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Electrophysiological correlates of the flexible allocation of visual working memory resources

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Abstract

1
2 Efficiently allocating capacity-limited cognitive resources is critical to guiding behavior
3 effectively. Although previous research has suggested that distractors are blocked from
4 memory access, recent work proposes a more flexible attentional filter that acts based
5 on item priority. Here, we investigated the electrophysiological correlates of flexible
6 attentional prioritization by manipulating the distribution of memory resources amongst
7 items. Across three experiments, we found that the contralateral delay activity (CDA), a
8 component typically associated with visual working memory (VWM) load, was affected
9 by both memory load and resource allocation. This allocation occurred as early as
10 during attentional selection, as indicated by the N2pc. Additionally, CDA amplitude was
11 well described when fit with a continuous power law function with load and resources
12 together, more so than when fit with either alone. Together, these findings suggest that
13 ERP markers of attentional selection and memory maintenance track attentional
14 prioritization in addition to VWM load.

1 More likely than not, it is much easier for you to recall the names of the
2 characters from the last television show that you watched than what you were wearing
3 while you watched it. This bias in memory is in part due to the fact that what we allocate
4 more attention to is remembered with greater detail¹. Indeed, numerous studies of long-
5 term memory have established that attention prioritizes relevant information to be
6 encoded into memory²⁻⁴. Attention also affects the maintenance and quality of
7 information stored over shorter periods of time, such as in visual working memory⁵⁻⁷
8 (VWM). In fact, given that VWM is limited in capacity, several models of VWM have
9 suggested that attention may play a critical role in determining what information gains
10 access to these finite storage resources⁸⁻¹¹.

11 One potential mechanism through which attention may drive working memory
12 performance is by filtering out irrelevant distractors¹². Filtering efficiency has been
13 quantified using measurements of electrophysiological brain activity related to working
14 memory storage, specifically an event-related potential (ERP) called the contralateral
15 delay activity¹³⁻¹⁶ (CDA). CDA amplitude increases with the number of items stored in
16 VWM, saturating as memory load increases beyond a few items¹⁷. Interestingly, when
17 distractors are presented alongside targets in a memory display, lower-capacity
18 individuals exhibit larger CDA amplitudes than those with higher capacities, reflecting
19 the fact that they have encoded and stored more distractors in memory¹⁶. This finding
20 has been taken as evidence that poor filtering efficiency, resulting in unnecessary
21 storage, is a critical determinant of VWM capacity.

22 Several recent studies have demonstrated that it is also possible to bias
23 attentional resources toward and away from certain items in a flexible manner,

1 independent of the need to filter out irrelevant distractor items. This bias can be induced
2 by associating certain stimuli with monetary incentives, or by simply varying instructions
3 indicating the probability that an item will be probed on any given trial⁷. For example,
4 spatial cues¹⁸ or feature-based cues¹⁹ can be used to change the likelihood that a given
5 item will be probed. In this way, the proportion of attentional resources allocated to any
6 given memory item can continuously vary anywhere between 0 and 100%.

7 In these past studies^{18,19}, it was found that working memory performance (i.e.,
8 raw error = 1/ precision) was best predicted by the likelihood that an item would be
9 probed on a given trial, independent of the overall memory load. These findings support
10 the idea that attentional resources can be continuously allocated across items, even
11 when they are of very low priority. Importantly, this relationship between probe likelihood
12 and memory precision, which followed a power law, could also account for changes in
13 performance across loads; for example, the change in precision from one to two items
14 was consistent with each item only receiving half as many attentional resources. This
15 framework suggests that attention does more than just restrict or grant access to VWM;
16 rather, it also flexibly distributes resources amongst memory items based on their
17 respective priorities. In other words, how attention is allocated between targets is as
18 important to memory performance as whether or not it is allocated to distractors²⁰.

19 If attention can be flexibly allocated across items in VWM, how might this be
20 reflected by neural measures of attention and VWM maintenance? There is evidence
21 that the CDA is well-described by a saturation model, which predicts a continuous
22 increase in CDA amplitude that saturates as set size becomes larger, instead of
23 increasing discretely and plateauing at memory capacity¹⁷. This finding suggests that

1 the CDA, much like VWM performance, may be more flexibly affected by memory load
2 than previously thought. Yet, it is currently unknown whether the CDA is also flexibly
3 affected by the prioritization of memory items instead of, or in addition to, changes in
4 memory load.

5 Prioritization could also be tracked by ERP components that precede memory
6 maintenance, such as attentional selection and suppression. That is, one way that
7 flexible prioritization could be accomplished is through the specific up-weighting of goal-
8 relevant over irrelevant information (as opposed to down-weighting of goal-irrelevant
9 information). Attentional selection can be tracked by the N2pc, a lateralized component
10 which specifically reflects the enhancement of an item²¹⁻²³. Alternatively, it could be that
11 prioritization is accomplished through the active suppression or down-weighting of goal
12 irrelevant information. This can be measured by the distractor positivity (P_D): a
13 lateralized component that is observed when distractors are presented laterally in the
14 stimulus display²⁴⁻²⁷. These two components can thus be used to disentangle the
15 underlying mechanisms of prioritization: whether through selective enhancement of
16 relevant information (N2pc) or suppression of irrelevant information (P_D).

17 Consequently, to determine the effect of resource allocation on the CDA, as well
18 as whether prioritization is driven by selective enhancement of high-priority items or
19 inhibition of low-priority items, we conducted three experiments in which the allocation
20 of memory resources across items was manipulated in a continuous-report delayed-
21 recall task. For these experiments, we use the term *memory load* to refer to the number
22 of items with greater than zero percent likelihood of being probed. We use the terms
23 *resource allocation* or *probability* to refer to the likelihood that one item, or a set of

1 items, will be probed. In Experiment 1, we examined how changes in resource
2 allocation amongst memory items influenced the CDA in comparison to the typical effect
3 of memory load. To do this, participants were asked to remember the colors of four
4 laterally presented items that were either equally likely to be probed, or where a spatial
5 cue indicated that one item was more likely to be probed than the others. Thus, while
6 participants should always be allocating 100% of memory resources to these items, how
7 the resources are distributed across items varied. In Experiments 2 and 3, we took
8 advantage of an attribute of the CDA, $N2pc$, and P_D – that these components are only
9 sensitive to laterally presented stimuli and not stimuli presented on the vertical midline –
10 to separately manipulate the effects of memory load and resource allocation on the
11 CDA. In Experiment 2, two items were presented laterally and two vertically, and a
12 featural cue indicated whether the lateral or vertical items were more likely to be probed.
13 Thus, this design allowed us to manipulate the proportion of memory resources
14 specifically allocated to lateral items. In Experiment 3, we tested whether the CDA
15 reflects the allocation of memory resources even in the absence of prioritization cues.
16 To do so, we manipulated the total number of items to-be-remembered (four or six),
17 while systematically changing the number of items presented laterally. In this way, we
18 could simultaneously manipulate lateral memory load and proportion of memory
19 resources allocated to the lateral items.

20 **Methods**

21 **Participants**

22 All participants gave written informed consent of the procedures as approved by
23 a university ethics review board. Participants received partial course credit or paid

1 remuneration (\$15/hour) for participating. Consistent with prior research^{15,16,28}, we
2 aimed for a sample size of 20 participants (right handed, normal-color vision, no history
3 of mental illness). To reach these targets a total of 30 participants were run in
4 Experiment 1, 33 in Experiment 2, and 28 in Experiment 3. Data were replaced if > 35%
5 of trials were removed due to EEG artifacts (10 in Experiment 1, 6 in Experiment 2, and
6 4 in Experiment 3). Additionally, in Experiments 2 and 3 data were replaced if average
7 residual HEOG activity was > 4 μ V (6 in Experiment 2 and 4 in Experiment 3; see
8 Electrophysiological Recording and Analysis). Distinct samples (N = 20) were used for
9 each experiment (Exp 1: $M_{age} = 22.0$, $SD_{age} = 3.0$, 10 male; Exp 2: $M_{age} = 22.6$, $SD_{age} =$
10 4.2, 9 male; Exp 3: $M_{age} = 21.6$, $SD_{age} = 3.9$, 3 male).

11 **Stimuli and Procedures**

12 All tasks were completed on a Windows PC with a 41-cm NEC MultiSync LCD
13 2090UXi computer monitor (1600 x 1200 pixels, 60 Hz refresh rate) in a private testing
14 room. Stimuli were rendered using Psychopy v1.90.3 (Peirce, 2007) and presented on a
15 grey background (RGB = 128 128 128) with a central fixation dot (radius of 0.3° visual
16 angle). Viewing distance was approximately 57 cm (no chin rest was used). In all
17 experiments, participants first completed a standard change detection task²⁹. However,
18 these data are not included in the analyses below.

19 The colors for the squares in the continuous report VWM tasks were chosen
20 pseudo-randomly from a 360-degree isoluminant color wheel (CIE L*a*b* color space, [L
21 = 70, a = -6, b = 14, radius = 49]), which was calibrated to the testing monitor using a
22 chroma meter (Konica Minolta CS-100A; Konica Minolta Sensing Americas, Inc.,

1 Ramsey, New Jersey). On every trial the memory stimuli colors were separated by at
2 least 30 degrees on the color wheel.

3 **Experiment 1.**

4 ***Visual working memory task with spatial-based prioritization cues (Figure*** 5 ***2A).***

6 Each trial began with a centrally presented arrow ($3^\circ \times 3^\circ$, 200 ms), indicating
7 which half of the screen contained the target stimuli. Next, a fixation screen was
8 presented for a random interval (200 – 500 ms) followed by the memory array
9 consisting of four squares on both sides of the screen ($1^\circ \times 1^\circ$, 4° from fixation,
10 separated by 1° , 150 ms). One or four of the laterally presented squares appeared with
11 a horizontal spatial line cue (2° long \times 1° wide, 2° from fixation) depending on the
12 condition (both sides of the screen included a cue to balance visual input). At the
13 beginning of each block, participants were given instructions on the cue-validity (i.e., the
14 probability the cued item would be probed). There were three conditions: In the 1-
15 Cue/100%-Valid condition, the one cued item would always be the target; In the 4-
16 Cues/100%-Valid condition, all four items could potentially be the target, resulting in
17 approximately 25% of memory resources being allocated toward each item; In the 1-
18 Cue/50%-Valid condition, the one cued item would be probed on 50% of trials and any
19 of the remaining three items would be probed on the other 50%.

20 Following the memory array, a fixation dot was presented for 900 ms followed by
21 the response screen, wherein a colour wheel (diameter of 7°) appeared around the
22 task-relevant lateral stimuli. Black outlines appeared at the same locations as the
23 memory array (line width of 1 pixel), with one outline bolded (line width of 3 pixels)

1 indicating the target location for the color response. Participants made their choice by
2 clicking on the color wheel with the mouse. As the mouse was moved around the color
3 wheel, the probed square outline was filled with the presently selected color.

4 There were a total of 960 trials: 240 in both the 1-Cue/100%-Valid and 4-
5 Cues/100%-Valid Conditions, and 480 in the 1-Cue/50%-Valid condition, which allowed
6 for 240 valid trials, split equally between the left and right sides of the screen. One
7 participant's data consisted of only 840 trials due to a recording error. Participants were
8 given a self-paced break every 25 trials.

9 **Experiment 2.**

10 ***Luminance matching task.***

11 In both Experiments 2 and 3 participants first completed a subjective luminance-
12 matching task in which a staircase method was used to match the brightness of 12
13 colors from the color wheel with a grey color. These individual luminance-matched
14 greys were used as placeholder colors in both experiments (see Supplemental
15 Materials for more information).

16 ***Visual working memory task with feature-based prioritization cues (Figure*** 17 ***3A).***

18 After pressing any key, trials began by a written cue (1.5° tall, 800 ms) indicating
19 the likelihood that the color of a shape (square or circle) would be probed on that trial
20 (100% or 75% valid). There were two cue instructions, such that it was either 100% or
21 75% likely that the color of a certain shape would be tested. Cued shape was
22 counterbalanced across participants. These cues led to an implicit probability for the

1 non-cued shape. For example, if it were 100% likely that the color of a square would be
2 probed, then there was a 0% chance that a circle would be probed

3 Next, there was a jittered fixation screen (500 – 1,000 ms) followed by the
4 memory array (200 ms) consisting of 8 shapes. Four shapes were always presented
5 laterally (two left and two right) and four vertically (two top and two bottom; 3° from
6 fixation to center of the cluster). Two shapes within a cluster were presented 1.2° apart
7 vertically (center to center). There were always two colored squares (1° x 1°, black
8 outline width of 1 pixel) and two colored circles (diameter of 1°) presented. If colored
9 squares were presented laterally, then colored circles were presented vertically and vice
10 versa. The remaining four items were filled with the subjectively luminance-matched
11 grey and were always the un-cued shape. Shapes were presented in all possible
12 position configurations equally (16 unique positions).

13 After the memory array was presented, there was a delay screen with a fixation
14 dot (900 ms). The response screen (similar to Experiment 1) was unsped. The
15 probed shape was chosen pseudo-randomly from the top or bottom shape in a cluster,
16 depending on the probability cue. Every 50 trials participants were presented with a
17 break screen. All participants received 20 practice trials.

18 There were a total of four conditions that varied by the probability that the color of
19 the shape presented on the lateral would be probed at test: 100%, 75%, 25%, and 0%.
20 Participants completed a total of 816 trials (100% lateral: 200, 0% lateral: 200, 75%
21 lateral: 208, 25% lateral: 208). One participant completed 806 trials due to a
22 programming error, and another completed 807 trials due to an interruption to the
23 recording session.

1 **Experiment 3.**

2 ***Visual working memory task with lateralized resource and load***

3 ***manipulation (Figure 5A).***

4 Participants were instructed to remember the colors of all of the squares in the
5 memory array, and that each square was equally likely to be probed. Each trial began
6 with a jittered fixation screen (500 –1,500 ms) followed by the lateralized memory array
7 (200 ms). There were three conditions defined by the proportion of memory resources
8 allocated toward the lateral items. 1) Load 4 with three colored squares presented in a
9 vertical cluster to the left or right of fixation (1° x 1°, black outline width of 1 pixel, 1.2°
10 apart center-to-center, 3° from fixation to center of the group of squares) and one
11 colored square presented vertically. This condition reflects 75% of attention to the
12 lateral while maintaining a total of 4 items in memory. 2) Load 4 with one square
13 presented laterally and three squares on the vertical, resulting in 25% lateral attention.
14 3) Load 6 with three squares presented laterally and 3 vertically, resulting in 50% of
15 attention to the lateral. For all memory arrays there were an equivalent number of
16 luminance-matched grey squares presented opposite to the colored squares. Counter-
17 balancing of stimuli positions was the same as in Experiment 2.

18 Next, there was a 900 ms delay period consisting of a fixation screen followed by
19 the probe screen (same as in Experiment 2). Participants were then given feedback
20 after their response (800 ms), where ‘Correct’ was considered within 40° on the target
21 color. Participants completed a total of 900 trials, 300 of each condition
22 counterbalanced across the 16 possible position combinations. There were 12 practice
23 trials and self-paced breaks were given every 50 trials.

1 EEG Recording and Pre-Processing

2 All EEG pre-processing was done in MATLAB with the EEGLAB³⁰ (Version
3 14.0.0b), and ERPLAB³¹ (Version 6.1.2) toolboxes. EEG was DC recorded at a 512 Hz
4 sampling rate from a 64 Ag/AgCl electrode cap placed at the standard 10-20 sites³².
5 The signal was online referenced to the common mode sense (CMS) and the driven
6 right leg (DRL) electrodes. Data were re-referenced off-line to the average of the
7 mastoids, baseline corrected to -200 ms before memory array onset, and filtered with a
8 40-Hz low-pass and 0.1-Hz high-pass Butterworth filter (slope: 12dB/octave). For
9 illustrative purposes only, data were low-pass filtered at 30-Hz. Data were epoched
10 between -200 and 1,050 (Experiment 1) or -200 and 1,100 ms (Experiment 2) ms, time-
11 locked to the memory array.

12 **Artifact rejection.**

13 Horizontal electro-oculogram (HEOG) was recorded from bipolar external
14 electrodes placed laterally beside the eyes. Vertical electro-oculogram (VEOG) was
15 recorded as the difference between external electrodes placed below the eyes and FP1
16 or FP2. Participants were instructed not to blink or move their eyes from the start of
17 each trial to the appearance of the response screen. We used an automated artifact-
18 rejection procedure to remove trials with VEOG activity greater than $\pm 80 \mu\text{V}$ or HEOG
19 activity greater than $\pm 32 \mu\text{V}$ (using a step function) between stimuli onset and the end of
20 the trial. We also removed trials in which the voltage over posterior channels (P1/2,
21 P3/4, P5/6, P7/8, P9/10, PO3/O4, PO8/O7, and O1/2) was $\pm 100 \mu\text{V}$. In the final sample
22 an average of 21.4% of trials rejected in Experiment 1, ($SD = 10.4\%$), 11.6% in

1 Experiment 2 ($SD = 7.8\%$), and 13.3% in Experiment 3 ($SD = 10.1\%$). Across studies,
2 each participant had more than 100 trials in each ERP condition bin.

3 In Experiments 2 and 3 we also replaced participants whose average residual
4 HEOG activity (relative to the side of the lateralized memory array) was greater than 4
5 μV between memory array onset and the end of the epoch. On average across
6 conditions, the absolute residual HEOG was 1.61 μV ($SD = 1.02 \mu\text{V}$) in Experiment 2
7 and 1.61 μV ($SD = 1.00 \mu\text{V}$) in Experiment 3. This means that the deviation in lateral
8 eye movements was less than $\pm 0.1^\circ$ relative to the location of the lateralized memory
9 array in both experiments, and that the estimated voltage propagation was overall less
10 than 0.1 μV at posterior electrodes^{33–35}.

11 **Data Analysis**

12 **Behavioral data.**

13 Performance was assessed using the trial-by-trial raw response error (i.e., the
14 difference in degrees between the color of the probed item and the participant's
15 response) and was computed using the standard deviation of response errors. Lower
16 values reflect more precise responding. We predicted that as the amount of memory
17 resources provided to an item increased, error would decrease, following a power-
18 law^{18,19,36}. To test this, we fitted the behavioral data across all experiments to a power-
19 law function:

$$20 \quad y \propto ax^{-k}$$

21 Bayesian information criterion (BIC) values were computed to compare model
22 fits. Raw error values were calculated using custom scripts in MATLAB. Goodness of fit
23 was computed using nonlinear least squares regression in MATLAB's Curve-Fitting

1 Toolbox using a bisquare robust fitting procedure with the group data averaged across
2 conditions. Degrees of freedom-adjusted- R^2 and root mean square error (*RMSE*) values
3 are also reported.

4 **ERP data.**

5 Difference waves were calculated as contralateral minus ipsilateral activity in
6 each condition. In Experiment 1, laterality was determined in reference to the pre-cued
7 side of the screen. In Experiments 2 and 3, laterality was determined in reference to the
8 side of the screen on which the colored lateral items were presented.

9 We measured difference wave activity at five posterior electrode pairs: P3/4,
10 P7/8, PO7/O8, PO3/O4, and O1/2³⁷. Across all experiments, there was no significant
11 Condition x Channel interaction for any of the ERP components ($F_s < 2.24$, $p_s > .055$,
12 $\eta^2_p < .106$). Therefore, we averaged activity across these electrode sites for all ERP
13 measurements.

14 For each ERP component of interest, we ran a repeated-measures ANOVA on
15 the mean condition amplitudes. Follow-up linear contrasts and fits were completed in
16 Experiments 2 and 3 for the N2pc and CDA. Greenhouse-Geisser corrected degrees of
17 freedom and p values are reported. Two-tailed post-hoc t-tests were Bonferroni-
18 corrected. Cohen's d is reported where appropriate. Bayesian repeated-measures
19 ANOVAs and post-hoc tests are reported where applicable (r scale prior width of 0.5,
20 default Cauchy prior centered on 0, 10,000 Monte Carlo samples). Bayes factors (BF_{10})
21 are presented as the marginal likelihood for the alternative model compared to the null
22 model³⁸. Statistical analyses were completed using JASP Version 0.8.4³⁹, MATLAB
23 R2017a, and R version 3.5.1⁴⁰ in RStudio version 1.1.456⁴¹.

1 In Experiment 2, we predicted a correlation between ERPs and behavior, such
2 that as N2pc /CDA amplitudes increased, responses would become more precise. To
3 examine this, we ran a repeated measures correlation analysis using the *rmcorr*
4 package in R⁵². Each participant provided three data points for the 100%, 75%, and
5 25% lateral memory resource conditions. We obtained the repeated measures
6 correlation coefficient between raw error for all trials in each condition and the mean
7 amplitude of the N2pc and the mean amplitude of the CDA.

8 **Modelling CDA data.**

9 In Experiments 2 and 3, to examine whether the CDA increased continuously
10 relative to load and resource allocation, we fitted the CDA amplitudes to a power-law
11 (we obtained an identical pattern of results using a saturation model¹⁷, although with
12 worse overall fits). Mean CDA amplitudes were fit to three different models: 1) CDA
13 amplitude was compared to lateral memory load alone; 2) CDA amplitude was
14 compared to the proportion of resources allocated to the lateral items; 3) CDA amplitude
15 was compared to a weighted-product of the number of lateral items held in VWM and
16 the amount of memory resources allocated to them. The weighted-product values were
17 calculated by the following formula:

18 % of lateral resources × number of lateral items

19 For example, in Experiment 2 when it was 25% likely that a lateral item would be
20 probed, then 25% × 2 items were stored in memory, resulting in a weighted score of 0.5.
21 The weighted-product values for each condition in Experiment 2 were: 0, 0.5, 1.5, and
22 2. In Experiment 3, the lateralization procedure influenced the amount of memory
23 resources allocated toward the lateral items (i.e., when 3 of 6 items were presented

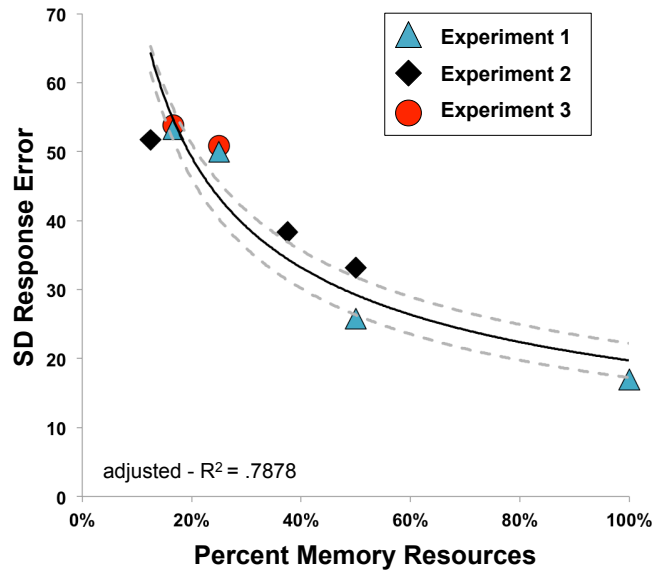
1 laterally, 50% of memory resources were allocated toward those items: $3 \times 50\% = 1.5$).
2 Therefore, there were 3 weighted-product values: 0.25, 2.25, and 1.5. In total, there
3 were 7 data points across the two studies. Model fits were completed using the Curve
4 Fitting Toolbox in MATLAB and custom MATLAB scripts to calculate BIC values to
5 compare model fits.

6 **Results**

7 **Behavioral: Experiments 1 - 3**

8 Because we manipulated proportion of memory resources per item across all
9 experiments, and were interested in how behavior changed as a function of resource
10 allocation, behavioural results were collapsed across all three experiments.

11 To compare how performance changed as a function of resource allocation, all
12 data points were fitted to a power law function. Consistent with past findings^{18,19}, this
13 provided a good fit (Figure 1), with the model accounting for around 79% of the variance
14 in the data, adjusted- $R^2 = .788$, $RMSE = 6.263$. These results demonstrate that the
15 proportion of memory resources allocated to an individual item was highly predictive of
16 behavioral precision for that item. Moreover, percent of memory resources allocated to
17 an item better predicted behavioral precision than memory load alone: adjusted- $R^2 =$
18 $.431$, $RMSE = 10.97$, $\Delta BIC = 9.71$. Thus, regardless of the behavioural manipulation
19 (i.e., spatial cues; feature-based cues; memory load), error is strongly predicted by the
20 percentage of resources allocated.



1

2 *Figure 1.* Standard deviation of raw response error by percent memory resources in each
3 experiment, fit with a power law. Dashed grey lines represent fits performed on the 95%
4 confidence interval of the condition means.

5

6 ERPs

7

Experiment 1

8

In Experiment 1, we sought to examine how the prioritization of some items over

9

others affected the CDA. Four lateral memory items were always presented, and spatial

10

cues indicated the number of items to be remembered, as well as the likelihood of a

11

given item to be probed. Based on past demonstrations that the CDA primarily reflects

12

VWM load, we should observe a larger CDA amplitude in the 4-Cues/100%-Valid

13

condition than the 1-Cue/100%-Valid condition; remembering four items results in a

14

larger CDA than remembering a single item. What remains an open question is how the

15

CDA changes when resources are distributed unequally across the four memory items.

16

Thus, comparing the 4-Cues/100%-Valid condition to the 1-Cue/50%-Valid condition

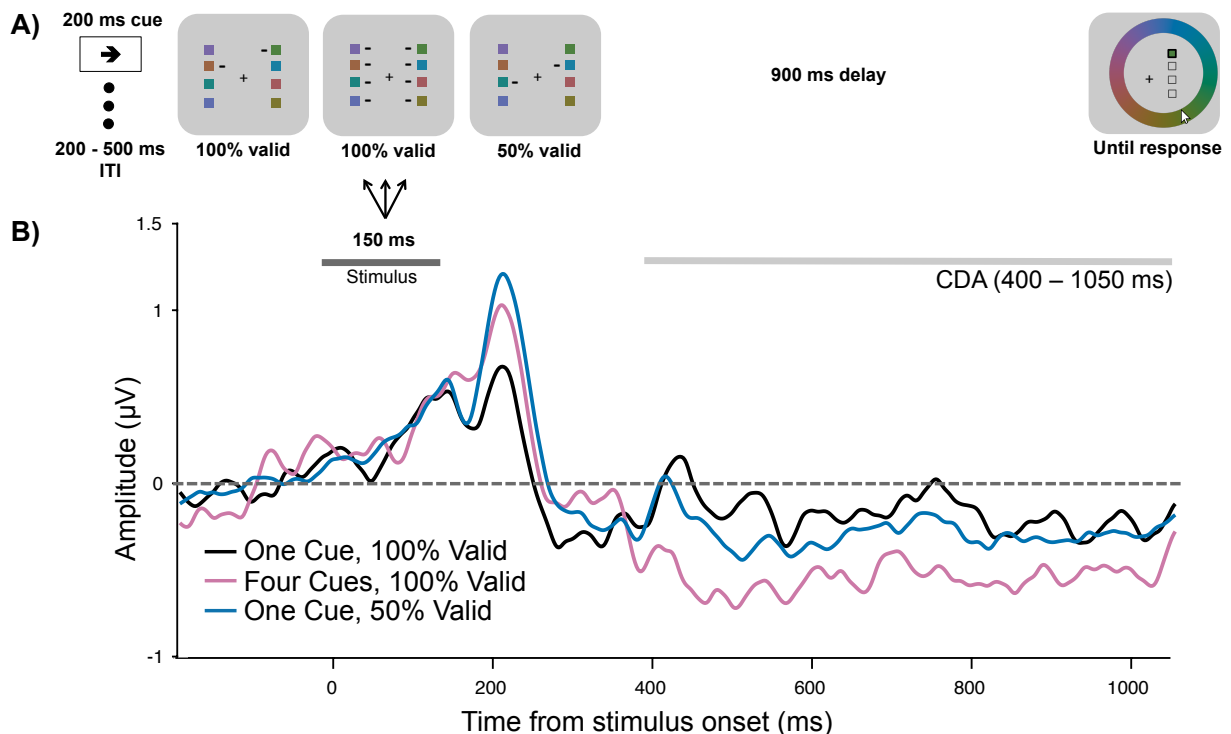
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provides an initial test of how resource allocation affects CDA amplitude.

18

CDA.

1 The spatial prioritization cues influenced CDA amplitude (Figure 2B; main effect
 2 of Condition, $F(2,38) = 5.83$, $p = .006$, $\eta^2_p = .235$, $BF_{10} = 6.98$). Consistent with a
 3 memory load effect, there was a more negative CDA amplitude when all four items were
 4 cued ($M = -0.545 \mu\text{V}$, $SD = 0.659 \mu\text{V}$), than when one item was cued at 100% validity
 5 ($M = -0.168$, $SD = 0.698 \mu\text{V}$), $t(19) = 3.43$, $p_{\text{bonf}} = .008$, $d = 0.767$, $BF_{10} = 14.943$. CDA
 6 amplitude in the 1-Cue/50%-Valid condition ($M = -0.285 \mu\text{V}$, $SD = 0.522 \mu\text{V}$) was not
 7 significantly different from the 1-Cue/100%-Valid condition, $t(19) = 0.981$, $p_{\text{bonf}} = 1$, $d =$
 8 0.219 , $BF_{10} = 0.355$, or from the 4-Cues/100%-Valid condition, $t(19) = 2.377$, $p_{\text{bonf}} =$
 9 $.084$, $d = 0.532$, $BF_{10} = 2.196$. While the CDA amplitude in the 1-Cue/50%-Valid
 10 condition was numerically smaller than in the 4-Cues/100%-Valid condition, this
 11 difference was not born out in the inferential statistics. Instead, the CDA amplitude in
 12 the 1-Cue/50%-Valid condition appeared to be in between the amplitudes of the other
 13 conditions (i.e., between holding one and four items in memory).



14

1 *Figure 2.* A) Task schematic of Experiment 1. Each trial began with a lateralization cue followed
2 by a jittered ITI consisting of a fixation dot. Conditions were blocked and cue probability
3 instructions provided at the beginning of each block. After a delay, participants made a
4 response to the probed square on the color wheel with the mouse. B) Grand average difference
5 waveform (N = 20) at the average of 5 posterior channel pairs, time-locked to stimuli onset.
6 Positive is plotted up. Filtered at 30 Hz for visualization purposes only.
7

8 **Experiment 2**

9 In Experiment 1 we replicated the typical effect of memory load on CDA
10 amplitude and the behavioral effect of resource allocation on memory precision.
11 However, the effects of resource allocation on CDA amplitude were less clear, as both
12 high and low probability items were presented together laterally, resulting in a mixed
13 electrophysiological signal. To better isolate the effects of prioritization on CDA
14 amplitude, in Experiment 2 we separated the items in the memory array along the
15 horizontal and vertical midlines by employing feature-based cues. Specifically, all
16 memory arrays comprised two items presented laterally, and two presented on the
17 vertical midline, with the lateral items either 100%, 75%, 25%, or 0% likely to be probed,
18 depending on the shape of those items. Because lateralized ERP components are only
19 sensitive to laterally presented stimuli, we could systematically manipulate the
20 proportion of lateral memory resources and thus its effect on the N2pc, P_D, and CDA.

21 **N2pc.**

22 The different cueing levels influenced the amplitude of the N2pc (Figure 3B; main
23 effect of Condition, $F(3,57) = 8.11$, $p < .001$, $\eta^2_p = .299$, $BF_{10} = 176.69$). Overall N2pc
24 amplitude was more negative when the item was 100% ($M = -0.331 \mu\text{V}$, $SD = 0.783 \mu\text{V}$)
25 likely to be probed than when it was 0% likely to be probed ($M = 0.172 \mu\text{V}$, $SD = 0.646$
26 μV), $t(19) = 3.582$, $p_{\text{bonf}} = .012$, $d = 0.801$, $BF_{10} = 20.173$. The N2pc was also larger
27 when the lateral item was 75% likely ($M = -0.262 \mu\text{V}$, $SD = 0.791 \mu\text{V}$) compared to 0%

1 likely to be probed, $t(19) = 3.643$, $p_{\text{bonf}} = .010$, $d = 0.815$, $BF_{10} = 22.741$. There was no
2 significant difference between N2pc amplitude in the 75% and 25% ($M = 0.032 \mu\text{V}$, SD
3 $= 0.615 \mu\text{V}$) conditions or any other condition, $p_s > .065$, $d_s < 0.634$, $BF_{s10} < 4.86$.
4 However, the overall N2pc amplitude did become linearly more negative as item priority
5 increased, adjusted- $R^2 = .983$, $RMSE = .0315$, linear contrast: $t(19) = 4.81$, $p < .001$,
6 suggesting that individuals could flexibly allocate their attention toward an item
7 depending on how important it was to the trial. Interestingly, fractional area latency did
8 not differ between conditions, $F(1.814, 29.027) = 1.698$, $p = .202$, $\eta^2_p = .096$, $BF_{10} =$
9 $.435$. Therefore, participants were not selecting high probability items any faster than
10 low probability items.

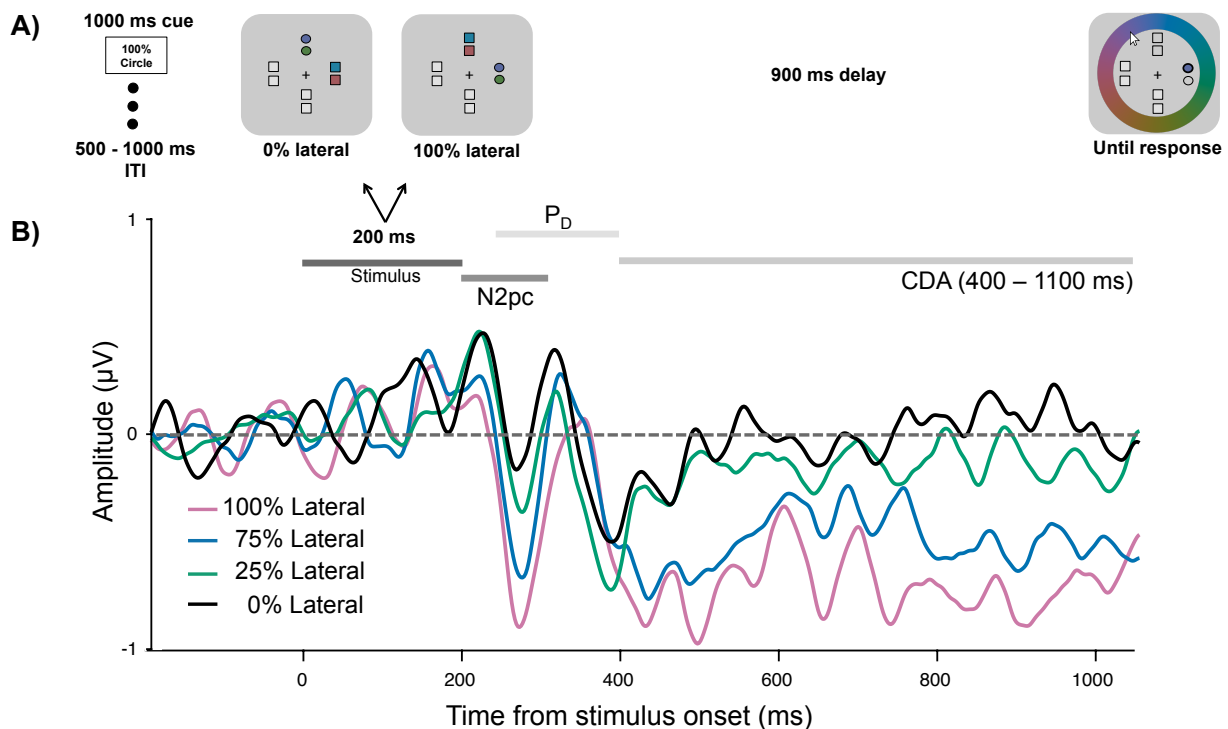
11 **P_D.**

12 Permutation tests indicated that the positive area of the grand average waveform
13 between 250 – 400 ms was not significantly different from noise in any of the conditions,
14 100%: $p = .529$, 75%: $p = .30$, 25%: $p = .306$, 0%: $p = .087$. Although the P_D was not
15 significant, it could be that priority still had an influence on its amplitude. There was a
16 small but non-significant effect of priority on the positive area of the P_D, $F(1.84, 34.96) =$
17 2.95 , $p = .070$, $\eta^2_p = .134$, $BF_{10} = 1.36$. Therefore, there was little evidence of active
18 attentional suppression in this task.

19 **CDA.**

20 Similar to the N2pc, priority affected the amplitude of the CDA (main effect of
21 Condition, $F(2.09, 39.74) = 7.43$, $p = .002$, $\eta^2_p = .281$, $BF_{10} = 251.951$). More information
22 was stored in VWM when the item was 100% likely to be probed ($M = -0.696 \mu\text{V}$, $SD =$
23 $0.809 \mu\text{V}$) than 0% ($M = -0.028 \mu\text{V}$, $SD = 0.382 \mu\text{V}$), $t(19) = 3.323$, $p_{\text{bonf}} = .021$, $d =$

1 0.743, $BF_{10} = 12.198$. Similarly, the CDA was more negative in the 100% condition than
 2 the 25% condition ($M = -0.042 \mu V$, $SD = 0.347 \mu V$), $t(19) = -3.118$, $p_{\text{bonf}} = .034$, $d = -$
 3 0.697, $BF_{10} = 8.249$. When an item was 75% likely to be probed, the CDA amplitude (M
 4 $= -0.618 \mu V$, $SD = 0.792 \mu V$) was marginally more negative than in the 25% and 0%
 5 conditions, $t_s < 2.87$, $p_{\text{bonfs}} < .075$, $d_s < 0.641$, $BF_{s10} > 4.30$. No other post-hoc
 6 comparisons were significant, $t_s < 0.133$, $p_{\text{bonfs}} = 1$, $d_s < 0.104$, $BF_{s10} < 0.235$.
 7 However, similar to the N2pc, CDA amplitude was linearly related to priority, adjusted-
 8 $R^2 = .906$, $RMSE = .1106$, linear contrast: $t(19) = 4.36$, $p < .001$. Therefore, the more
 9 likely an item was to be probed, the more information about that item was stored in
 10 VWM as tracked by the CDA.



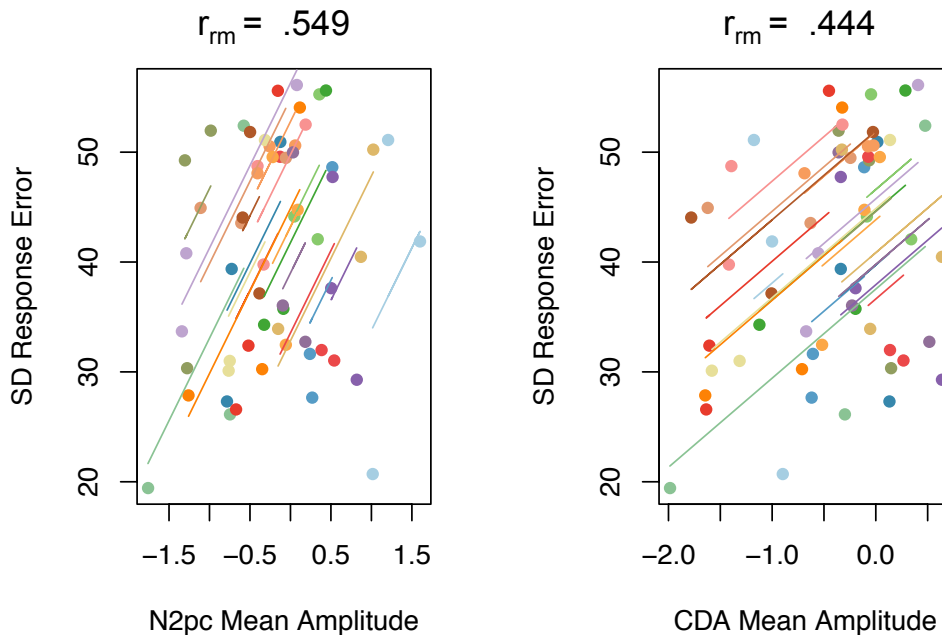
11
 12 *Figure 3.* A) Task schematic of Experiment 2. Each trial began with a feature-based cue
 13 followed by a jittered ITI consisting of a fixation dot. In this example, it was 100% likely that the
 14 color of a circle would be probed. The stimulus display consisted of 2 colored shapes on the
 15 lateral and 2 on the vertical. In the present example, if squares were presented on the lateral,
 16 0% of memory resources should be allocated toward them. If circles were presented on the

1 lateral, 100% should be allocated. After a delay, participants made a response to the probed
2 shape on the color wheel with the mouse. B) Grand average difference waveform (N = 20) at
3 the average of 5 posterior channel pairs, time-locked to stimuli onset. Positive is plotted up.
4 Filtered at 30 Hz for visualization purposes only.

5
6

N2pc and CDA amplitudes predict behavioral precision.

7 To examine whether memory resource-related changes in N2pc and CDA
8 amplitudes predicted changes to VWM response error, a repeated-measures correlation
9 was performed between mean amplitude and response error across three lateral
10 resource conditions (25%, 75%, and 100%). It was found that attention, as measured by
11 the N2pc, toward the lateral shapes predicted how precisely the color of the probed
12 shape was reported, $r_{rm}(39) = 0.549$, 95% CI = [.282, .737], $p < .001$ (Figure 4A).
13 There was also a correlation between raw error and mean amplitude of the CDA, $r_{rm}(39)$
14 = 0.444, 95% CI = [0.150, 0.666], $p = .004$ (Figure 4B). These findings indicate more
15 precise reports of the probed color were associated with larger neural responses related
16 to attentional enhancement (N2pc) and memory maintenance (CDA).



17

1 *Figure 4.* Repeated-measures correlations plots. Each colored line is the fit for three data points
2 from each individual participant from the 100%, 75%, and 25% lateral likelihood conditions. A)
3 Correlation between N2pc mean amplitude and standard deviation (SD) of raw response error.
4 Lower SD indicates more precise responding. B) Correlation between CDA mean amplitude and
5 SD of response error.
6

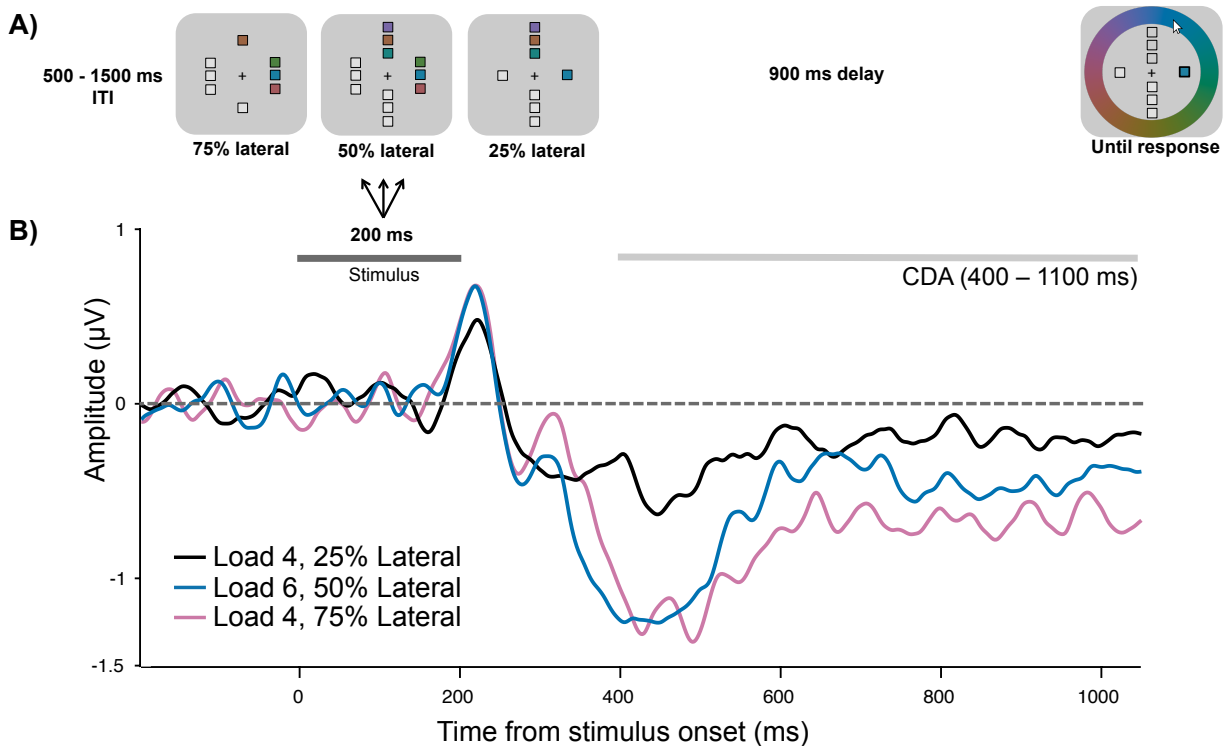
7 **Experiment 3**

8 Experiment 2 provided evidence that attentional prioritization not only affects the
9 behavioral precision in a delayed-recall task, it is also associated with a proportional
10 increase in the amplitude of ERP components associated with attentional enhancement
11 (N2pc) and memory maintenance (CDA). Interestingly, previous studies have found that
12 the effect of load on behavioral precision is identical to those of prioritization; thus,
13 splitting resources across two items results in similar memory precision as an item with
14 50% cue validity¹⁸. Consequently, to test whether the CDA similarly reflects resource
15 allocation in the absence of prioritization cues we manipulated how many items were
16 presented laterally, and how many vertically. There were three conditions: one item
17 lateral and three vertical (Load 4, 25% lateral), three items lateral and one vertical (Load
18 4, 75% lateral), and three items lateral and three items vertical (Load 6, 50% lateral).
19 Thus, these last two conditions had the same lateral memory load and a change in the
20 proportion of memory resources allocated to those items. Comparing across these three
21 conditions allowed us to examine how both lateral memory load and the proportion of
22 lateral memory resources affected the CDA, independent of cueing effects.

23 **CDA.**

24 CDA amplitude was affected by Condition (Figure 5B), $F(2,38) = 7.60$, $p = .002$,
25 $\eta^2_p = .286$, $BF_{10} = 24.313$, such that the amplitude was more negative when 75% of
26 memory resources were allocated to three lateral items ($M = -0.775 \mu\text{V}$, $SD = 0.637 \mu\text{V}$)
27 than when 25% were allocated to one lateral item ($M = -0.252 \mu\text{V}$, $SD = 0.541 \mu\text{V}$), $t(19)$

1 = 3.401, $p_{bonf} = .009$, $d = 0.760$, $BF_{10} = 14.168$. When 50% of memory resources were
 2 allocated to three lateral items ($M = -0.565 \mu V$, $SD = .595 \mu V$), the CDA amplitude was
 3 not different from either of the other two conditions, $t_s < 2.27$, $p_s > .105$, $d_s < 0.508$,
 4 $BF_{S10} < 1.83$. Although participants were holding three lateral items in memory in this
 5 condition, the CDA amplitude was not significantly different from when only one lateral
 6 item was in memory (in contrast to when three lateral items were held in memory with
 7 75% of memory resources). Additionally, CDA amplitude was linearly related to the
 8 proportion of lateral resources, adjusted- $R^2 = .9067$, $RMSE = .0963$, $t(19) = 3.4$, $p =$
 9 $.009$, such that amplitude became more negative as the amount of resources increased.
 10 Together, these findings suggest that even in the absence of prioritization cues, the
 11 CDA may reflect a combination of memory load *and* the amount of attention/memory
 12 resources allocated toward these items.



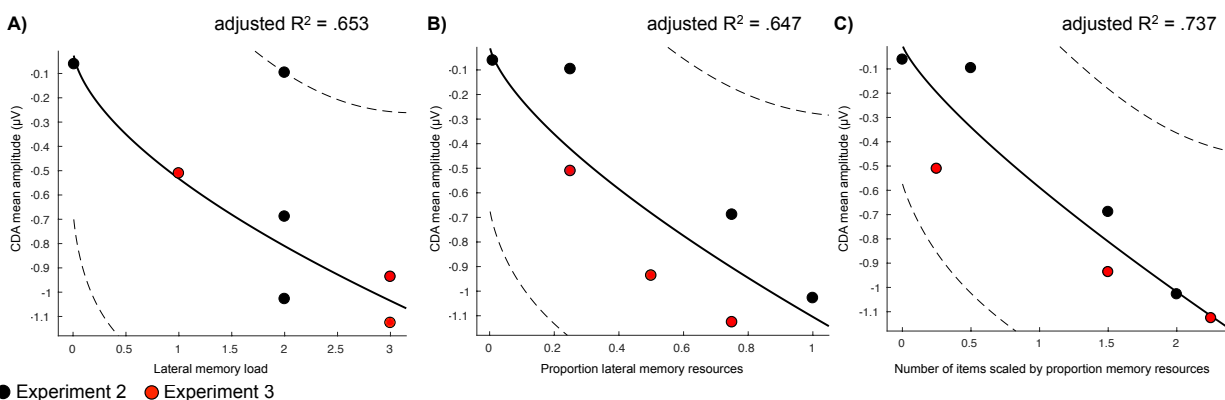
13

1 *Figure 5.* A) Task schematic of Experiment 3. Participants were told to remember the colors of
2 all of the squares. Each trial began with a jittered ITI consisting of a fixation dot. There were 3
3 conditions differing in overall memory load (4 or 6) and by how many items were presented on
4 the lateral (1 or 3). After a delay, participants made a response to the probed shape on the color
5 wheel with the mouse. B) Grand average difference waveform (N = 20) at the average of 5
6 posterior channel pairs, time-locked to stimuli onset. Positive is plotted up. Filtered at 30 Hz for
7 visualization purposes only.

8 **CDA amplitude continuously reflects both VWM load and resource allocation**

10 Across three experiments, the manipulation of resource allocation – whether by
11 spatial cues, feature-based cues, or memory load – affected the amplitude of the CDA.
12 Although these effects were sometimes small, they are consistent with previous
13 behavioral findings (also observed here) that the magnitude of the effect on memory
14 performance depends on the magnitude of the change in resource allocation. However,
15 although small changes in resource allocation may only produce small effects, these
16 effects tend to follow a predictable pattern along a continuous power-law in behavioral
17 studies¹⁸. Thus, it is possible that the effect of resource allocation on ERP measures of
18 memory maintenance should similarly follow a continuous pattern, wherein the
19 amplitude of the CDA changes with the proportion of resources allocated to laterally-
20 presented items. It is also possible that, although resource allocation is a better
21 predictor of memory performance than load alone, CDA amplitude may reflect a mixture
22 of signals that combine effects of load *and* resource allocation. To examine this
23 prediction, we tested whether the CDA amplitudes observed in Experiments 2 and 3
24 (which involved the same stimulus displays) were best described by one of three
25 models: one in which CDA amplitude was predicted by load alone, another with
26 resource allocation alone, and a model using a scaled combination of memory load and
27 resource allocation (see Methods).

1 When CDA amplitudes were compared to memory load alone (Figure 6A), the
 2 model only accounted for 65% of the variance in the data, adjusted- $R^2 = 0.653$, $RMSE =$
 3 0.255 , $BIC = -14.44$. This was similar when CDA amplitudes were fit with proportion of
 4 memory resources alone (Figure 6B), adjusted- $R^2 = 0.647$, $RMSE = 0.257$, $BIC = -$
 5 18.64 . However, when fitting CDA amplitude to the weighted sum of both memory load
 6 and proportion memory resources, we observed the best fit (Figure 6C), adjusted- $R^2 =$
 7 0.737 , $RMSE = 0.222$, $BIC = -21.28$. This demonstrates that the amplitude of the CDA
 8 follows a predictable continuous function that is affected both by the number of lateral
 9 items to be remembered, and by the proportion of total resources allocated to those
 10 items.



11
 12 **Figure 6.** Power-law models and fits. Dotted lines represent 95% CIs of the model fit. Black dots
 13 represent condition means from Experiment 2 and red dots from Experiment 3. A) Fit between
 14 CDA mean amplitude and lateral memory load. B) Fit between CDA amplitude and proportion
 15 lateral memory resources. C) Fit between CDA amplitude and number of items scaled for both
 16 memory load and memory resources.

17 18 **General Discussion**

19 In the current study, we sought to examine the effect of attentional prioritization
 20 on the CDA, as well use attention-related ERPs to determine whether prioritization was
 21 driven by selective enhancement or suppression. In Experiment 1, we found that the
 22 CDA amplitude is somewhat reduced when prioritizing one item over others than when

1 all items are prioritized equally. In Experiment 2, we implemented a stronger
2 manipulation of resource allocation using a systematic lateralization procedure^{26,51},
3 demonstrating that the CDA tracked overall proportion of memory resources allotted.
4 Additionally, we found that the N2pc was also reflective of priority, providing evidence
5 that the allocation of neural resources toward to-be remembered items occurs via
6 attentional enhancement. Moreover, both N2pc and CDA amplitudes correlated with
7 individuals' behavioral precision in this task, demonstrating that both components can
8 be used to predict how well individuals are able to recall a memory item. Finally, in
9 Experiment 3 we manipulated the proportion of memory resources that should be
10 allocated to lateral items by controlling the relative proportion of memory array items
11 presented laterally. Consistent with the first two experiments, we found that CDA
12 amplitude tracked the proportion of memory resources that should have been allocated
13 toward the lateral items in the stimulus display.

14 When comparing across Experiments 2 and 3, we also found that CDA
15 amplitudes were best predicted by a weighted sum of memory load and resources. This
16 relationship followed a continuous power law, similar to previous behavioral
17 findings^{7,18,19}. Importantly, these model fits showed that when accounting for both load
18 and memory resources there was a better fit than when considering only load or
19 resources in isolation. This novel finding points to the CDA as a proxy of more than
20 memory load alone, suggesting that this component may also reflect the total amount of
21 memory resources allocated to each item, and therefore, the fidelity of those
22 representations.

1 One potential argument against the resource allocation interpretation is that
2 instead of flexibly distributing resources across all items in the display, individuals were
3 selectively encoding items in the display depending on the likelihood that they would
4 become the target (i.e. preferentially encoding the higher priority items). One argument
5 against this interpretation comes from the absence of timing differences in the N2pc in
6 Experiment 2. Previous studies have shown that in visual search tasks, high-probability
7 targets are selected first, resulting in an earlier N2pc^{47,53}. Based on this logic, one would
8 expect that participants might select the higher-priority items first, resulting in a change
9 in the onset of the lateral N2pc depending on whether the high-priority items were
10 presented on the lateral or vertical midline. That is, if participants were encoding more
11 high-priority items, these items should be selected first (consistent with high-probability
12 targets in search tasks). In contrast to this hypothesis, there was no difference in the
13 timing of the N2pc across conditions in Experiment 2, suggesting that all items were
14 being attended to at the same time, regardless of their priority.

15 In addition, the findings of Experiment 3 demonstrate that resource allocation
16 affects the CDA amplitude even in the absence of explicit prioritization cues. That is,
17 even though all items were equally likely to be probed, the CDA amplitude towards
18 three lateral items was reduced when resources had to be spread across additional
19 vertical items. It is possible that participants could decide to encode only a subset of
20 items on each trial. However, rather than being a confound specific to a resource
21 allocation interpretation, fluctuations in CDA amplitude across trials is likely a feature of
22 all CDA measurements⁴², as changes in the number of items and amount of information
23 encoded may occur due to spontaneous fluctuations in attention^{5,54,55}, or top-down

1 strategies^{56,57}. In other words, although the experiments presented here may include
2 some measure of strategic differences in resource allocation across trials, *spontaneous*
3 changes in resource allocation across trials, as opposed to the systematic changes
4 across conditions demonstrated here, may be a feature of past CDA studies that has
5 been previously unexplored.

6 There are several implications that arise from these findings. First, the CDA has
7 frequently been used to estimate the number of items stored in memory, such that it has
8 been used as a proxy for filtering efficiency^{16,58}. However, we show that the CDA at
9 least in part reflects flexible prioritization and allocation of memory resources towards
10 to-be remembered items. Therefore, it is possible that studies that have used the CDA
11 as an all-or-none marker of WM filtering may be over- or under-estimating the number
12 of items that individuals have stored in memory, without accounting for resource
13 allocation.

14 The results also speak to the role of attentional enhancement in prioritization. In
15 Experiment 2 we found that the N2pc, but not the P_D, tracked the priority of the
16 lateralized stimuli, while also predicting the behavioural precision of memory report. This
17 suggests that when using feature-based cues, participants relied on up-weighting
18 relevant information depending on their respective priorities, in comparison to down-
19 weighting irrelevant information using active suppression. This is consistent with
20 previous findings which found that when given a pre-cue that indicated to participants to
21 up or down-regulate memory encoding processes, it was only possible to up-regulate
22 processing to benefit performance³. Additionally, it has been found that when using

1 reward to prioritize items, only target selection was impacted and not distractor
2 suppression⁵⁹.

3 Our finding is also consistent with a recent study that suggests the N2pc reflects
4 enhancement of items at the spatial focus of attention, instead of an overall attentional
5 shift toward the lateral⁶⁰. Interestingly, we did not find attention-related components in
6 Experiments 1 and 3, pointing to the importance of having a pre-cue to be able to
7 allocate attention accordingly, suggesting perhaps that resource allocation may occur
8 later in the presence of simultaneous spatial cues (Experiment 1) or no cues
9 (Experiment 3). Future studies should further examine the N2pc as a potential marker of
10 the flexible allocation of neural resources for attentional enhancement according to item
11 priority.

12 Our findings also stress the importance of flexible attentional control in
13 prioritization, which may be a limiting factor in overall VWM capacity and performance.
14 Namely, previous work has focused on the link between unnecessary memory storage
15 of distractors and VWM capacity^{61,62}. However, a reanalysis of these data found that
16 attentional control processes involved in filtering distractors better predicted memory
17 capacity than unnecessary storage itself²⁰. These attentional control processes are
18 thought to arise from the bilateral prefrontal cortex and left basal ganglia^{61,62}. Thus,
19 while future studies should investigate the role of frontal-related ERP components to
20 VWM resource allocation, our findings that the N2pc amplitude changes as a function of
21 priority and predicts behavioural precision provide further evidence that attentional
22 enhancement driven by top-down attentional control may be critical to determining VWM
23 performance.

1 Although previous studies have established a clear link between filtering ability
2 and VWM performance, our findings suggest that the role of attention in VWM
3 performance goes beyond filtering distractors. Consequently, one limitation of the
4 filtering account is that the effect can only be observed when there are distractors
5 present in the display. It is known, however, that memory performance differs amongst
6 individuals even when the display consists only of targets (i.e. capacity effects).
7 Therefore, a full account of working memory performance should require a mechanism
8 wherein resources are allocated amongst items when they are all relevant to the task¹¹.
9 The results of Experiment 3 speak to the existence of such a mechanism, as even in the
10 absence of prioritization (or filtering) cues, the CDA still best reflected the overall
11 proportion of resources allocated toward the lateral items. This was of course also
12 influenced by how many items were being held in memory, as demonstrated by the
13 model fit of CDA amplitude with resources and load together. However, a full account of
14 VWM performance will need to understand the control mechanisms that select and
15 prioritize targets, in addition to (or irrespective of) the requirement to filter distractors.

16 Finally, the current results provide with some information about the neural origins
17 of the CDA. The finding that the CDA follows a power-law when fit with both resources
18 and memory load is consistent with the saturation model of delay period activity
19 proposed by Bays¹⁷. In this model, as input increases, neuronal activity also increases.
20 However, as the input becomes large, it produces a smaller increment in neuronal
21 activity¹⁷. This results in activity saturating at some maximum level. Although the power-
22 law examined here tests a similar pattern, the current experiments did not test a large
23 enough range of set sizes to delineate between capacity-limited models and limitless

1 models. Moreover, it could be that prioritization is only possible within a limited range of
2 stored items. Regardless, the results of the experiments presented here indicate the
3 need to consider resource allocation in addition to overall load in neural and behavioral
4 models of VWM.

References

- 1 1. Chun, M. M. & Turk-Browne, N. B. Interactions between attention and memory. *Current*
2 *Opinion in Neurobiology* **17**, 177–184 (2007).
- 3 2. deBettencourt, M. T., Norman, K. A. & Turk-Browne, N. B. Forgetting from lapses of
4 sustained attention. *Psychon Bull Rev* **25**, 605–611 (2017).
- 5 3. Sundby, C. S., Woodman, G. F. & Fukuda, K. Electrophysiological and behavioral
6 evidence for attentional up-regulation, but not down-regulation, when encoding
7 pictures into long-term memory. *Mem Cogn* (2018). doi:10.3758/s13421-018-0871-z
- 8 4. Turk-Browne, N. B., Golomb, J. D. & Chun, M. M. Complementary attentional components
9 of successful memory encoding. *NeuroImage* **66**, 553–562 (2013).
- 10 5. Adam, K. C. S., Mance, I., Fukuda, K. & Vogel, E. K. The contribution of attentional lapses
11 to individual differences in visual working memory capacity. *Journal of Cognitive*
12 *Neuroscience* **27**, 1601–1616 (2015).
- 13 6. Fukuda, K. & Vogel, E. K. Individual differences in recovery time from attentional
14 capture. *Psychological Science* **22**, 361–368 (2011).
- 15 7. Klyszejko, Z., Rahmati, M. & Curtis, C. E. Attentional priority determines working
16 memory precision. *Vision Research* **105**, 70–76 (2014).
- 17 8. Awh, Vogel, E. K. & Oh, S.-H. Interactions between attention and working memory.
18 *Neuroscience* **139**, 201–208 (2006).
- 19 9. Cowan, N. *et al.* On the capacity of attention: Its estimation and its role in working
20 memory and cognitive aptitudes. *Cogn Psychol* **51**, 42–100 (2005).
- 21 10. Engle, R. W. Working memory capacity as executive attention. *Curr Dir Psychol Sci* **11**,
22 19–23 (2002).
- 23

- 1 11. Fukuda, K., Woodman, G. F. & Vogel, E. K. Individual differences in visual working
2 memory capacity: Contributions of attentional control to storage. *Mechanisms of*
3 *Sensory Working Memory: Attention and Performance XXV* 105 (2015).
- 4 12. Cowan, N. & Morey, C. C. Visual working memory depends on attentional filtering.
5 *Trends in Cognitive Sciences* **10**, 139–141 (2006).
- 6 13. Luck, S. J. & Vogel, E. K. Visual working memory capacity: From psychophysics and
7 neurobiology to individual differences. *Trends in Cognitive Sciences* 391 (2013).
8 doi:10.1016/j.tics.2013.06.006
- 9 14. McCollough, A. W., Machizawa, M. G. & Vogel, E. K. Electrophysiological measures of
10 maintaining representations in visual working memory. *Cortex* **43**, 77–94 (2007).
- 11 15. Vogel, E. K. & Machizawa, M. G. Neural activity predicts individual differences in visual
12 working memory capacity. *Nature* **428**, 748–751 (2004).
- 13 16. Vogel, E. K., McCollough, A. W. & Machizawa, M. G. Neural measures reveal individual
14 differences in controlling access to working memory. *Nature* **438**, 500–503 (2005).
- 15 17. Bays, P. M. Reassessing the evidence for capacity limits in neural signals related to
16 working memory. *Cereb Cortex* **28**, 1432–1438 (2018).
- 17 18. Emrich, S. M., Lockhart, H. A. & Al-Aidroos, N. Attention mediates the flexible allocation
18 of visual working memory resources. *J Exp Psychol Hum Percept Perform* **43**, 1454–
19 1465 (2017).
- 20 19. Dube, B., Emrich, S. M. & Al-Aidroos, N. More than a filter: Feature-based attention
21 regulates the distribution of visual working memory resources. *J Exp Psychol Hum*
22 *Percept Perform* **43**, 1843–1854 (2017).

- 1 20. Emrich, S. M. & Busseri, M. A. Re-evaluating the relationships among filtering activity,
2 unnecessary storage, and visual working memory capacity. *Cogn Affect Behav Neurosci*
3 **15**, 589–597 (2015).
- 4 21. Eimer. The N2pc component as an indicator of attentional selectivity.
5 *ELECTROENCEPHALOGRAPHY AND CLINICAL NEUROPHYSIOLOGY* **99**, 225–234 (1996).
- 6 22. Hickey, C., McDonald, J. J. & Theeuwes, J. Electrophysiological evidence of the capture of
7 visual attention. *Journal of Cognitive Neuroscience* **18**, 604–613 (2006).
- 8 23. Hickey, C., Zoest, W. van & Theeuwes, J. The time course of exogenous and endogenous
9 control of covert attention. *Exp Brain Res* **201**, 789–796 (2010).
- 10 24. Burra, N. & Kerzel, D. The distractor positivity (Pd) signals lowering of attentional
11 priority: Evidence from event-related potentials and individual differences.
12 *Psychophysiol* **51**, 685–696 (2014).
- 13 25. Gaspar, J. M. & McDonald, J. J. Suppression of salient objects prevents distraction in
14 visual search. *J. Neurosci.* **34**, 5658–5666 (2014).
- 15 26. Hickey, C., Di Lollo, V. & McDonald, J. J. Electrophysiological indices of target and
16 distractor processing in visual search. *Journal of Cognitive Neuroscience* **21**, 760–775
17 (2008).
- 18 27. Sawaki, R. & Luck, S. J. Active suppression after involuntary capture of attention.
19 *Psychon Bull Rev* **20**, 296–301 (2013).
- 20 28. Fukuda, K., Kang, M.-S. & Woodman, G. F. Distinct neural mechanisms for spatially
21 lateralized and spatially global visual working memory representations. *Journal of*
22 *Neurophysiology* **116**, 1715–1727 (2016).

- 1 29. Luck, S. J. & Vogel, E. K. The capacity of visual working memory for features and
2 conjunctions. *Nature* **390**, 279–281 (1997).
- 3 30. Delorme, A. & Makeig, S. EEGLAB: An open source toolbox for analysis of single-trial
4 EEG dynamics including independent component analysis. *J. Neurosci. Methods* **134**, 9–
5 21 (2004).
- 6 31. Lopez-Calderon, J. & Luck, S. J. ERPLAB: An open-source toolbox for the analysis of
7 event-related potentials. *Front Hum Neurosci* **8**, (2014).
- 8 32. *BioSemi ActiveTwo System Amsterdam, The Netherlands*.
- 9 33. Gaspelin, N. & Luck, S. J. Combined electrophysiological and behavioral evidence for the
10 suppression of salient distractors. *Journal of Cognitive Neuroscience* **30**, 1265–1280
11 (2018).
- 12 34. Lins, O. G., Picton, T. W., Berg, P. & Scherg, M. Ocular artifacts in EEG and event-related
13 potentials I: Scalp topography. *Brain Topogr* **6**, 51–63 (1993).
- 14 35. McDonald, J. J. & Ward, L. M. Spatial relevance determines facilitatory and inhibitory
15 effects of auditory covert spatial orienting. *Journal of Experimental Psychology: Human*
16 *Perception and Performance* **25**, 1234 (1999).
- 17 36. Bays, P. M. & Husain, M. Dynamic shifts of limited working memory resources in human
18 vision. *Science* **321**, 851–854 (2008).
- 19 37. Hakim, N., Adam, K. C. S., Gunseli, E., Awh, E. & Vogel, E. K. Dissecting the neural focus of
20 attention reveals distinct processes for spatial attention and object-based storage in
21 visual working memory. *Psychol Sci* **30**, 526–540 (2019).
- 22 38. van Doorn, J. *et al*. The JASP guidelines for conducting and reporting a bayesian
23 analysis. *PsyArXiv* (2019). doi:10.31234/osf.io/yqxfr

- 1 39. JASP Team. *JASP*. (2018).
- 2 40. R Core Team. *R: A language and environment for statistical computing*. (2017).
- 3 41. RStudio Team. *RStudio: Integrated Development for R*. (2015).
- 4 42. Adam, K. C. S., Robison, M. K. & Vogel, E. K. Contralateral delay activity tracks
5 fluctuations in working memory performance. *Journal of Cognitive Neuroscience* **30**,
6 1229–1240 (2018).
- 7 43. Ikkai, A., McCollough, A. & Vogel, E. Contralateral delay activity provides a neural
8 measure of the number of representations in visual working memory. *JOURNAL OF*
9 *NEUROPHYSIOLOGY* **103**, 1963–1968 (2010).
- 10 44. Kiss, M., Velzen, J. V. & Eimer, M. The N2pc component and its links to attention shifts
11 and spatially selective visual processing. *Psychophysiology* **45**, 240–249 (2008).
- 12 45. Luck, S. J. & Hillyard, S. A. Spatial filtering during visual search: Evidence from human
13 electrophysiology. *Journal of Experimental Psychology: Human Perception and*
14 *Performance* **20**, 1000–1014 (1994).
- 15 46. Mazza, V., Turatto, M. & Caramazza, A. Attention selection, distractor suppression and
16 N2pc. *Cortex* **45**, 879–890 (2009).
- 17 47. Woodman, G. F. & Luck, S. J. Electrophysiological measurement of rapid shifts of
18 attention during visual search. *Nature* **400**, 867 (1999).
- 19 48. Luck, S. J. *An introduction to the event-related potential technique*. (MIT press, 2014).
- 20 49. Feldmann-Wüstefeld, T. & Vogel, E. K. Neural evidence for the contribution of active
21 suppression during working memory filtering. *Cereb Cortex* (2018).
22 doi:10.1093/cercor/bhx336

- 1 50. Gaspar, J. M., Christie, G. J., Prime, D. J., Jolicoeur, P. & McDonald, J. J. Inability to suppress
2 salient distractors predicts low visual working memory capacity. *Proceedings of the*
3 *National Academy of Sciences* **113**, 3693–3698 (2016).
- 4 51. Sawaki, R., Geng, J. J. & Luck, S. J. A common neural mechanism for preventing and
5 terminating the allocation of attention. *J. Neurosci.* **32**, 10725–10736 (2012).
- 6 52. Bakdash, J. Z. & Marusich, L. R. Repeated measures correlation. *Front Psychol* **8**, (2017).
- 7 53. Woodman, G. F. & Luck, S. J. Serial deployment of attention during visual search. *Journal*
8 *of Experimental Psychology: Human Perception and Performance* **29**, 121–138 (2003).
- 9 54. deBettencourt, M. T., Keene, P. A., Awh, E. & Vogel, E. K. Real-time triggering reveals
10 concurrent lapses of attention and working memory. *Nature Human Behaviour* **1**
11 (2019). doi:10.1038/s41562-019-0606-6
- 12 55. van den Berg, R., Shin, H., Chou, W.-C., George, R. & Ma, W. J. Variability in encoding
13 precision accounts for visual short-term memory limitations. *Proc. Natl. Acad. Sci. U.S.A.*
14 **109**, 8780–8785 (2012).
- 15 56. Cusack, R., Lehmann, M., Veldsman, M. & Mitchell, D. J. Encoding strategy and not visual
16 working memory capacity correlates with intelligence. *Psychonomic Bulletin & Review*
17 **16**, 641–647 (2009).
- 18 57. Linke, A. c., Vicente-Grabovetsky, A., Mitchell, D. j. & Cusack, R. Encoding strategy
19 accounts for individual differences in change detection measures of VSTM.
20 *Neuropsychologia* **49**, 1476–1486 (2011).
- 21 58. Awh, E. & Vogel, E. K. The bouncer in the brain. *Nature neuroscience* **11**, 5–6 (2008).

- 1 59. Hickey, C., Chelazzi, L. & Theeuwes, J. Reward has a residual impact on target selection
2 in visual search, but not on the suppression of distractors. *Visual Cognition* **19**, 117–128
3 (2011).
- 4 60. Zivony, A., Allon, A. S., Luria, R. & Lamy, D. Dissociating between the N2pc and
5 attentional shifting: An attentional blink study. *Neuropsychologia* **121**, 153–163 (2018).
- 6 61. Liesefeld, A. M., Liesefeld, H. R. & Zimmer, H. D. Intercommunication between prefrontal
7 and posterior brain regions for protecting visual working memory from distractor
8 interference. *Psychol Sci* **25**, 325–333 (2014).
- 9 62. McNab, F. & Klingberg, T. Prefrontal cortex and basal ganglia control access to working
10 memory. *Nat Neurosci* **11**, 103–107 (2008).
- 11