Results and discussion

Behavioral performance was again assessed as the corrected hit rate (Rouder et al., 2011) and is shown in Figure 2c. Set size significantly reduced change detection accuracy, $F(1.54, 16.93) = 41.04$, $p < 0.001$. Because subjects were generally worse at detecting changes in the words, there was a significant effect of stimulus type, $F(1, 11) = 27.20$, $p < 0.001$, and an interaction of set size and stimulus type due to particularly poor performance when remembering a large set size of words, $F(1.77, 19.47) = 20.17$, $p < 0.001$. Estimated capacity for colored rectangles was slightly higher than Experiment 1, $M = 3.14$, $SE = 0.20$, and significantly lower for words, $M = 2.14$, $SE = 0.25$, $t(11) = 5.74$, $p < 0.001$.

Extending the findings of Experiment 1, we found that the words in Experiment 2 elicited a capacity-limited pattern of CDA, similar to what has repeatedly been found with simple colored objects. This can be seen in Figure 2b–d. The CDA was computed identically to Experiment 1, and we again found a main effect of set size because the CDA amplitude increased as set size increased, $F(3, 33) = 11.81$, $p < 0.001$, as well as a main effect of stimulus type, $F(1, 11) = 4.90$, $p = 0.049$, because the CDA was larger for words than colored rectangles. These effects also varied by electrode, $Fs > 2.80$, $p < 0.007$, such that the difference between stimulus types was present only at OL/OR and T5/T6, and the set size effect

[1]Comparing ERPs for words and letters irrespective of target hemifield showed a sustained difference over central and parietal electrodes beginning at approximately 650 ms after the memory sample display and persisting until the memory test array, as well as a larger frontal P1 for letters. The mean amplitude of the late positivity for electrodes Cz, Pz, PO3, and PO4 between 650 ms and 1,500 ms verified that letters elicited more positivity than colors, $F(1, 11) = 5.90$, $p = 0.033$, with no interactions between stimulus type and either electrode or set, $Fs < 1.22$, $ps > 0.31$. The mean amplitude measured for electrodes Fz, F3, and F4 between 120 ms and 300 ms showed more positivity for letters than colors, $F(1, 11) = 12.27$, $p = 0.005$, which did not interact with set size or electrode, $Fs < 0.81$, $ps > 0.41$.

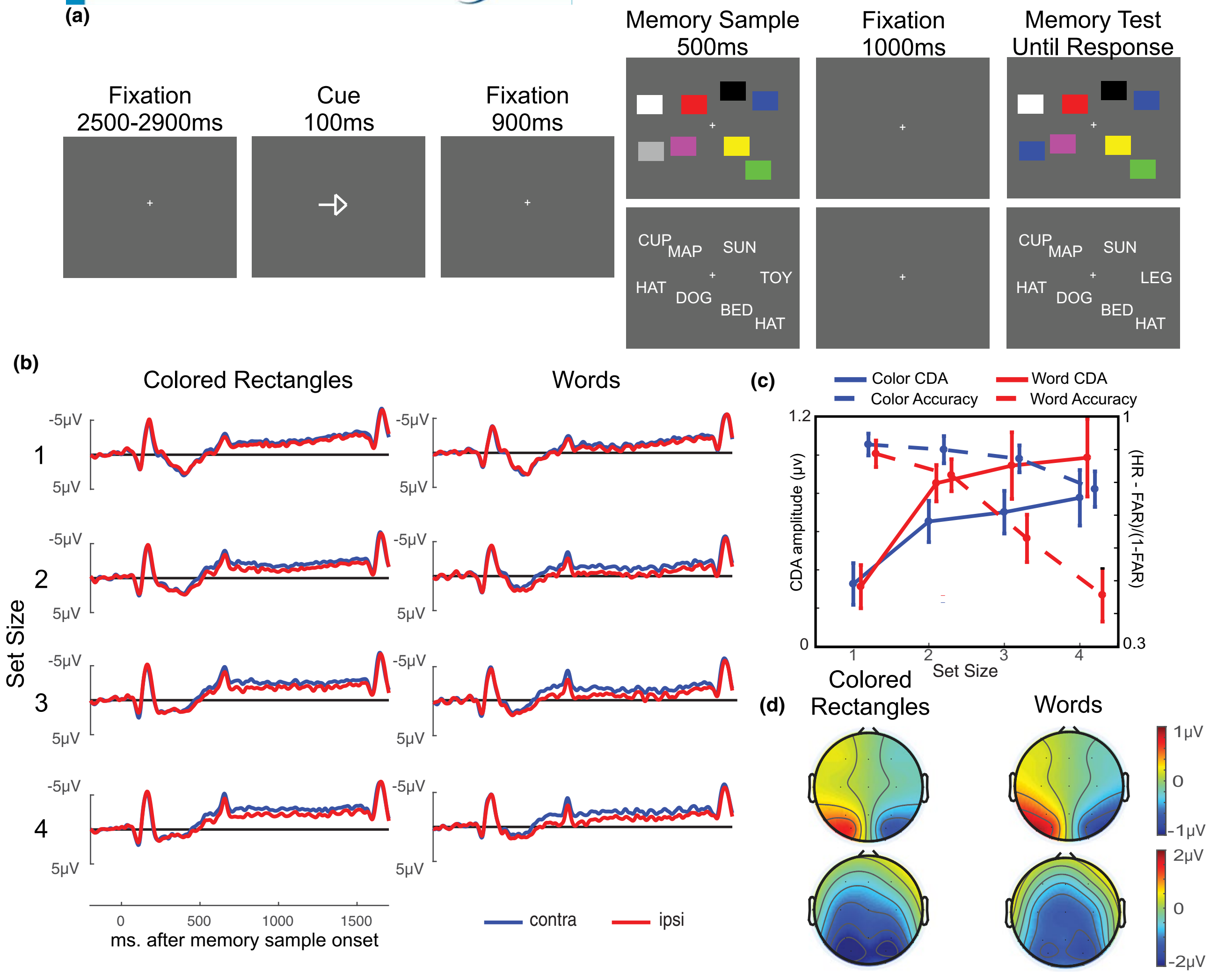

FIGURE 2 (a) Illustrative depiction (not to scale) of trial stimuli in Experiment 2. (b) Contralateral and ipsilateral waveforms, averaged over electrode pairs PO3/PO4, O1/O2, OL/OR, and T5/T6, separated by set size and stimulus type. (c) Mean CDA amplitudes and memory accuracy for each stimulus type and set size. (d). Topographical maps for each stimulus type for the CDA interval, 300–1,500 ms. Upper plots show contra–ipsi voltage distributions, and lower plots show voltage distributions irrespective of attended hemifield

was most pronounced at OL/OR. The CDA overall was largest at OL/OR and smallest at O1/O2 as well resulting in a main effect of electrode, $F(3, 33) = 6.93$, $p < 0.001$. Importantly, set size and stimulus type did not interact with each other, $F(3, 33) = 1.50$, $p = 0.23$, nor was there a three-way interaction, $F(9, 99) = 1.28$, $p = 0.26$. These results extend the findings of Experiment 1, showing that verbal stimuli—three-letter words—elicit a load-dependent CDA.[2] As in Experiment 1, behavioral accuracy, $r(10) = 0.82$, $p = 0.001$, and CDA amplitudes, $r(10) = 0.85$, $p < 0.001$, for the two stimulus types were correlated across observers, lending support to the conclusion that both stimuli were stored visually.

4 | GENERAL DISCUSSION

In the current study, we found that, despite their linguistic associations, both letters and short words elicited a load-dependent CDA, the canonical measure of storage in VWM. Somewhat surprisingly, the amplitude of the CDA was larger for words than for colored rectangles, despite poorer change detection performance. This fits with the general notion that working memory capacity is reduced for more complex objects (Alvarez & Cavanagh, 2004). Although it is well established that the CDA is a good measure of different

[2]Although the CDA did not differ importantly based on the stimulus type, other ERP components do appear to be different. Contrasting word- and color-related ERPs showed that the words elicited a broadly distributed frontal positivity. The mean amplitude for the positivity, measured the same way as in Experiment 1, showed a more positive potential for words compared to colored rectangles, $F(1, 11) = 5.45$, $p = 0.039$, but this varied by electrode and set size, $F(2.54, 27.90) = 4.59$, $p = 0.01$. Analysis at each electrode showed that the difference seemed to disappear at higher set sizes for Cz, $F(3, 33) = 2.55$, $p = 0.07$, with main effects of stimulus type at parietal electrodes, $Fs(1, 11) > 3.74$, $ps < 0.08$.

capacity limits of individuals (Vogel & Machizawa, 2004; Vogel et al., 2005), this is evidently not the case when comparing across stimulus types, arguably because more complex stimuli demand more available capacity (Perez, Ashby, Awh, & Vogel, as cited in Fukuda, Awh, et al., 2010; Awh, Barton, & Vogel, 2007). However, this cannot explain the larger amplitude for word stimuli, given that these differences occurred even at set sizes beyond working memory capacity.

There appear to be two ways to account for this finding. One is that more visual information is encoded about words than colors, similarly to what has been argued for real-world objects by Brady et al. (2016). Although somewhat counterintuitive, given that memory performance was worse for words than colored squares, it is possible that more features are encoded per item in these cases, despite equivalent or even fewer items being encoded overall, which would reduce change detection performance (Awh et al., 2007; Wilson, Adamo, Barense, & Ferber, 2012). A second possibility is that the difference reflects demands on spatial attention, given that words require discrimination of higher spatial frequencies and the processing of multiple features per item, which may require sustained spatial attention. The CDA has previously been linked to spatial attention in search (Emrich et al., 2009) and is enlarged when orientation-defined targets are lower in contrast (Töllner, Conci, Rusch, & Müller, 2013). Encoding of colored stimuli into working memory, on the other hand, is not affected by contrast (Ikkai et al., 2010). If this is the case, our data may reflect overlapping components, one reflecting focused spatial attention and one reflecting memory storage (see Becke, Müller, Vellage, Schoenfeld, & Hopf, 2015).

The CDA is considered to be a marker of VWM storage (Luria et al., 2016; McCollough et al., 2007; Vogel & Machizawa, 2004; but see Berggren & Eimer, 2016; Eimer & Kiss, 2010; Katus & Eimer, 2015), and so the present results fit with the possibility that participants store alphanumeric and verbal stimuli in VWM during change detection tasks such as the one used here. These results also fit well with fMRI studies that show recruitment of posterior parietal cortex (PPC) for both simple visual stimuli and for verbal stimuli (Majerus et al., 2011, 2014 ; Todd & Marois, 2004), suggesting that PPC could participate in maintaining diverse codes (Xu, 2017).

Whereas alphanumeric stimuli have been foundational in visual cognition research, they are often considered to be phonological stimuli (Henson et al., 2000; Majerus et al., 2014). Although phonological storage of verbal materials appears to be the modal view of how visually presented alphanumeric characters and words are stored (Baddeley, 2003), there is also evidence for lasting visual coding of such materials. Logie and colleagues (2000) found that fewer items are recalled from lists of visually similar words and letter pairs compared to visually dissimilar word and letter pairs, suggesting the involvement of VWM in the short-term representation of visual materials (see also Posner, Boies, Eichelman, & Taylor, 1969). Fiebach, Rissman, and D'Esposito (2006) showed that an area in left inferotemporal cortex, which is selectively activated by words compared to nonwords, showed load-sensitive activation when visually presented words are stored in working memory. Furthermore, similarities in BOLD responses for stimuli that recruit VWM (colored squares) and visually presented words have been shown by Majerus and colleagues. Majerus et al. (2011) showed that maintaining letters in working memory produces a load-dependent, opponent activation pattern between the intraparietal sulcus and temporal-parietal junction, similar to what is observed for colored squares (Todd & Marois, 2004). Majerus et al. (2014) have further shown that it is possible to decode working memory load (number of items stored) between colored squares and visually presented letter strings using fMRI, notably from the intraparietal sulcus. These results support the present findings of similar working memory mechanisms involved in retaining information about words and visual stimuli over short delays.

How might our results be useful for understanding reading? Our experiments required the mere memorization of letters and words over a brief delay, whereas reading demands that participants parse orthographic forms from visual input and translate these into semantic or phonological codes (Coltheart, Rastle, Perry, Landon, & Ziegler, 2001). Processing of individual words, as measured by eye movements (Rayner, 1998), and ERPs, such as the N400 (Kutas & Federmeier, 2011), is affected not only by that word's frequency, but also its relationship to neighboring words (Dambacher & Kliegl, 2007). Whether these interactions reflect concurrent visual processing or not is debated, with models favoring serial word recognition as well as concurrent word processing (Murray, Fischer, & Tatler, 2013; Reichle, Liversedge, Pollatsek, & Rayner, 2009; Trukenbrod & Engbert, 2012; Wang & Inhoff, 2013; White, Palmer, & Boynton, 2018). Given its load sensitivity, the CDA could provide a useful additional measure of the amount of visual information being concurrently processed during sentence comprehension.

Finally, it is worth noting that, while letters and words did not differ from colored rectangles in their ability to elicit a CDA, we observed differences in ERPs that have been associated with long-term recognition memory (Rugg & Curran, 2007; Rugg & Doyle, 1992). Given that no memory retrieval was required at the encoding of the memory sample arrays, these ERPs may reflect the automatic recognition of familiar forms for letters and possibly the activation of semantic memory for words, due to cumulative priming.

ACKNOWLEDGEMENTS

The present work was supported by the National Institutes of Health (R01-EY025275, R01-EY019882, R01-MH110378, P30-EY08126). We are grateful to Chong Zhao for his help with data collection.

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How to cite this article: Rajsic J, Burton JA, Woodman GF. Contralateral delay activity tracks the storage of visually presented letters and words. *Psychophysiology*. 2018;e13282. https://doi.org/10.1111/psyp.13282