

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23

The contralateral delay activity tracks the storage of visually presented letters and words

Jason Rajsic¹, Jane A. Burton², & Geoffrey F. Woodman^{1,2}

¹ Department of Psychological Sciences

² Neuroscience Program

Vanderbilt University

Accepted: July 26, 2018 at Psychophysiology

Word count: 4,336

Abstract: 223

Please address correspondence to:

Jason Rajsic

221 Wilson Hall

111 21st Ave., Nashville TN, 37240

jason.rajsic@vanderbilt.edu

24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45

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 letter stimuli in seminal investigations of visual attention and memory, it is unknown whether VWM for letters also elicits a typical load-sensitive CDA. Given their close associations with language and phonological codes, it is possible that participants store letter stimuli phonologically, and not visually. Participants completed a standard visual change-detection task while their event-related potentials 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, letter, 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 also elicit the electrophysiological marker of VWM encoding and storage.

46 A given stimulus can often be coded in many ways. Written letters and words are a
47 particularly good example of this. Becoming literate involves becoming fluent in
48 automatically transforming these visual stimuli into acoustic and semantic codes
49 (Tanenhaus, Flanigan, & Seidenberg, 1980; Humphreys, Evett, & Taylor, 1982; Booth,
50 Perfetti, & MacWhinney, 1999). Indeed, dedicated areas of cortex appear to underlie the
51 recognition of these special stimuli (McCandliss, Cohen, & Dehaene, 2003; Ossowski &
52 Behrmann, 2015). Because of their dual identity, either visual or verbal codes might be
53 stored in working memory when attempting to remember recently encountered letters and
54 words. In the present study, we ask whether these linguistically meaningful stimuli elicit
55 an electrophysiological component associated with the storage of visual information in
56 working memory: the contralateral delay activity (CDA: Vogel & Machizawa, 2004;
57 2005; Ikkai, McCollough, Vogel, 2010; see Luria, Balaban, Awh, & Vogel, 2016 for a
58 review).

59 The CDA is a sustained negativity recorded over occipital-parietal electrodes that
60 is present when visual information has been encoded into visual working memory, also
61 referred to as the sustained posterior contralateral negativity (SPCN; Dell'Acqua, Sessa,
62 Jolicœur, & Robitaille, 2006; Jolicœur, Sessa, Dell'Acqua, & Robitaille, 2006). It is
63 typically maximal over lateral parieto-occipital electrodes (OL/OR, or PO7/PO8) and
64 begins approximately 300ms after stimulus onset, typically sustaining through blank
65 retention intervals. Its hallmark feature is its sensitivity to memory load; the amplitude of
66 the CDA will increase with the number of to-be-remembered stimuli, but does not
67 increase further once the capacity of working memory is reached (Vogel & Machizawa,
68 2004). The CDA has been most often studied using colored stimuli (Vogel & Machizawa,

69 2004; Vogel, McCollough, & Machizawa, 2005), but oriented bars and gratings
70 (McCollough, Machizawa, & Vogel, 2007; Woodman & Vogel, 2008; Machizawa, Goh,
71 & Driver, 2012), simple shapes (Fukuda, Awh, & Vogel, 2010; Luria & Vogel, 2011a),
72 moving targets (Drew & Vogel, 2008), and photographs of real-world objects (Schimdt,
73 MacNamara, Proudfit, & Zelinsky, 2014; Brady, Störmer, & Alvarez, 2016; Xie &
74 Zhang, 2018; Galvez-Pol, Calvo-Merino, Capilla, & Forster, 2018) have also been shown
75 to elicit a load-dependent CDA. However, it is not clear whether the memorization of
76 alphanumeric stimuli elicits a load-dependent CDA.

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

88 The presence or absence of a load-dependent CDA for letters and words would
89 provide information about how these stimuli are maintained in memory. On the one hand,
90 one might expect that participants store visually presented letters and words
91 phonologically, as is assumed in many experiments on verbal memory (Henson, Burgess,

92 & Frith, 1999; Baddeley, 2003; Majerus et al., 2014). In this case, the CDA should not
93 scale with set size as these items would not be stored in VWM. On the other hand,
94 participants could instead opt to store arrays of verbal material in a visual format.
95 Previous work has shown a CDA during visual search through arrays of letters (Emrich,
96 Al-Aidroos, Pratt, & Ferber, 2009; Luria & Vogel, 2011b), and for to-be reported targets
97 (Jolicoeur et al., 2006; Jolicoeur, Brisson, & Robitaille, 2008; Wiegand et al., 2013).
98 Regarding the use of VWM to store words, Predovan et al., 2009 (see also Prime et al.,
99 2011) found a CDA for sets of letters whose amplitude was smaller when the letter sets
100 formed a word, which could mean that VWM stores chunked visual stimuli, but could
101 also reflect a higher probability of phonological coding for words in place of VWM
102 storage. By manipulating set size, and comparing results to stimuli known to elicit visual
103 storage, we aim to provide a strong test of the hypothesis that VWM participates in the
104 temporary storage of alphanumeric and verbal stimuli. If arrays of verbal material are
105 indeed stored in VWM, a load sensitive CDA should be observed for verbal stimuli as
106 well as more typical VWM stimuli (i.e., colored rectangles).

107 In the current study, we measured the amplitude of the CDA while subjects stored
108 a well-studied stimulus in memory (highly discriminable colored squares; Vogel &
109 Machizawa, 2004; Vogel, McCollough, & Machizawa, 2007) and while subjects
110 remembered simple linguistic stimuli (i.e., uppercase letters in Experiment 1 and short
111 words in Experiment 2). Given that the CDA appears to track the number of visual
112 representations being maintained, the presence of a load-dependent CDA for linguistic
113 materials would suggest common storage mechanisms for linguistic stimuli and visual
114 stimuli during short retention intervals. On the other hand, if linguistic stimuli are

115 automatically recoded and stored phonologically, then a load-dependent CDA will not
116 arise, suggesting that storage of alphanumeric and verbal stimuli utilizes verbal working
117 memory exclusively.

118 **Experiment 1**

119 In Experiment 1, we directly compared the amplitude of the CDA for colored
120 squares and uppercase consonants. If lowercase consonants are encoded and stored
121 verbally, then we should not see a load-dependent CDA. On the other hand, if these
122 stimuli are encoded and stored visually, then we would expect to see the CDA amplitude
123 increase as more stimuli are stored in working memory, up until visual working memory
124 capacity is reached.

125 **Participants**

126 Twenty volunteers from the Vanderbilt community participated in exchange for
127 financial compensation. All participants provided informed consent. Participants were
128 recruited until a pre-established sample size of twelve participants remained after data-
129 driven rejection criteria were applied (detailed below). This resulted in the data of eight
130 volunteers being excluded due to excessive eye movement and muscular artifacts. We
131 chose twelve participants with approximately 200 trials per cell of the experimental
132 design to be consistent with seminal studies of the CDA using colored squares as
133 memoranda (Vogel & Machizawa, 2005; McCullough, Vogel, & Machizawa, 2007).

134 Methods**135 Apparatus**

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

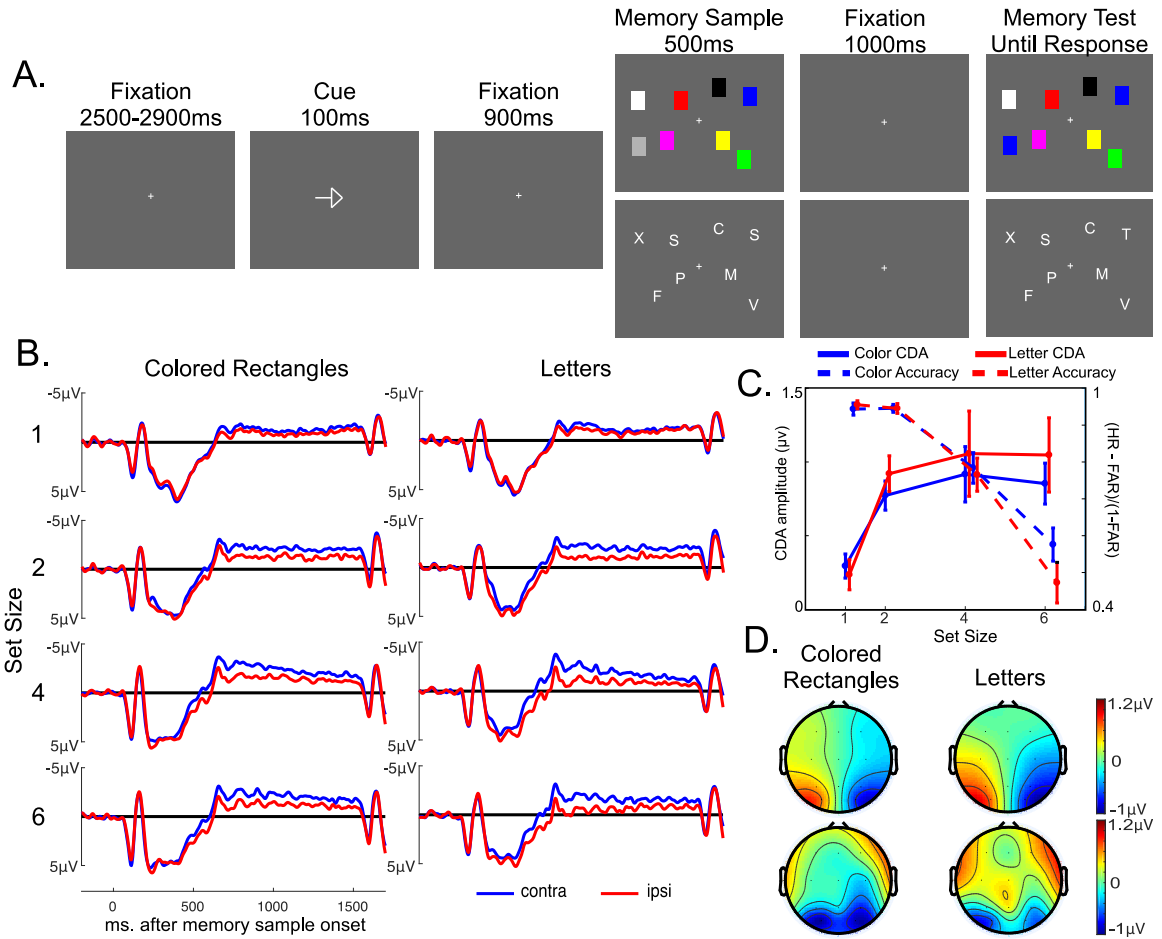
140 The EEG recordings were obtained with a 20-channel cap (Electro-cap
141 International, OH), embedded with tin electrodes that make contact with the skin through
142 electrode gel. Two electrodes were placed at the outer canthi of each eye for recording
143 horizontal eye movements. One tin electrode was placed approximately 2.5 cm below the
144 right eyelid to measure blinks. All impedences were below 4k Ω . During recording, the
145 right mastoid electrode served as an online reference, and signals were re-referenced to
146 the average of the right and left mastoids offline (Luck, 2005). Signals were amplified
147 20,000 times (SA Instrumentation Co., CA), with a high-pass filter of 0.01 Hz and a low-
148 pass filter of 100 Hz and sampled at 250 Hz for digitization.

149 Stimuli

150 Stimuli were presented using Matlab and the Psychophysics Toolbox (Kleiner,
151 Brainard, Pelli, Ingling, Murray, & Broussad, 2007). Experimental trials consisted of four
152 types of displays: a fixation display, a cue display, a memory sample display, and a
153 memory test display (see Figure 1A) on gray backgrounds (37 cd/m²). The fixation
154 display consisted of a white fixation cross (44 cd/m²; 0.2°) in the center of the screen.
155 The cue display consisted of a white arrow (44 cd/m²; 0.8° wide and 0.4° tall) in the
156 center of the screen facing either left or right. Memory sample displays comprised a

157 fixation cross (44 cd/m^2 ; 0.2°) and bilateral sets of either 1, 2, 4, or 6 colored rectangles
158 (red ($7 = \text{cd/m}^2$, $x = 0.58$, $y = 0.34$), green ($27 = \text{cd/m}^2$, $x = 0.27$, $y = 0.59$), blue ($6 =$
159 cd/m^2 , $x = 0.15$, $y = 0.08$), magenta ($12 = \text{cd/m}^2$, $x = 0.25$, $y = 0.14$), yellow ($39 = \text{cd/m}^2$,
160 $x = 0.44$, $y = 0.51$), gray ($11 = \text{cd/m}^2$, $x = 0.26$, $y = 0.28$), white ($44 = \text{cd/m}^2$, $x = 0.26$, $y =$
161 0.28), or black ($0.5 = \text{cd/m}^2$, $x = 0.27$, $y = 0.31$), sampled without replacement), or 1, 2, 4,
162 or 6 uppercase consonants printed in Arial font (C, F, M, P, S, T, V, or X, colored in
163 white, 44 cd/m^2 , sampled without replacement). Sizes of the two stimuli were equated by
164 using the bounding box surrounding each letter as the possible sizes of colored rectangles
165 (approx. 0.34° wide and 0.4° tall on average). Stimuli were randomly placed in the left or
166 right hemifield by placing them along the circumference of one of three progressively
167 eccentric imaginary circles (2° , 3.8° , 5.5° radius), centered on fixation, such that only
168 three stimuli could be presented on a given circle's circumference. To ensure that all
169 stimuli were placed away from the midline, stimuli only appeared within 60 degree arcs,
170 centered on the horizontal midline (i.e., between two and four o'clock on the right of
171 fixation, and between eight and ten o'clock on the left of fixation). To prevent any
172 overlap, 10 degrees of radial jitter was added to stimulus placement between successive
173 eccentricities. For a given memory sample display, all items were either colored
174 rectangles or letters. Memory test displays were identical to memory sample displays,
175 except that one item, on either the cued or uncued side, could change relative to the
176 memory sample display on a given trial.

177



178

179

Figure 1. The task and results of Experiment 1. Illustrative depiction of trial

180

stimuli in Experiment 1 (A). Contralateral and ipsilateral waveforms, averaged over

181

electrode pairs PO3/PO4, O1/O2, OL/OR, and T5/T6, separated by Set Size and Stimulus

182

Type (B). Mean CDA amplitudes and memory accuracy for each stimulus type and set

183

size (C). Topographical maps for each stimulus type for the CDA interval, 300ms –

184

1500ms. Upper plots show contra – ipsi voltage distributions and lower plots show scalp

185

distributions irrespective of attended hemifield (D).

186

187 **Procedure**

188 Participants completed 1536 trials, over the course of 4 blocks. Within each
189 block, participants completed runs of 50 trials, after which they were encouraged to take
190 a short break. **Both conditions (set size and stimulus type) were varied randomly**
191 **from trial to trial.** Trials all comprised the following events: an inter-trial blank display
192 for 2200ms, +/- 200ms of jitter, a 500ms fixation display, a 100ms cue display, a 900ms
193 fixation display, a 500ms memory sample display, a 1000ms fixation display, and a
194 memory test display that persisted until a response was entered. Participants were
195 instructed to maintain fixation throughout the trial, and to restrict their blinks to the
196 period between their responses and the onset of the arrow-cue on the next trial.
197 Participants were to attend the stimuli in the hemifield indicated by the arrow cue on that
198 trial, and to report, upon the memory test display, whether an item in the attended
199 hemifield had changed or none had. Responses were entered using the right hand, with a
200 button for each of the two decisions (change, no change). No articulatory suppression
201 was used, as this is known to discourage verbal coding (Logie, Della Sala, Wynn, &
202 Baddeley, 2000).

203 **Data Analysis**

204 Voltages were baseline corrected by subtracting the mean of the 200ms preceding
205 each trial. Epochs with artifacts due to blinks, saccades, and amplifier saturation were
206 rejected using a two-step method (Woodman & Luck, 2003). The first step is rejecting
207 trials with artifacts, and in the second step we calculated the averaged horizontal
208 electroculogram (HEOG) for left and right cue trials. If this averaged HEOG exceeded
209 +/- 3 μ V, then the subject was excluded from the analyses, as were subjects for whom

210 more than 33% of epochs contained artifacts were rejected from further analysis. This led
211 to the exclusion of eight participants, and on average 5.44% of trials ($SD = 5.79\%$) of
212 trials were excluded for those participants who were included.

213 Voltage values were re-referenced to the average of the left and right mastoids.
214 Event-related potentials (ERPs) were calculated for each condition and each participant,
215 excluding epochs marked with artifacts, using Matlab, and inferential statistics were
216 calculated using JASP (JASP Team, 2018). Greenhouse-Geisser corrections were applied
217 in all cases where the assumption of sphericity was violated. To identify an appropriate
218 temporal window for calculating the CDA amplitude, we plotted the grand average
219 contralateral and ipsilateral ERPs time-locked to the memory sample display for
220 electrodes OL/OR, where the CDA is typically maximal (Vogel & Machizawa, 2005), as
221 recommended by Woodman (2010). These plots showed that the contralateral and
222 ipsilateral difference extended until the memory test display onset, justifying a 350ms-
223 1500ms window (see Figure 1B). To identify electrodes contributing to the CDA, we
224 created topographical plots of the contra-ipsi difference wave amplitude in the identified
225 time window. These plots showed that while the CDA was indeed maximal at OL/OR,
226 contralateral negativity was also present at surrounding electrodes O1/O2, PO3/PO4, and
227 T5/T5 (see Figure 1D). Topographical ERP plots were generated using the `topoplot()`
228 function from EEGLAB (Delorme & Makeig, 2004).

229 **Results and Discussion**

230 Memory performance was quantified using the method recommended by Rouder,
231 Morey, Morey, & Cowan (2011); $(Hit\ Rate - False\ Alarm\ Rate)/(1 - False\ Alarm\ Rate)$.
232 Memory for both colored rectangles and letters was affected by set size, $F(1.20, 13.15) =$

233 87.84, $p < .001$, with memory for letters suffering slightly more than memory for colors
234 as set size increased, $F(1.49, 16.33) = 3.22$, $p = .078$, see Figure 1A. Taking the
235 maximum k estimate from all set sizes for each participant, the average capacity for
236 colored rectangles was 2.47, $SE = 0.14$, and was 2.40 for letters, $SE = 0.13$, $t(11) = 0.67$,
237 $p = .36$.

238 The CDA was computed as the mean voltage of the difference wave (ipsilateral –
239 contralateral) between 350ms and 1500ms following memory sample onset at electrode
240 pairs PO3/PO4, O1/O2, OL/OR, and T5/T6 (see Figure 1B-C). A repeated-measures
241 ANOVA revealed two main effects: CDA amplitude increased with set size, $F(1.85,$
242 $20.38) = 9.37$, $p = .002$, and was larger at OL/OR and T5/T6, $F(1.94, 21.30) = 9.92$, $p <$
243 $.001$. Critically, neither the main effect nor interactions involving the factor of stimulus
244 type (colored squares versus letters) were significant ($p > .26$). Given that both stimulus
245 types elicited a load-dependent CDA, these data are consistent with the conclusion that
246 letter stimuli are encoded and maintained using the same neural mechanisms as colored
247 rectangles, that is, visual working memory¹.

¹ Comparing ERPs for words and letters irrespective of target hemifield showed a sustained difference over central and parietal electrodes beginning at approximately 650ms 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 650ms and 1500ms verified that letters elicited more positivity than colors, $F(1, 11) = 5.90$, $p = .033$, with no interactions between stimulus type and either electrode or set, $F_s < 1.22$, $p_s > .31$. The mean amplitude measured for electrodes Fz, F3, and F4 between 120ms and 300ms showed more

248 Although our sample is not ideal for correlational analyses, we examined the
249 relationships between performance and CDA amplitudes between stimulus types. We did
250 this because these measures should be related under the hypothesis that all stimulus types
251 are similarly stored in memory. Average accuracy for colored rectangles was correlated
252 with average letter accuracy, $r(10) = .55, p = .063$, and CDA amplitude was likewise
253 correlated between stimulus types, $r(10) = .69, p = .001$. Thus, further support for the
254 conclusion that both stimulus types were stored in VWM comes from significant
255 correlations between performance and ERPs.

256

257

Experiment 2

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

positivity for letters than colors, $F(1, 11) = 12.27, p = .005$, which did not interact with
set size nor electrode, $F_s < 0.81, p_s > .41$.

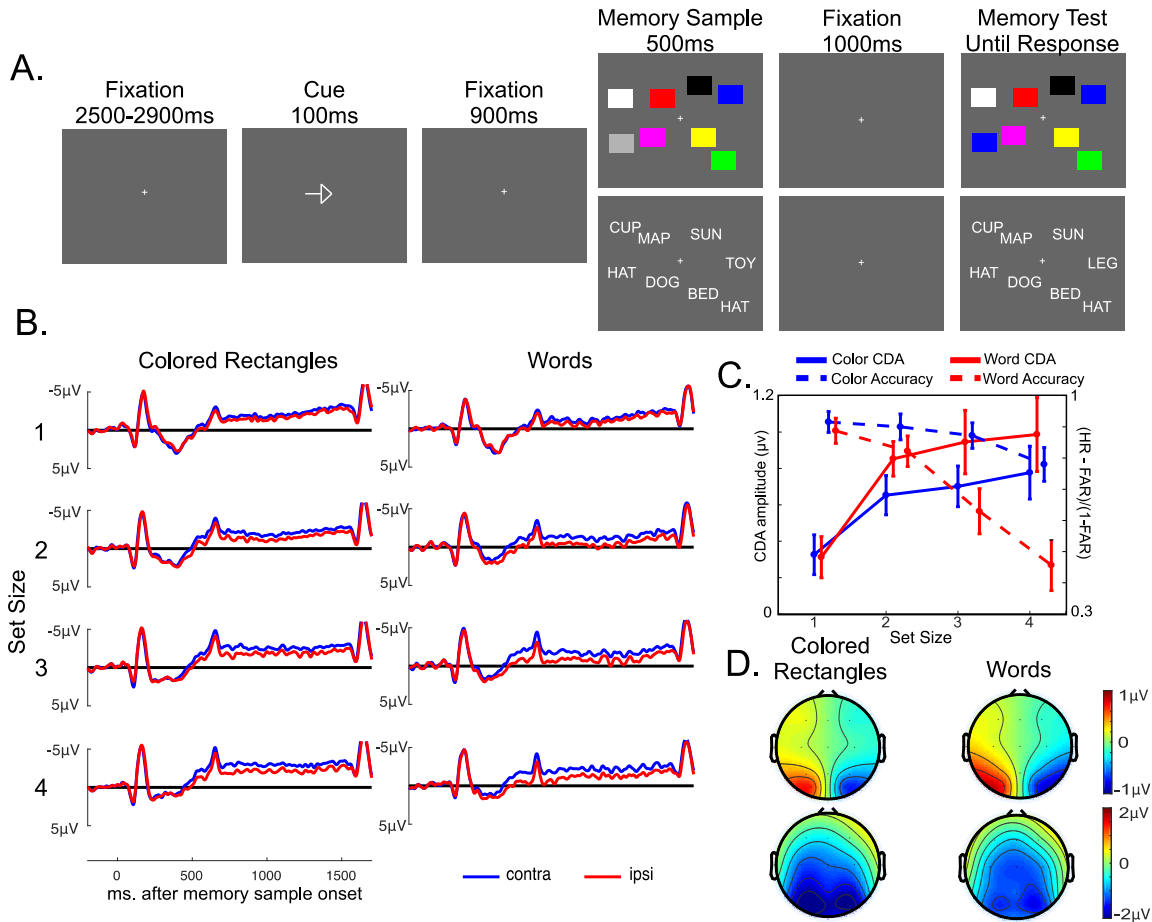
265 **Method**

266 **Participants**

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

271 **Stimuli**

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



282

283 **Figure 2.** Illustrative depiction (not to scale) of trial stimuli in Experiment 2 with
 284 stimulus timings (A). Contralateral and ipsilateral waveforms, averaged over electrode
 285 pairs PO3/PO4, O1/O2, OL/OR, and T5/T6, separated by set size and stimulus type (B).
 286 Mean CDA amplitudes and memory accuracy for each stimulus type and set size (C).
 287 Topographical maps for each stimulus type for the CDA interval, 300ms – 1500ms.
 288 Upper plots show contra - ipsi voltage distributions and lower plots show voltage
 289 distributions irrespective of attended hemifield (D).

290

291 **Results**

292 Behavioral performance was again assessed as the corrected hit rate (Rouder,
293 Morey, Morey, & Cowan, 2011), and is shown in Figure 2C. Set size significantly
294 reduced change detection accuracy, $F(1.54, 16.93) = 41.04, p < .001$. Because subjects
295 were generally worse at detecting changes in the words, there was a significant effect of
296 stimulus type, $F(1, 11) = 27.20, p < .001$, and an interaction of set size and stimulus type
297 due to particularly poor performance when remembering a large set size of words,
298 $F(1.77, 19.47) = 20.17, p < .001$. Estimated capacity for colored rectangles was slightly
299 higher than Experiment 1, $M = 3.14, SE = 0.20$, and significantly lower for words, $M =$
300 $2.14, SE = 0.25, t(11) = 5.74, p < .001$.

301 Extending the findings of Experiment 1, we found that the words in Experiment 2
302 elicited a capacity-limited pattern of CDA, similar to what has repeatedly been found
303 with simple colored objects. This can be seen in Figure 2B-D. The CDA was computed
304 identically to Experiment 1, and we again found a main effect of set size because the
305 CDA amplitude increased as set size increased, $F(3, 33) = 11.81, p < .001$, as well as a
306 main effect of stimulus type, $F(1, 11) = 4.90, p = .049$, because the CDA was larger for
307 words than colored rectangles. These effects also varied by electrode, $F_s > 2.80, p < .007$,
308 such that the difference between stimulus types was present only at OL/OR and T5/T6,
309 and the set size effect was most pronounced at OL/OR. The CDA overall was largest at
310 OL/OR and smallest at O1/O2 as well resulting in a main effect of electrode, $F(3, 33) =$
311 $6.93, p < .001$. Importantly, set size and stimulus type did not interact with each other,
312 $F(3, 33) = 1.50, p = .23$, nor was there a three-way interaction, $F(9, 99) = 1.28, p = .26$.
313 These results extend the findings of Experiment 1, showing that verbal stimuli – three-

314 letter words – elicit a load-dependent CDA². As in Experiment 1, behavioral accuracy,
315 $r(10) = .82, p = .001$, and CDA amplitudes, $r(10) = .85, p < .001$, for the two stimulus
316 types were correlated across observers, lending support to the conclusion that both
317 stimuli were stored visually.

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, $F(1, 11) = 5.45, p = .039$, but this varied by electrode and set size, $F(2.54, 27.90) = 4.59, p = .01$. Analysis at each electrode showed that the difference seemed to disappear at higher set sizes for Cz, $F(3, 33) = 2.55, p = .07$, with main effects of stimulus type at parietal electrodes, $F_s(1, 11) > 3.74, p_s < .08$.

318 **General Discussion**

319 In the current study, we found that, despite their linguistic associations, both
320 letters and short words elicited a load-dependent CDA, the canonical measure of storage
321 in visual working memory. Somewhat surprisingly, the amplitude of the CDA was larger
322 for words than for colored rectangles, despite poorer change detection performance. This
323 fits with the general notion that working memory capacity is reduced for more complex
324 objects (Alvarez & Cavanagh, 2004). Although it is well established that the CDA is a
325 good measure of different capacity limits of individuals (Vogel & Machizawa, 2004;
326 Vogel, McCollough, & Machizawa, 2005), this is evidently not the case when comparing
327 across stimulus types, arguably because more complex stimuli demand more available
328 capacity (Perez, Ashby, Awh, & Vogel, as cited in Fukuda, Awh, Vogel, 2010; Awh,
329 Barton, & Vogel, 2007). However, this cannot explain the *larger* amplitude for word
330 stimuli, given that these differences occurred even at set sizes beyond working memory
331 capacity.

332 There appear to be two ways to account for this finding. One is that more visual
333 information is encoded about words than colors, similarly to what has been argued for
334 real-world objects by Brady, Störmer, & Alvarez (2016). Although somewhat counter-
335 intuitive, given that memory performance was worse for words than colored squares, it is
336 possible that more features are encoded per item in these cases, despite equivalent, or
337 even fewer, items being encoded overall, which would reduce change detection
338 performance (Awh, Barton, & Vogel, 2007; Wilson, Adamo, Barense, & Ferber, 2012).
339 A second possibility is that the difference reflects demands on spatial attention, given that
340 words require discrimination of higher spatial frequencies and the processing of multiple

341 features per item, which may require sustained spatial attention. The CDA has previously
342 been linked to spatial attention in search (Emrich, Al-Aidroos, Pratt, & Ferber, 2009) and
343 is enlarged when orientation-defined targets are lower in contrast (Töllner, Conci, Rusch,
344 & Müller, 2013). Encoding of colored stimuli into working memory, on the other hand, is
345 not affected by contrast (Ikkai, McCollough, & Vogel, 2010). If this is the case, our data
346 may reflect overlapping components, one reflecting focused spatial attention, and one
347 reflecting memory storage (see Becke et al., 2015).

348 The CDA is considered to be a marker of visual working memory storage (Vogel
349 & Machizawa, 2004; McCollough, Machizawa, & Vogel, 2007; Luria, Balaban, Awh, &
350 Vogel, 2016; but see Eimer & Kiss, 2010; Katus & Eimer, 2015; Berggren & Eimer,
351 2016), and so the present results fit with the possibility that participants store
352 alphanumeric and verbal stimuli in visual working memory during change detection tasks
353 such as the one used here. These results also fit well with fMRI studies that show
354 recruitment of posterior parietal cortex (PPC) for both simple visual stimuli and for
355 verbal stimuli (Todd & Marois, 2004; Majerus et al., 2011; 2014), suggesting that PPC
356 could participate in maintaining diverse codes (Xu, 2017).

357 Whereas alphanumeric stimuli have been foundational in visual cognition
358 research, they are often considered to be phonological stimuli (Henson, Burgess, & Frith,
359 1999; Majerus et al., 2014). Although phonological storage of verbal materials appears to
360 be the modal view of how visually presented alphanumeric characters and words are
361 stored (Baddeley, 2003), there is also evidence for lasting visual coding of such materials.
362 Logie, Della Sala, Wynn, & Baddeley (2000) found that fewer items are recalled from
363 lists of visually similar words and letter pairs compared to visually dissimilar word and

364 letter pairs, suggesting the involvement of visual working memory in the short-term
365 representation of visual materials (see also Posner, Boies, Eichelman, & Taylor, 1969).
366 Fiebach, Rissman, & D'Esposito (2006) showed that an area in left inferotemporal
367 cortex, which is selectively activated by words compared to non-words, showed load-
368 sensitive activation when visually presented words are stored in working memory.
369 Furthermore, similarities in BOLD responses for stimuli that recruit visual working
370 memory (colored squares) and visually presented words have been shown by Majerus and
371 colleagues. Majerus et al. (2011) showed that maintaining letters in working memory
372 produces a load-dependent, opponent activation pattern between the intra-parietal sulcus
373 and temporal-parietal junction, similar to what is observed for colored squares (Todd &
374 Marois, 2004). Majerus et al. (2014) have further shown that it is possible to decode
375 working memory load (number of items stored) between colored squares and visually
376 presented letter strings using fMRI, notably from the intra-parietal sulcus. These results
377 support the present findings of similar working memory mechanisms involved in
378 retaining information about words and visual stimuli over short delays.

379 How might our results be useful for understanding reading? Our experiments
380 required the mere memorization of letters and words over a brief delay, whereas reading
381 demands that participants parse orthographic forms from visual input and translate these
382 into semantic or phonological codes (Coltheart, Rastle, Perry, Landon, & Ziegler, 2001).
383 Processing of individual words, as measured by eye movements (Rayner 1998), and
384 ERPs, such as the N400 (Kutas & Federmeier, 2011), is affected by that word's
385 frequency, but also its relationship to neighboring words (Dambacher & Kliegl, 2007).
386 Whether these interactions reflect concurrent visual processing or not is debated, with

387 models favoring serial word recognition as well as concurrent word processing (Reichle,
388 Liversedge, Pollatsek, & Rayner, 2009; Trukenbrod & Engbert, 2012; Murray, Fischer, &
389 Tatler, 2013; Wang & Inhoff, 2013; White, Palmer, & Boynton, 2018). Given its load-
390 sensitivity, the CDA could provide a useful additional measure of the amount of visual
391 information being concurrently processed during sentence comprehension.

392 Finally, it is worth noting that while letters and words did not differ from colored
393 rectangles in their ability to elicit a CDA, we observed differences in ERPs that have
394 been associated with long-term recognition memory (Rugg & Doyle, 1992; Rugg &
395 Curran, 2007). Given that no memory retrieval was required at the encoding of the
396 memory sample arrays, these ERPs may reflect the automatic recognition of familiar
397 forms, for letters, and possibly the activation of semantic memory for words, due to
398 cumulative priming.
399

400

Acknowledgements

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

404

405

406

References

407

Alvarez, G. A., & Cavanagh, P. (2004). The capacity of visual short-term memory is set both by visual information load and by number of objects. *Psychological science*, 15(2), 106-111.

409

410

Awh, E., Barton, B., & Vogel, E. K. (2007). Visual working memory represents a fixed number of items regardless of complexity. *Psychological science*, 18(7), 622-628.

411

412

Baddeley, A. (2003). Working memory: Looking back and looking forward. *Nature Reviews Neuroscience*, 4, 829-839.

413

414

Balota, D. A., Yap, M. J., & Cortese, M. J. (2006). Visual word recognition: The journey from features to meaning (a travel update). In *Handbook of Psycholinguistics (Second Edition)* (pp. 285-375).

416

417

Becke, A., Müller, M. Vellage, A., Schoenfeld, M. A., Hopf, J-M. (2015). Neural sources of visual working memory maintenance in human parietal and ventral extrastriate visual cortex. *NeuroImage*, 110(15), 78-86.

419

420

Berggren, N., & Eimer, M. (2016). Does contralateral delay activity reflect working memory storage or the current focus of spatial attention within visual working memory?. *Journal of cognitive neuroscience*, 28(12), 2003-2020.

422

423

Booth, J. R., Perfetti, C. A., & MacWhinney, B. (1999). Quick, automatic, and general activation of orthographic and phonological representations in young readers. *Developmental psychology*, 35(1), 3-19.

425

426

Brady, T. F., Störmer, V. S., & Alvarez, G. A. (2016). Working memory is not fixed-capacity: More active storage capacity for real-world objects than for simple stimuli. *Proceedings of the National Academy of Sciences*, 113(27), 7459-7464.

428

- 429 Browne, C., Culligan, B. & Phillips, J. (2013). The New General Service List. Retrieved
430 from: <http://www.newgeneralservicelist.org>.
- 431 Carlisle, N. B., Arita, J. T., Pardo, D., & Woodman, G. F. (2011). Attentional templates
432 in visual working memory. *Journal of Neuroscience*, 31(25), 9315-9322.
- 433 Coltheart, M., Rastle, K., Perry, C., Langdon, R., & Ziegler, J. (2001). DRC: a dual route
434 cascaded model of visual word recognition and reading aloud. *Psychological*
435 *Review*, 108(1), 204-256.
- 436 Craik, F. I., & Tulving, E. (1975). Depth of processing and the retention of words in
437 episodic memory. *Journal of experimental Psychology: General*, 104(3), 268-294.
- 438 Dambacher, M. & Kliegl, R. (2007). Synchronizing timelines: Relations between fixation
439 durations and N400 amplitudes during sentence reading. *Brain Research*, 1155,
440 147-162.
- 441 Dell'Acqua, R., Sessa, P., Jolicœur, P., & Robitaille, N. (2006). Spatial attention freezes
442 during the attention blink. *Psychophysiology*, 43(4), 394-400.
- 443 Delorme, A. & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of
444 single-trial EEG dynamics including independent component analysis. *Journal of*
445 *Neuroscience Methods*, 134(1). 9-21.
- 446 Drew, T., & Vogel, E. K. (2008). Neural measures of individual differences in selecting
447 and tracking multiple moving objects. *Journal of Neuroscience*, 28(16), 4183-
448 4191.
- 449 Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity.
450 *Psychological review*, 96(3), 433-458.

- 451 Eimer, M., & Kiss, M. (2010). An electrophysiological measure of access to
452 representations in visual working memory. *Psychophysiology*, *47*(1), 197-200.
- 453 Emrich, S. M., Al-Aidroos, N., Pratt, J., & Ferber, S. (2009). Visual search elicits the
454 electrophysiological marker of visual working memory. *PloS one*, *4*(11), e8042.
- 455 Eriksen, B. A., & Eriksen, C. W. (1974). Effects of noise letters upon the identification of
456 a target letter in a nonsearch task. *Perception & psychophysics*, *16*(1), 143-149.
- 457 Eriksen, C. W., & Hoffman, J. E. (1973). The extent of processing of noise elements
458 during selective encoding from visual displays. *Perception & Psychophysics*,
459 *14*(1), 155-160.
- 460 Fiebach, C. J., Rissman, J., & D'Esposito, M. (2006). Modulation of inferotemporal
461 cortex activation during verbal working memory maintenance. *Neuron*, *51*(2),
462 251-261.
- 463 Fukuda, K., Vogel, E., Mayr, U., & Awh, E. (2010). Quantity, not quality: The
464 relationship between fluid intelligence and working memory capacity.
465 *Psychonomic bulletin & review*, *17*(5), 673-679.
- 466 Galvez-Pol, A., Calvo-Merino, B., Capilla, A., & Forster, B. (2018). Persistent
467 recruitment of somatosensory cortex during active maintenance of hand images in
468 working memory. *NeuroImage*, *174*(1), 153-163.
- 469 Henson, R. N. A., Burgess, N., & Frith, C. D. (2000). Recoding, storage, rehearsal and
470 grouping in verbal short-term memory: an fMRI study. *Neuropsychologia*, *38*(4),
471 426-440.
- 472 Humphreys, G. W., Evett, L. J., & Taylor, D. E. (1982). Automatic phonological priming
473 in visual word recognition. *Memory & Cognition*, *10*(6), 576-590.

- 474 Ikkai, A., McCollough, A. W., & Vogel, E. K. (2010). Contralateral delay activity
475 provides a neural measure of the number of representations in visual working
476 memory. *Journal of neurophysiology*, *103*(4), 1963-1968.
- 477 JASP Team (2018). JASP (Version 0.8.6)[Computer software].
- 478 Jolicoeur, P., Brisson, B., & Robitaille, N. (2008). Dissociation of N2pc and sustained
479 posterior contralateral negativity in a choice response task. *Brain Research*, *1215*,
480 160-172.
- 481 Jolicoeur, P., Sessa, P., Dell'Acqua, R., & Robitaille, N. (2006). On the control of visual
482 spatial attention: Evidence from human electrophysiology. *Psychological*
483 *research*, *70*(6), 414-424.
- 484 Katus, T., & Eimer, M. (2015). Lateralized delay period activity marks the focus of
485 spatial attention in working memory: evidence from somatosensory event-related
486 brain potentials. *Journal of Neuroscience*, *35*(17), 6689-6695.
- 487 Kleiner, M., Brainard, D., Pelli, D., Ingling, A., Murray, R., & Broussard, C. (2007).
488 What's new in Psychtoolbox-3. *Perception*, *36*(14), 1.
- 489 Kutas, M., & Federmeier, K. D. (2011). Thirty years and counting: finding meaning in
490 the N400 component of the event-related brain potential (ERP). *Annual Review of*
491 *Psychology*, *62*, 621-647.
- 492 Lavie, N., & Tsal, Y. (1994). Perceptual load as a major determinant of the locus of
493 selection in visual attention. *Perception & psychophysics*, *56*(2), 183-197.
- 494 Logie, R. H., Della Sala, S., Wynn, V., & Baddeley, A. D. (2000). Visual similarity
495 effects in immediate verbal serial recall. *The Quarterly Journal of Experimental*
496 *Psychology Section A*, *53*(3), 626-646.

- 497 Luck, S. J. (2005). *An introduction to the event-related potential technique*. Cambridge,
498 MA: MIT Press.
- 499 Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features
500 and conjunctions. *Nature*, 390(6657), 279.
- 501 Luria, R., Balaban, H., Awh, E., & Vogel, E. K. (2016). The contralateral delay activity
502 as a neural measure of visual working memory. *Neuroscience & Biobehavioral*
503 *Reviews*, 62, 100-108.
- 504 Luria, R. & Vogel, E. K. (2011a). Shape and color conjunction stimuli are represented as
505 bound objects in visual working memory. *Neuropsychologia*, 49(6), 1632-1639.
- 506 Luria, R. & Vogel, E. K. (2011b). Visual search demands dictate reliance on working
507 memory storage. *The Journal of Neuroscience*, 31(6), 6207-6199.
- 508 Machizawa, M. G., Goh, C. C., & Driver, J. (2012). Human visual short-term memory
509 precision can be varied at will when the number of retained items is low.
510 *Psychological science*, 23(6), 554-559.
- 511 Majerus, S., Attout, L., D'Argembeau, A., Degueldre, C., Fias, W., Maquet, P., ... &
512 Phillips, C. (2011). Attention supports verbal short-term memory via competition
513 between dorsal and ventral attention networks. *Cerebral Cortex*, 22(5), 1086-
514 1097.
- 515 Majerus, S., Cowan, N., Péters, F., Van Calster, L., Phillips, C., & Schrouff, J. (2014).
516 Cross-modal decoding of neural patterns associated with working memory:
517 Evidence for attention-based accounts of working memory. *Cerebral Cortex*,
518 26(1), 166-179.

- 519 McCandliss, B. D., Cohen, L., & Dehaene, S. (2003). The visual word form area:
520 expertise for reading in the fusiform gyrus. *Trends in cognitive sciences*, 7(7),
521 293-299.
- 522 McCollough, A. W., Machizawa, M. G., & Vogel, E. K. (2007). Electrophysiological
523 measures of maintaining representations in visual working memory. *Cortex*,
524 43(1), 77-94.
- 525 Meyer, D. E., & Schvaneveldt, R. W. "Facilitation in recognizing pairs of words:
526 evidence of a dependence between retrieval operations. *Journal of Experimental*
527 *Psychology*, 90(2), 227-234.
- 528 Murray, W. S., Fischer, M. H., & Tatler, B. W. (2013). Serial and parallel processes in
529 eye movement control: Current controversies and future direction. *The Quarterly*
530 *Journal of Experimental Psychology*, 66, 417-428.
- 531 Neisser, U. (1964). Visual search. *Scientific American*, 210(6), 94-103.
- 532 Ossowski, A. & Behrmann, M. (2015). Left hemisphere specialization for word reading
533 potentially causes, rather than results from, a left lateralized bias for high spatial
534 frequency visual information. *Cortex*, 72, 27-39.
- 535 Predovan, D., Prime, D., Arguin, M., Gosselin, F., Dell'Acqua, R., & Jolicœur, P. (2009).
536 On the representation of words and nonwords in visual short - term memory:
537 Evidence from human electrophysiology. *Psychophysiology*, 46(1), 191-199.
- 538 Peterson, L., & Peterson, M. J. (1959). Short-term retention of individual verbal items.
539 *Journal of Experimental Psychology*, 58(3), 193-198.

- 540 Posner, M. I., Boies, S. J., Eichelman, W. H., & Taylor, R. L. (1969). *Retention of visual*
541 *and name codes of single letters. Journal of experimental psychology, 79*(1, Pt. 2),
542 1-16.
- 543 Prime, D., Dell'Acqua, R., Arguin, M., Gosselin, F., & Jolicœur, P. (2011). Spatial layout
544 of letters in nonwords affects visual short - term memory load: Evidence from
545 human electrophysiology. *Psychophysiology, 48*(3), 430-436.
- 546 Rayner, K. (1998). Eye movements in reading and information processing: 20 years of
547 research. *Psychological Bulletin, 124*(3), 372-422.
- 548 Reichle, E. D., Liversedge, S. P., Pollatsek, A., & Rayner, K. (2009). Encoding multiple
549 words simultaneously in reading is implausible. *Trends in cognitive sciences,*
550 *13*(3), 115-119.
- 551 Rouder, J. N., Morey, R. D., Morey, C. C., & Cowan, N. (2011). How to measure
552 working memory capacity in the change detection paradigm. *Psychonomic*
553 *Bulletin & Review, 18*(2), 324-330.
- 554 Rugg, M. D., & Curran, T. (2007). Event-related potentials and recognition memory.
555 *Trends in cognitive sciences, 11*(6), 251-257.
- 556 Rugg, M. D., & Doyle, M. C. (1992). Event-related potentials and recognition memory
557 for low-and high-frequency words. *Journal of cognitive neuroscience, 4*(1), 69-
558 79.
- 559 Schmidt, J., MacNamara, A., Proudfit, G. H., & Zelinsky, G. J. (2014). More target
560 features in visual working memory leads to poorer search guidance: Evidence
561 from contralateral delay activity. *Journal of vision, 14*(3), 1-19.

- 562 Schneider, W., & Shiffrin, R. M. (1977). Controlled and automatic human information
563 processing: I. Detection, search, and attention. *Psychological review*, 84(1), 1-66.
- 564 Shiffrin, R. M., & Schneider, W. (1977). Controlled and automatic human information
565 processing: II. Perceptual learning, automatic attending and a general theory.
566 *Psychological review*, 84(2), 127-190.
- 567 Sperling, G. (1960). The information available in brief visual presentations.
568 *Psychological monographs: General and applied*, 74(11), 1-29.
- 569 Sternberg, S. (1966). High-speed scanning in human memory. *Science*, 153(3736), 652-
570 654.
- 571 Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of*
572 *experimental psychology*, 18(6), 643.
- 573 Tanenhaus, M. K., Flanigan, H. P., & Seidenberg, M. S. (1980). Orthographic and
574 phonological activation in auditory and visual word recognition. *Memory &*
575 *Cognition*, 8(6), 513-520.
- 576 Todd, J. J., & Marois, R. (2004). Capacity limit of visual short-term memory in human
577 posterior parietal cortex. *Nature*, 428(6984), 751-754.
- 578 Töllner, T., Conci, M., Rusch, T., & Müller, H. J. (2013). Selective manipulation of
579 target identification demands in visual search: The role of stimulus contrast in
580 CDA activations. *Journal of Vision*, 13(3), 1-13.
- 581 Treisman, A., & Sato, S. (1990). Conjunction search revisited. *Journal of Experimental*
582 *Psychology: Human Perception and Performance*, 16(3), 459-478.
- 583 Trukenbrod, H. A., & Engbert, R. (2012). Eye movements in a sequential scanning task:
584 Evidence for distributed processing. *Journal of Vision*, 12(1), 1-12.

- 585 Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences
586 in visual working memory capacity. *Nature*, 428(6984), 748-751.
- 587 Vogel, E. K., McCollough, A. W., & Machizawa, M. G. (2005). Neural measures reveal
588 individual differences in controlling access to working memory. *Nature*,
589 438(7067), 500-503.
- 590 Wang, C. & Inhoff, A. W. (2013). Extraction of linguistic information from successive
591 words during reading: Evidence for spatially distributed lexical processing:
592 *Journal of Experimental Psychology: Human Perception and Performance*, 39(3),
593 662-677.
- 594 Waugh, N. C., & Norman, D. A. (1965). Primary memory. *Psychological review*, 72(2),
595 89-104.
- 596 White, A. L. , Palmer, J., & Boynton, G. M. (2018). Evidence of serial processing in
597 visual word recognition. *Psychological Science*, doi: 0956797617751898
- 598 Wiegand, I., Töllner, T., Habekost, T., Dyrholm, M., Müller, H. K., & Finke, K. (2013).
599 Distinct neural markers of TVA-based visual processing speed and short-term
600 storage capacity parameters. *Cerebral Cortex*, 24(8), 1967-1978.
- 601 Wilson, K. E., Adamo, M., Barense, M. D., & Ferber, S. (2012). To bind or not to bind:
602 Addressing the question of object representation in visual short-term memory.
603 *Journal of Vision*, 12(8), 1-16.
- 604 Woodman, G. F. (2010). A brief introduction to the use of event-related potentials in
605 studies of perception and attention. *Attention, Perception, & Psychophysics*,
606 72(8), 2031-2046.

- 607 Woodman, G. F., Carlisle, N. B., & Reinhart, R. M. (2013). Where do we store the
608 memory representations that guide attention?. *Journal of Vision, 13*(3), 1-17.
- 609 Woodman, G. F., & Vogel, E. K. (2008). Selective storage and maintenance of an
610 object's features in visual working memory. *Psychonomic bulletin & review,*
611 *15*(1), 223-229.
- 612 Xie, W., & Zhang, W. (2018). Familiarity speeds up visual short-term memory
613 consolidation: Electrophysiological evidence from contralateral delay activities.
614 *Journal of cognitive neuroscience, 30*(1), 1-13.
- 615 Xu, Y. (2017). Reevaluating the sensory account of visual working memory storage.
616 *Trends in cognitive sciences, 21*(10), 794-815.
- 617 Yantis, S., & Jonides, J. (1990). Abrupt visual onsets and selective attention: voluntary
618 versus automatic allocation. *Journal of Experimental Psychology: Human*
619 *perception and performance, 16*(1), 121.
- 620 Zhang, W., & Luck, S. J. (2008). Discrete fixed-resolution representations in visual
621 working memory. *Nature, 453*(7192), 233-235.