Electrophysiological correlates of the flexible allocation of visual working memory resources

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Abstract

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

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

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

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

independent of the need to filter out irrelevant distractor items. This bias can be induced by associating certain stimuli with monetary incentives, or by simply varying instructions indicating the probability that an item will be probed on any given trial[7]. For example, spatial cues[18] or feature-based cues[19] can be used to change the likelihood that a given item will be probed. In this way, the proportion of attentional resources allocated to any given memory item can continuously vary anywhere between 0 and 100%.

In these past studies[18,19], it was found that working memory performance (i.e., raw error = 1/ precision) was best predicted by the likelihood that an item would be probed on a given trial, independent of the overall memory load. These findings support the idea that attentional resources can be continuously allocated across items, even when they are of very low priority. Importantly, this relationship between probe likelihood and memory precision, which followed a power law, could also account for changes in performance across loads; for example, the change in precision from one to two items was consistent with each item only receiving half as many attentional resources. This framework suggests that attention does more than just restrict or grant access to VWM; rather, it also flexibly distributes resources amongst memory items based on their respective priorities. In other words, how attention is allocated between targets is as important to memory performance as whether or not it is allocated to distractors[20].

If attention can be flexibly allocated across items in VWM, how might this be reflected by neural measures of attention and VWM maintenance? There is evidence that the CDA is well-described by a saturation model, which predicts a continuous increase in CDA amplitude that saturates as set size becomes larger, instead of increasing discretely and plateauing at memory capacity[17]. This finding suggests that

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

Prioritization could also be tracked by ERP components that precede memory maintenance, such as attentional selection and suppression. That is, one way that flexible prioritization could be accomplished is through the specific up-weighting of goal-relevant over irrelevant information (as opposed to down-weighting of goal-irrelevant information). Attentional selection can be tracked by the N2pc, a lateralized component which specifically reflects the enhancement of an item[21–23]. Alternatively, it could be that prioritization is accomplished through the active suppression or down-weighting of goal irrelevant information. This can be measured by the distractor positivity (P_D): a lateralized component that is observed when distractors are presented laterally in the stimulus display[24–27]. These two components can thus be used to disentangle the underlying mechanisms of prioritization: whether through selective enhancement of relevant information (N2pc) or suppression of irrelevant information (P_D).

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

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

Methods

Participants

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

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

Stimuli and Procedures

All tasks were completed on a Windows PC with a 41-cm NEC MultiSync LCD 2090UXi computer monitor (1600 x 1200 pixels, 60 Hz refresh rate) in a private testing room. Stimuli were rendered using Psychopy v1.90.3 (Peirce, 2007) and presented on a grey background (RGB = 128 128 128) with a central fixation dot (radius of 0.3° visual angle). Viewing distance was approximately 57 cm (no chin rest was used). In all experiments, participants first completed a standard change detection task [29]. However, these data are not included in the analyses below.

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

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

Experiment 1.

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

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

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

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

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

Experiment 2.

Luminance matching task.

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

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

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

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

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

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

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

Experiment 3.

Visual working memory task with lateralized resource and load manipulation (Figure 5A).

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

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

EEG Recording and Pre-Processing

All EEG pre-processing was done in MATLAB with the EEGLAB[30] (Version 14.0.0b), and ERPLAB[31] (Version 6.1.2) toolboxes. EEG was DC recorded at a 512 Hz sampling rate from a 64 Ag/AgCl electrode cap placed at the standard 10-20 sites[32]. The signal was online referenced to the common mode sense (CMS) and the driven right leg (DRL) electrodes. Data were re-referenced off-line to the average of the mastoids, baseline corrected to -200 ms before memory array onset, and filtered with a 40-Hz low-pass and 0.1-Hz high-pass Butterworth filter (slope: 12dB/octave). For illustrative purposes only, data were low-pass filtered at 30-Hz. Data were epoched between -200 and 1,050 (Experiment 1) or -200 and 1,100 ms (Experiment 2) ms, time-locked to the memory array.

Artifact rejection.

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

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

In Experiments 2 and 3 we also replaced participants whose average residual HEOG activity (relative to the side of the lateralized memory array) was greater than 4 μV between memory array onset and the end of the epoch. On average across conditions, the absolute residual HEOG was 1.61 μV (*SD* = 1.02 μV) in Experiment 2 and 1.61 μV (*SD* = 1.00 μV) in Experiment 3. This means that the deviation in lateral eye movements was less than ± 0.1° relative to the location of the lateralized memory array in both experiments, and that the estimated voltage propagation was overall less than 0.1 μV at posterior electrodes[33–35].

Data Analysis

Behavioral data.

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

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

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

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

ERP data.

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

We measured difference wave activity at five posterior electrode pairs: P3/4, P7/8, PO7/O8, PO3/O4, and O1/2[37]. Across all experiments, there was no significant Condition x Channel interaction for any of the ERP components (Fs < 2.24, ps > .055, η^2_ps < .106). Therefore, we averaged activity across these electrode sites for all ERP measurements.

For each ERP component of interest, we ran a repeated-measures ANOVA on the mean condition amplitudes. Follow-up linear contrasts and fits were completed in Experiments 2 and 3 for the N2pc and CDA. Greenhouse-Geisser corrected degrees of freedom and p values are reported. Two-tailed post-hoc t-tests were Bonferroni-corrected. Cohen's d is reported where appropriate. Bayesian repeated-measures ANOVAs and post-hoc tests are reported where applicable (r scale prior width of 0.5, default Cauchy prior centered on 0, 10,000 Monte Carlo samples). Bayes factors (BF_{10}) are presented as the marginal likelihood for the alternative model compared to the null model[38]. Statistical analyses were completed using JASP Version 0.8.4[39], MATLAB R2017a, and R version 3.5.1[40] in RStudio version 1.1.456[41].

CDA.

In all experiments, the CDA was measured for each condition and participant as the mean amplitude during the delay period from 400 ms post-stimuli offset to the end of the trial[42,43] (Experiment 1: 1,050 ms; Experiments 2 and 3: 1,100 ms).

N2pc.

An N2pc was only observed in Experiment 2 and was measured from 200 – 300 ms post-stimuli onset[44–47]. To determine whether individuals were selecting the higher priority items any faster than the lower priority items, we also measured the negative 50% fractional area latency of the N2pc between 200 – 300 ms for each participant and condition [48].

P_D.

We predicted there to be a P_D in Experiment 2 exclusively, as this was the only task in which there were systematically lateralized distractors. In Experiment 2, we measured the P_D as the positively signed area from 250 – 400 ms[49,50]. Because the positively signed area is biased away from zero, we used a nonparametric permutation approach developed by Sawaki and colleagues[51] to determine the presence of the P_D. This method estimates the area of the waveform above zero that would be expected by noise alone, which can then be compared to the observed area of the grand-average P_D in each condition.

The *p* values for the permutation tests were estimated using the following formula with 1,000 permutations[33]:

$$p = \frac{\text{Number of permuted areas } \geq \text{observed area}}{\text{Total number of simulated permutations}}$$

EEG and behavior correlations.

In Experiment 2, we predicted a correlation between ERPs and behavior, such that as N2pc /CDA amplitudes increased, responses would become more precise. To examine this, we ran a repeated measures correlation analysis using the *rmcorr* package in R[52]. Each participant provided three data points for the 100%, 75%, and 25% lateral memory resource conditions. We obtained the repeated measures correlation coefficient between raw error for all trials in each condition and the mean amplitude of the N2pc and the mean amplitude of the CDA.

Modelling CDA data.

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

$$\% \text{ of lateral resources} \times \text{number of lateral items}$$

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

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

Results

Behavioral: Experiments 1 - 3

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

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

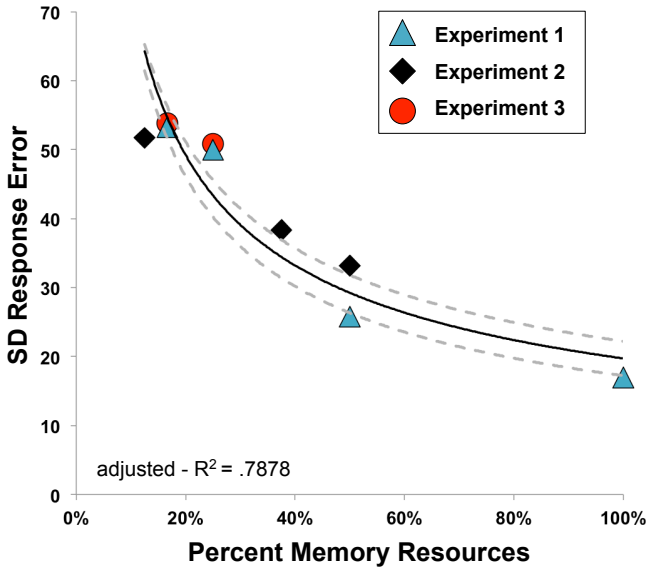

Figure 1. Standard deviation of raw response error by percent memory resources in each experiment, fit with a power law. Dashed grey lines represent fits performed on the 95% confidence interval of the condition means.

ERPs

Experiment 1

In Experiment 1, we sought to examine how the prioritization of some items over others affected the CDA. Four lateral memory items were always presented, and spatial cues indicated the number of items to be remembered, as well as the likelihood of a given item to be probed. Based on past demonstrations that the CDA primarily reflects VWM load, we should observe a larger CDA amplitude in the 4-Cues/100%-Valid condition than the 1-Cue/100%-Valid condition; remembering four items results in a larger CDA than remembering a single item. What remains an open question is how the CDA changes when resources are distributed unequally across the four memory items. Thus, comparing the 4-Cues/100%-Valid condition to the 1-Cue/50%-Valid condition provides an initial test of how resource allocation affects CDA amplitude.

CDA.

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

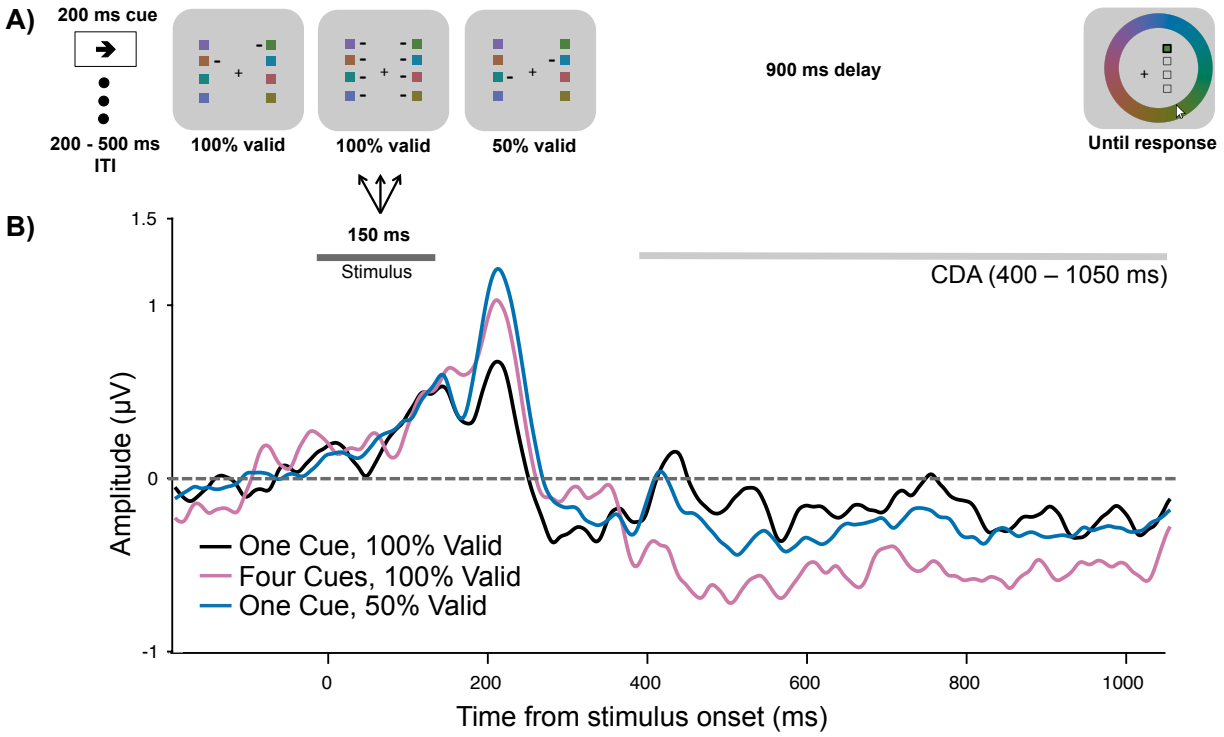

Figure 2. A) Task schematic of Experiment 1. Each trial began with a lateralization cue followed by a jittered ITI consisting of a fixation dot. Conditions were blocked and cue probability instructions provided at the beginning of each block. After a delay, participants made a response to the probed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

Experiment 2

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

N2pc.

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

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

P_D.

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

CDA.

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

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

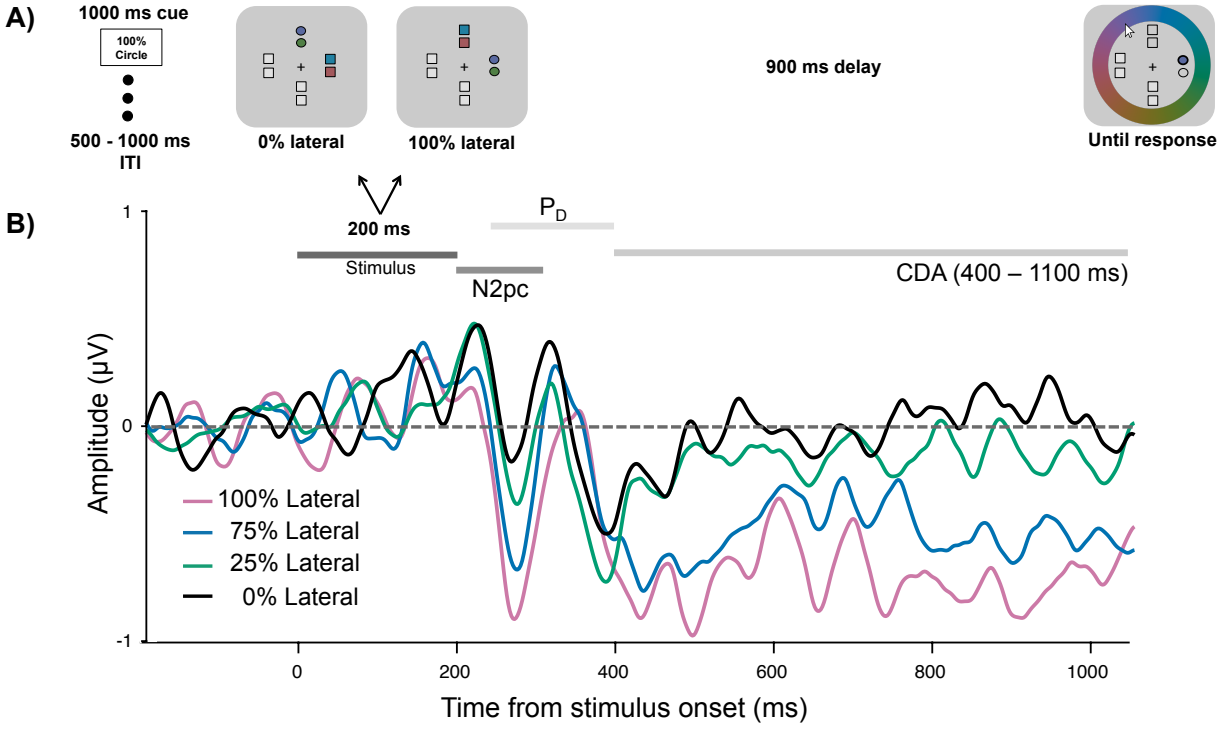

Figure 3. A) Task schematic of Experiment 2. Each trial began with a feature-based cue followed by a jittered ITI consisting of a fixation dot. In this example, it was 100% likely that the color of a circle would be probed. The stimulus display consisted of 2 colored shapes on the lateral and 2 on the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

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

N2pc and CDA amplitudes predict behavioral precision.

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

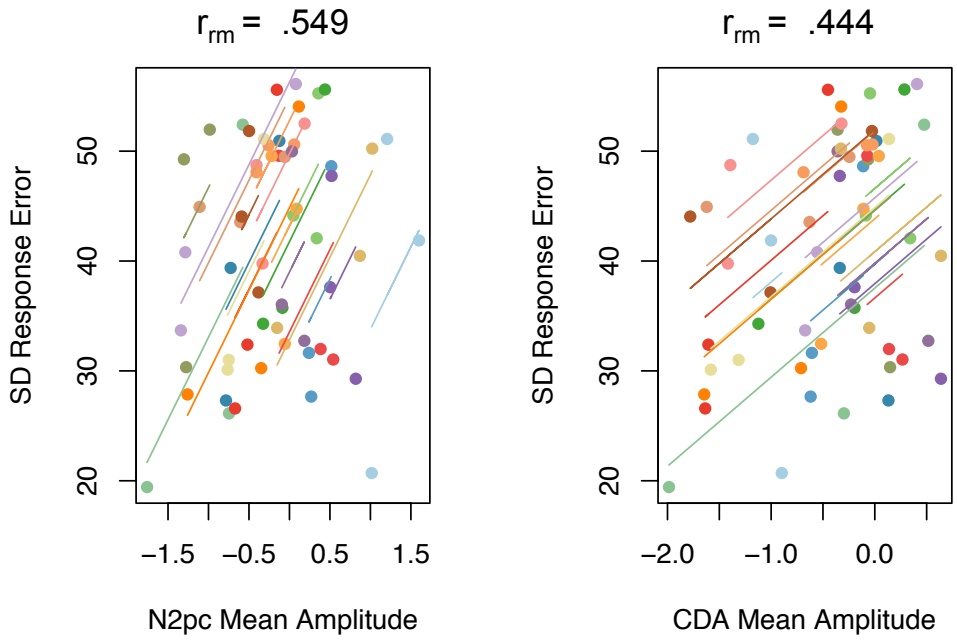

Figure 4. Repeated-measures correlations plots. Each colored line is the fit for three data points from each individual participant from the 100%, 75%, and 25% lateral likelihood conditions. A) Correlation between N2pc mean amplitude and standard deviation (SD) of raw response error. Lower SD indicates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

Experiment 3

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

CDA.

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

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

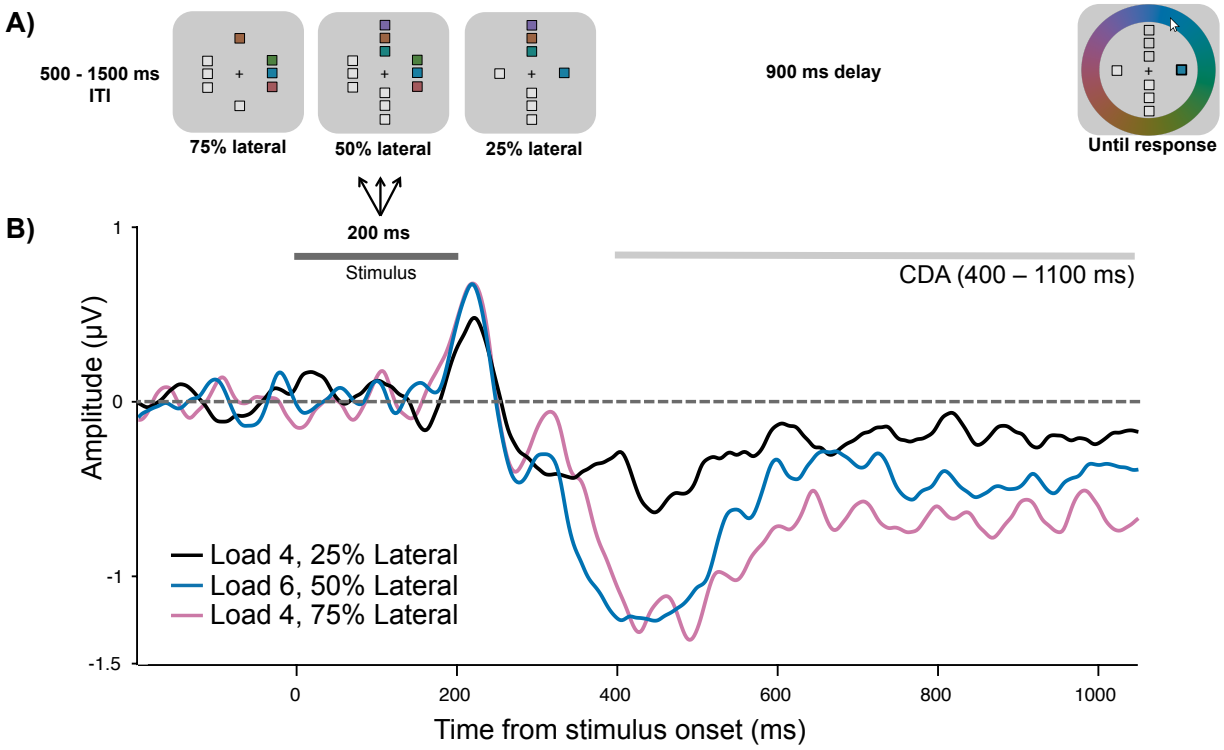

Figure 5. A) Task schematic of Experiment 3. Participants were told to remember the colors of all of the squares. Each trial began with a jittered ITI consisting of a fixation dot. There were 3 conditions differing in overall memory load (4 or 6) and by how many items were presented on the lateral (1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

CDA amplitude continuously reflects both VWM load and resource allocation

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

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

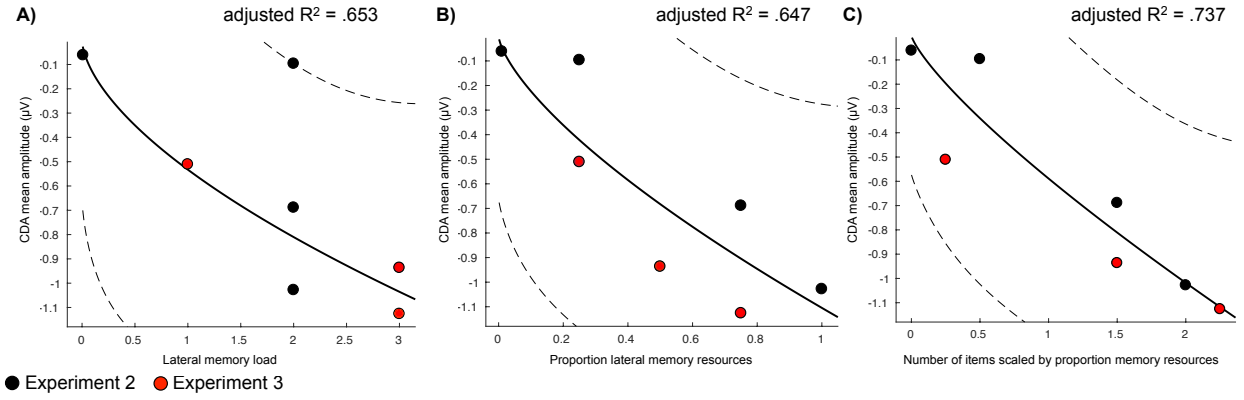

Figure 6. Power-law models and fits. Dotted lines represent 95% CIs of the model fit. Black dots represent condition means from Experiment 2 and red dots from Experiment 3. A) Fit between CDA mean amplitude and lateral memory load. B) Fit between CDA amplitude and proportion lateral memory resources.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

General Discussion

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

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

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

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

In addition, the findings of Experiment 3 demonstrate that resource allocation affects the CDA amplitude even in the absence of explicit prioritization cues. That is, even though all items were equally likely to be probed, the CDA amplitude towards three lateral items was reduced when resources had to be spread across additional vertical items. It is possible that participants could decide to encode only a subset of items on each trial. However, rather than being a confound specific to a resource allocation interpretation, fluctuations in CDA amplitude across trials is likely a feature of all CDA measurements[42], as changes in the number of items and amount of information encoded may occur due to spontaneous fluctuations in attention[5,54,55], or top-down

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

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

The results also speak to the role of attentional enhancement in prioritization. In Experiment 2 we found that the N2pc, but not the $P_{D,}$ tracked the priority of the lateralized stimuli, while also predicting the behavioural precision of memory report. This suggests that when using feature-based cues, participants relied on up-weighting relevant information depending on their respective priorities, in comparison to down-weighting irrelevant information using active suppression. This is consistent with previous findings which found that when given a pre-cue that indicated to participants to up or down-regulate memory encoding processes, it was only possible to up-regulate processing to benefit performance[3]. Additionally, it has been found that when using

reward to prioritize items, only target selection was impacted and not distractor suppression[59].

Our finding is also consistent with a recent study that suggests the N2pc reflects enhancement of items at the spatial focus of attention, instead of an overall attentional shift toward the lateral[60]. Interestingly, we did not find attention-related components in Experiments 1 and 3, pointing to the importance of having a pre-cue to be able to allocate attention accordingly, suggesting perhaps that resource allocation may occur later in the presence of simultaneous spatial cues (Experiment 1) or no cues (Experiment 3). Future studies should further examine the N2pc as a potential marker of the flexible allocation of neural resources for attentional enhancement according to item priority.

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

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

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

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

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