Electrophysiological correlates of the flexible allocation of visual working memory resources

Christine Salahub[1*], Holly A. Lockhart[1], Blaire Dube[2], Naseem Al-Aidroos[3], and Stephen M. Emrich[1]

[1]Department of Psychology, Brock University
St. Catharines, Ontario, Canada

[2]Department of Psychology, The Ohio State University
Columbus, Ohio, USA

[3] Department of Psychology, University of Guelph
Guelph, Ontario, Canada

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*Corresponding Author: Christine Salahub, christine.salahub@brocku.ca, Department of Psychology, Brock University, 1812 Sir Isaac Brock Way, L2S 3A1, St. Catharines, Ontario, Canada

1   Abstract

2   Visual working memory is a brief, capacity-limited store of visual information that is involved in

3   a large number of cognitive functions. To guide one's behavior effectively, one must efficiently

4   allocate these limited memory resources across memory items. Previous research has suggested

5   that items are either stored in memory or completely blocked from memory access. However,

6   recent behavioral work proposes that memory resources can be flexibly split across items based

7   on their level of task importance. Here, we investigated the electrophysiological correlates of

8   flexible resource allocation by manipulating the distribution of resources amongst systematically

9   lateralized memory items. We examined the contralateral delay activity (CDA), a waveform

10   typically associated with the number of items held in memory. Across three experiments, we

11   found that, in addition to memory load, the CDA flexibly tracks memory resource allocation.

12   This allocation occurred as early as attentional selection, as indicated by the N2pc. Additionally,

13   CDA amplitude was better-described when fit with a continuous model predicted by load and

14   resources together than when fit with either alone. Our findings show that electrophysiological

15   markers of attentional selection and memory maintenance not only track memory load, but also

16   the proportion of memory resources those items receive.

1   More likely than not, it is much easier for you to recall the names of the characters from

2   the last television show that you watched than what you were wearing while you watched it. This

3   bias in memory is in part due to the fact that what we allocate more attention to is remembered

4   with greater detail[1]. Indeed, numerous studies of long-term memory have established that

5   attention prioritizes relevant information to be encoded into memory[2–4]. Attention also affects the

6   maintenance and quality of information stored over shorter periods of time, such as in visual

7   working memory[5–7] (VWM). In fact, given that VWM is limited in capacity, several models of

8   VWM have suggested that attention may play a critical role in determining what information

9   gains access to these finite storage resources[8–11].

10   One potential mechanism through which attention may drive working memory

11   performance is by filtering out irrelevant distractors[12]. Filtering efficiency has been quantified

12   using measurements of electrophysiological brain activity related to working memory storage –

13   specifically an event-related potential (ERP) called the contralateral delay activity[13–16] (CDA).

14   CDA amplitude increases with the number of items stored in VWM, saturating as memory load

15   increases beyond a few items[17]. Interestingly, when distractors are presented alongside targets in

16   a memory display, lower-capacity individuals exhibit larger CDA amplitudes than those with

17   higher capacities, reflecting the fact that they have encoded and stored more distractors in

18   memory[16]. This finding has been taken as evidence that poor filtering efficiency, resulting in

19   unnecessary storage, is a critical determinant of VWM capacity.

20   Several recent studies have demonstrated that it is also possible to bias attentional

21   resources toward and away from certain items in a flexible manner, independent of the need to

22   filter out irrelevant distractor items. This bias can be induced by associating certain stimuli with

23   monetary incentives, or by simply varying instructions indicating the probability that an item will

1   be probed on any given trial[7]. In this way, the proportion of attentional resources allocated to any

2   given memory item can continuously vary anywhere between 0 and 100%. In these past

3   studies[18,19], it was found that working memory performance (i.e., raw error = 1/precision) was

4   best predicted by the likelihood that an item would be probed on a given trial, independent of the

5   overall memory load. Importantly, this relationship between probe likelihood and memory

6   precision, which followed a power-law, could also account for changes in performance across

7   loads; for example, the change in precision from one to two items was consistent with each item

8   only receiving half as many attentional resources. This framework suggests that attention does

9   more than just restrict or grant access to VWM; rather, it also flexibly distributes resources

10   amongst objects based on their respective priorities. In other words, how attention is allocated

11   between targets is as important to memory performance as whether or not it is allocated to

12   distractors[20,21].

13   If attention can be flexibly allocated across items in VWM, how might this be reflected

14   by neural measures of attention and VWM maintenance? There is evidence that the CDA is well-

15   described by a saturation model, which predicts a continuous increase in CDA amplitude that

16   saturates as set size becomes larger, instead of increasing discretely and plateauing at memory

17   capacity[17]. This finding suggests that the CDA, much like VWM performance, may be more

18   flexibly affected by memory load than previously thought. Yet, it is currently unknown whether

19   the CDA is also flexibly affected by the prioritization of memory items instead of, or in addition

20   to, changes in memory load.

21   Prioritization could also be tracked by ERP components that precede memory

22   maintenance, such as attentional selection and suppression. That is, one way that flexible

23   prioritization could be accomplished is through the specific up-weighting of goal-relevant over

4

1   irrelevant information (as opposed to down-weighting of goal-irrelevant information).

2   Attentional selection can be tracked by the N2pc, a lateralized component which specifically

3   reflects the enhancement of an item[22–24]. Alternatively, it could be that prioritization is

4   accomplished through the active suppression or down-weighting of goal irrelevant information.

5   This can be measured by the distractor positivity (P_D): a lateralized component that is observed

6   when distractors are presented laterally in the stimulus display[25–28]. These two components can

7   thus be used to disentangle the underlying mechanisms of prioritization: whether through

8   selective enhancement of relevant information (N2pc) or suppression of irrelevant information

9   (P_D).

10   Consequently, to determine the effect of resource allocation on the CDA, as well as

11   whether prioritization is driven by selective enhancement of high-priority items or inhibition of

12   low-priority items, we conducted three experiments in which the allocation of memory resources

13   across items was manipulated in a continuous-report delayed-recall task. For these experiments,

14   we use the term *memory load* to refer to the number of items with greater than zero percent

15   likelihood of being probed. We use the terms *resource allocation* or *probability* to refer to the

16   likelihood that one item, or a set of items, will be probed. In Experiment 1, we examined how

17   changes in resource allocation amongst memory items influenced the CDA in comparison to the

18   typical effect of memory load. To do this, participants were asked to remember the colors of four

19   laterally presented items that were either equally likely to be probed, or where a spatial cue

20   indicated that one item was more likely to be probed than the others (i.e. 50% or 100% likely to

21   be probed). Thus, while participants should always be allocating 100% of memory resources to

22   all four items, how the resources were distributed across items varied. If the CDA is unaffected

5

1   by resource allocation, and is only affected by memory load, then CDA amplitude should only

2   reflect the total number of items to be stored, regardless of attentional priority.

3   In Experiments 2 and 3, we took advantage of an attribute of the CDA, N2pc, and P_D –

4   that these components are only sensitive to laterally presented stimuli and not stimuli presented

5   on the vertical midline – to separately manipulate the effects of memory load and resource

6   allocation. In Experiment 2, two items were presented laterally and two vertically, and a featural

7   cue indicated whether the lateral or vertical items were more likely to be probed. Thus, this

8   design allowed us to manipulate the proportion of memory resources specifically allocated to

9   lateral items. If these ERP components reflect strategic resource allocation, then they should

10 increase in amplitude with increasing probe likelihood (i.e., greater resource allocation).

11 However, if these components are only affected by overall load, then item prioritization should

12 have no effect.

13   In Experiment 3, we tested whether the CDA reflects the allocation of memory resources

14 even in the absence of prioritization cues. To do so, we manipulated the total number of to-be-

15 remembered items (four or six), while systematically changing the number of items presented

16 laterally. In this way, we could simultaneously manipulate lateral memory load and proportion of

17 memory resources allocated to the lateral items. We predicted that if the CDA tracks resource

18 distribution across the lateral and vertical items, then CDA amplitude should reflect the

19 proportion of total memory resources allocated to lateral items in addition to lateral memory

20 load.

21 **Results**

22 **Behavioral: Experiments 1 - 3**

6

1   Because we manipulated proportion of memory resources per item across all three

2   experiments, and were interested in how behavior changed as a function of resource allocation,

3   behavioural results were collapsed across experiments.

4   To compare how performance changed as a function of resource allocation, all data

5   points were fit to a power-law function. Consistent with past findings[18,19], this provided a good

6   fit (Fig. 1), with the model accounting for around 79% of the variance in the data, adjusted-$R^2 =$

7   .79, *RMSE* = 6.26. These results demonstrate that the proportion of memory resources allocated

8   to an individual item was highly predictive of behavioral precision for that item. Moreover,

9   percent of memory resources allocated to an item better predicted behavioral precision than

10   memory load alone: adjusted-R^2 = .35, *RMSE* = 10.97, ΔBIC = 9.71. Thus, regardless of the

11   behavioural manipulation (i.e., spatial cues; feature-based cues; lateralized memory load),

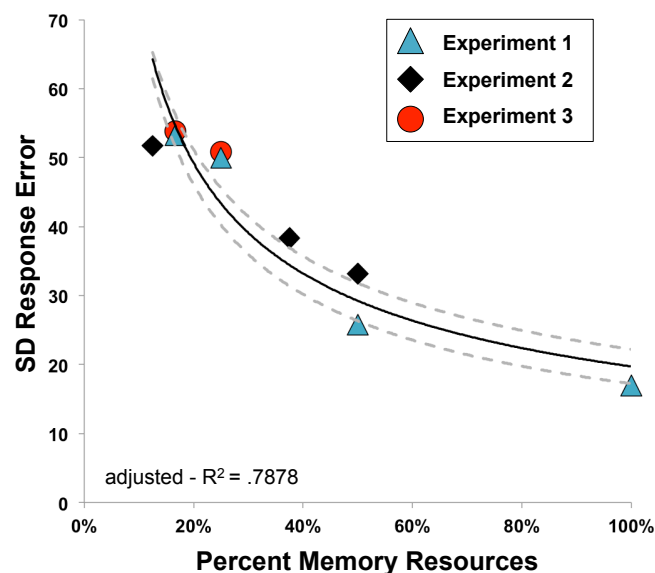12   precision is strongly predicted by the percentage of resources allocated to the probed item.

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.

13   **ERPs**

1   **Experiment 1**

2   In this experiment, we sought to examine how the prioritization of one item over the

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

4   indicated the number of items to be remembered, as well as the likelihood of a given item to be

5   probed (Fig. 2A). Based on past demonstrations that the CDA primarily reflects VWM load, we

6   expected there to be a larger CDA amplitude in the 4-Cues/100%-Valid condition than the 1-

7   Cue/100%-Valid condition; remembering four items results in a larger CDA than remembering a

8   single item. What remains an open question, however, is how the CDA changes when resources

9   are distributed unequally across the four memory items. Thus, comparing the 4-Cues/100%-

10   Valid and the 1-Cue/100%-Valid conditions to the 1-Cue/50%-Valid condition provides an

11   initial test of how resource allocation affects CDA amplitude.

12   **CDA.**

13   The spatial prioritization cues influenced CDA amplitude (Fig. 2B; main effect of

14   Condition, $F(2,38) = 5.83$, $p = .006$, $\eta^2_p = .24$, $BF_{10} = 6.94$). Consistent with a memory load

15   effect, there was a more negative CDA amplitude when all four items were cued ($M = -0.55$ μV,

16     $SD = 0.66$ μV), than when one item was cued at 100% validity ($M = -0.17$, $SD = 0.70$ μV), $t(19)$

17     $= 3.43$, $p = .003$, d $= 0.77$, $BF_{10} = 14.94$. CDA amplitude in the 1-Cue/50%-Valid condition ($M =$

18   -0.29 μV, $SD = 0.52$ μV) was not significantly different from the 1-Cue/100%-Valid condition,

19     $t(19) = 0.98$, $p_{bonf} = 1$, d $= 0.22$, $BF_{10} = 0.36$, or from the 4-Cues/100%-Valid condition, $t(19) =$

20   2.38, $p_{bonf} = .084$, d $= 0.53$, $BF_{10} = 2.20$. Thus, though the CDA amplitude in the 1-Cue/50%-

21   Valid condition was numerically smaller than in the 4-Cues/100%-Valid condition, this

22   difference was not born out in the inferential statistics. Instead, the CDA amplitude in the 1-

1 Cue/50%-Valid condition appeared to be in between the amplitudes of the other conditions (see
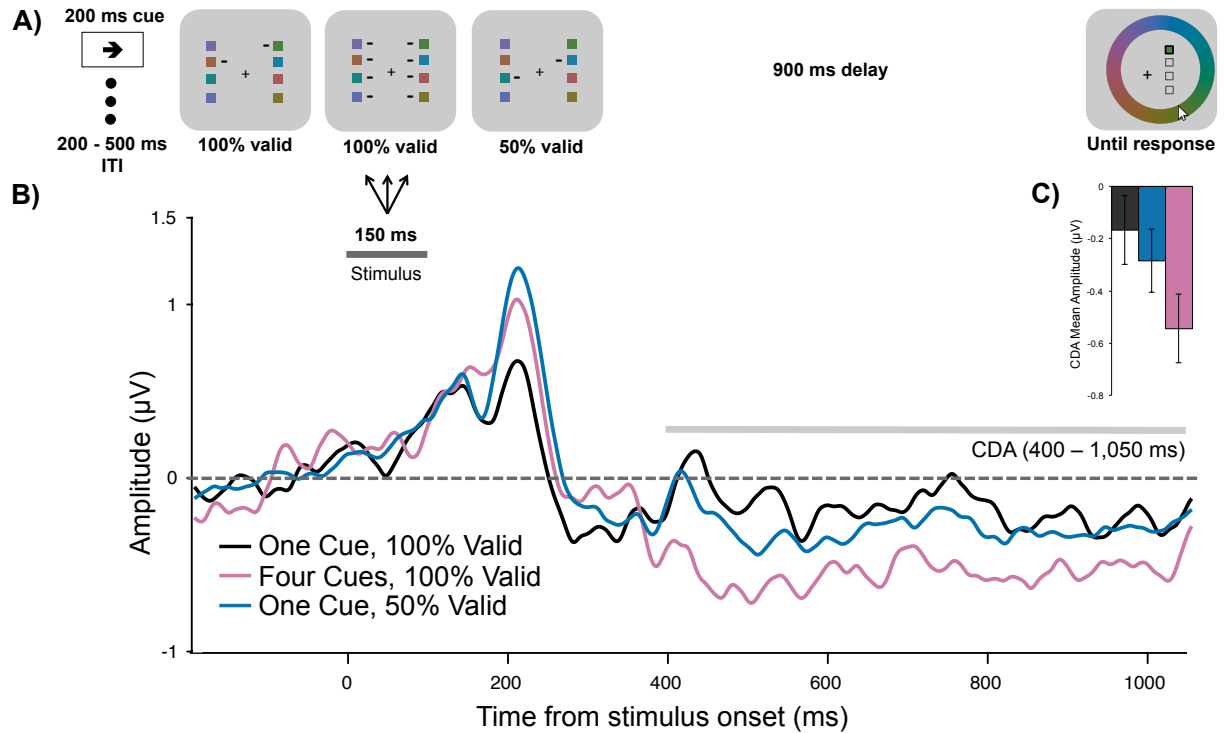
2 Fig. 2C).

Figure 2. A) Task schematic of Experiment 1.B) Grand average difference waveform (N = 20) at the average of 5 posterior channel pairs, time-locked to stimulus onset. Positive is plotted up. Filtered at 30 Hz for visualization purposes only. C) Bar chart of mean CDA amplitudes in each condition. Error bars reflect within-subject 95% confidence intervals.

3 **Experiment 2**

4   In Experiment 1, we replicated the typical effect of memory load on CDA amplitude and

5 the behavioral effect of resource allocation on memory precision. However, the effects of

6 resource allocation on CDA amplitude were less clear, as both high and low probability items

7 were presented together laterally, resulting in a mixed electrophysiological signal. To better

8 isolate the effects of prioritization on CDA amplitude, in Experiment 2 we separated the items in

9 the memory array along the horizontal and vertical midlines and used feature-based priority cues

10 (Fig. 3A). Specifically, all memory arrays comprised two items presented laterally, and two

11 presented on the vertical midline, with the lateral items either 100%, 75%, 25%, or 0% likely to

9

1 be probed, depending on the shape of those items. Because lateralized ERP components are only

2 sensitive to laterally presented stimuli, we could systematically manipulate the proportion of

3 lateral memory resources and thus its effect on the N2pc, P_D, and CDA. If these components

4 reflect strategic resource allocation, then their amplitudes should increase continuously with item

5 priority. However, if these components reflect memory load alone, then their amplitudes should

6 remain stable regardless of the priority manipulation.

7   **N2pc.**

8   Feature-based priority influenced the amplitude of the N2pc (Fig. 3B; main effect of

9 Condition, $F(2.17, 41.24) = 10.85$, $p < .001$, $\eta^2_p = .36$, $BF_{10} = 1871.28$). Overall N2pc amplitude

10 was more negative when the items were 100% ($M = -0.37$ µV, $SD = 0.74$ µV) likely to be probed

11 than when they were 0% ($M = 0.17$ µV, $SD = 0.58$ µV), $t(19) = 4.82$, $p < .001$, d = 1.08, $BF_{10} =$

12 238.64, or 25% likely to be probed ($M = 0.06$ µV, $SD = 0.52$ µV) , $t(19) = 3.22$, $p = .005$, d =

13 0.72, $BF_{10} = 10.02$. The N2pc was also larger when the lateral items were 75% likely ($M = -0.19$

14 µV, $SD = 0.72$ µV) compared to 0%, $t(19) = 3.32$, $p = .004$, d = 0.74, $BF_{10} = 12.21$, or 25% likely

15 to be probed, $t(19) = 2.57$, $p = .019$, d = 0.57, $BF_{10} = 3.05$. There were no significant differences

16 between N2pc amplitudes in any other condition comparison, $ps > .069$, ds < 0.44, $BFs_{10} < 1.08$.

17 However, the overall N2pc amplitude did become linearly more negative as item priority

18 increased, adjusted-$R^2 = .99$, $RMSE = 5.54$, linear contrast: $t(19) = 5.66$, $p < .001$, suggesting that

19 individuals could flexibly allocate their attention toward an item depending on how important it

20 was to the trial (see Fig. 3C). Interestingly, fractional peak latency did not differ between

21 conditions, $F(1.81, 29.03) = 1.70$, $p = .202$, $\eta^2_p = .10$, $BF_{01} = 2.29$. Therefore, participants were

22 not selecting high priority items any faster than low priority items.

23   **P_D.**

1   Permutation tests indicated that the positive area of the grand average waveform between

2   250 – 400 ms was not significantly different from noise in any of the conditions, 100%: $p = .529$,

3   75%: $p = .30$, 25%: $p = .306$, 0%: $p = .087$. Although the P_D was not significant, it could be that

4   priority still had an influence on its amplitude. There was a small but non-significant effect of

5   priority on the positive area of the P_D, $F(1.84, 34.96) = 2.95$, $p = .070$, $\eta^2_p = .13$, $BF_{10} = 1.36$.

6   Therefore, there was little evidence of active attentional suppression in this task.

7   **CDA.**

8   Similar to the N2pc, priority affected the amplitude of the CDA (main effect of

9   Condition, $F(2.02, 38.42) = 6.43$, $p = .004$, $\eta^2_p = .253$, $BF_{10} = 85.42$). More information was

10   stored in VWM when the items were 100% likely to be probed ($M = -0.69$ µV, $SD = 0.78$ µV)

11   than 0% ($M = -0.02$ µV, $SD = 0.41$ µV), $t(19) = 3.34$, $p = .003$, d = 0.75, $BF_{10} = 12.53$. Similarly,

12   the CDA was more negative in the 100% condition than the 25% condition ($M = -0.14$ µV, $SD = $

13   0.36 µV), $t(19) = 2.75$, $p = .013$, d = 0.61, $BF_{10} = 4.18$. When the items were 75% likely to be

14   probed, the CDA amplitude ($M = -0.49$ µV, $SD = 0.68$ µV) was more negative than in the 25%,

15   $t(19) = 2.15$, $p = .045$, d = 0.48, $BF_{10} = 1.52$, and 0% conditions, $t(19) = 2.38$, $p = .028$, d = 0.53,

16   $BF_{10} = 2.20$. No other comparisons were significant, ts < 0.18, ps > .18, ds < 0.31, BFs$_{10}$ < 0.52.

17   However, similar to the N2pc, CDA amplitude was linearly related to priority, adjusted-$R^2 = .99$,

18   $RMSE = .03$, linear contrast: $t(19) = 4.33$, $p < .001$ (see Fig. 3C). Therefore, the more likely the

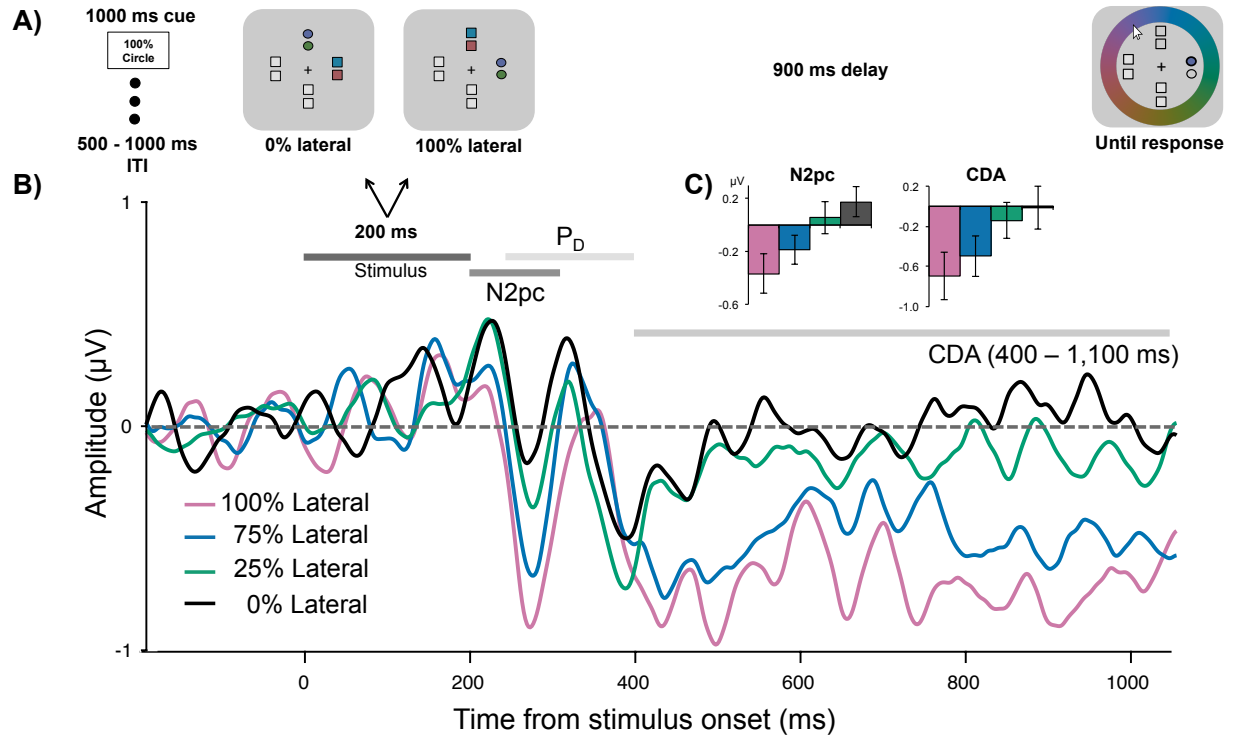19   items were to be probed, the greater the amplitude of the CDA.

Figure 3. A) Task schematic of Experiment 2. In this example, it was 100% likely that the color of a circle would be probed. B) Grand average difference waveform (N = 20) at the average of 5 posterior channel pairs, time-locked to stimuli onset. Filtered at 30 Hz for visualization purposes only. C) Bar chart of mean N2pc and CDA amplitudes in each condition. Error bars reflect within-subject 95% confidence intervals.

1   **N2pc and CDA amplitudes predict behavioral precision.**

2   To examine whether memory resource-related changes in N2pc and CDA amplitudes

3   predicted changes to VWM response error, a repeated-measures correlation was performed[29,30]

4   between mean amplitude and response error across three lateral resource conditions (25%, 75%,

5   and 100%). It was found that attention toward the lateral shapes, as measured by the N2pc,

6   predicted how precisely the color of the probed shape was reported, $r_{rm}(39) = 0.55$, 95% CI =

7   [.28, .74], $p = <.001$ (Fig. 4A). There was also a correlation between raw error and mean

8   amplitude of the CDA, $r_{rm}(39) = 0.44$, 95% CI = [0.15, 0.67], $p = .004$ (Fig. 4B). These findings

9   indicate that more precise reports of the probed color were associated with larger neural

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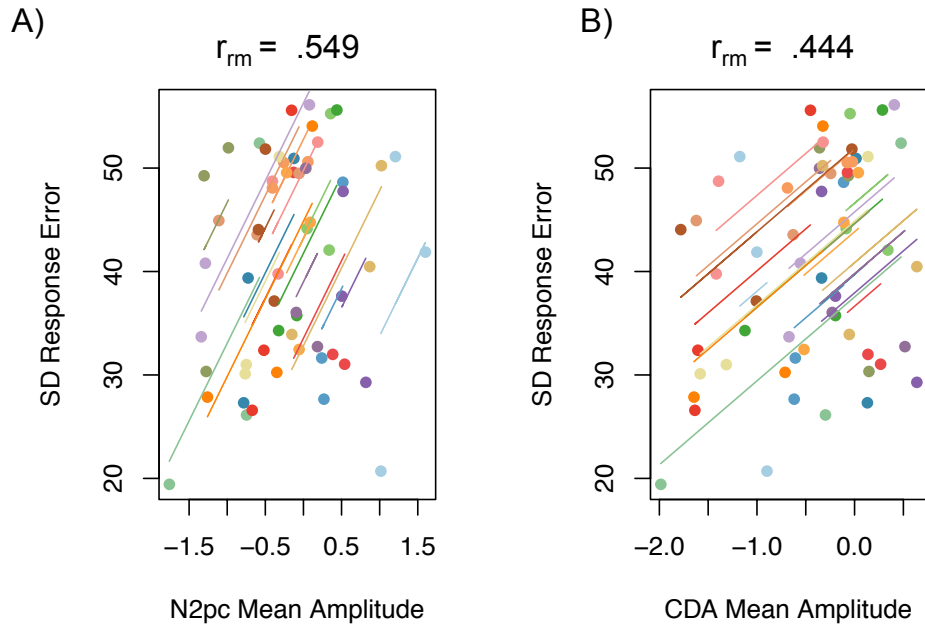
Figure 4. Repeated-measures correlations plots. Each colored line is the fit for three data points from each individual participant from the 100%, 75%, and 25% lateral likelihood conditions. A) Correlation between N2pc mean amplitude and standard deviation (SD) of raw response error. Lower SD indicates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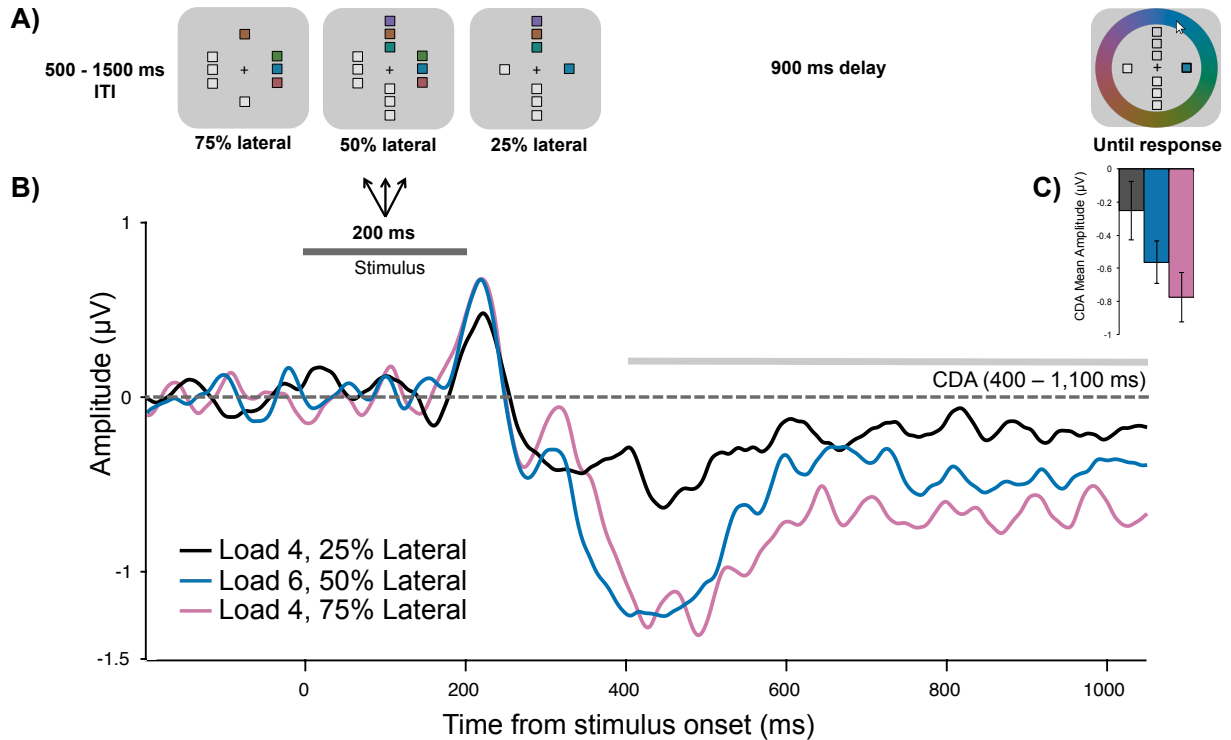
1   **Experiment 3**

2   Experiment 2 provided evidence that attentional prioritization not only affects behavioral

3   precision in a delayed-recall task, it is also associated with a proportional increase in the

4   amplitude of ERP components associated with attentional enhancement (N2pc) and memory

5   maintenance (CDA). Interestingly, previous studies have found that the effect of load on

6   behavioral precision is identical to those of prioritization; thus, splitting resources across two

7   items results in similar memory precision as an item with 50% cue validity[18]. Consequently, to

8   test whether the CDA similarly reflects resource allocation in the absence of prioritization cues

9   we manipulated how many items were presented laterally, and how many vertically (Fig. 5A).

10   There were three conditions: one item lateral and three vertical (Load 4, 25% lateral), three items

11   lateral and one vertical (Load 4, 75% lateral), and three items lateral and three items vertical

12   (Load 6, 50% lateral). Thus, these last two conditions had the same lateral memory load but a

1   change in the proportion of memory resources allocated to those items. We predicted that CDA

2   amplitude would become more negative as the proportion of lateral memory resources increased.

3   **CDA.**

4   CDA amplitude was affected by Condition (Fig. 5B), $F(2,38) = 7.60$, $p = .002$, $\eta^2_p = .29$,

5    $BF_{10} = 24.31$, such that the amplitude was more negative when 75% of memory resources were

6   allocated to three lateral items ($M = -0.78$ μV, $SD = 0.64$ μV) than when 25% were allocated to

7   one lateral item ($M = -0.25$ μV, $SD = 0.54$ μV), $t(19) = 3.4$, $p = .003$, d = 0.76, $BF_{10} = 14.17$.

8   When 50% of memory resources were allocated to three lateral items ($M = -0.57$ μV, $SD = .60$

9   μV), the CDA amplitude was more negative than when 25% of resources were allocated to one

10   item, $t(19) = 2.27$, $p = .035$, d = 0.51, $BF_{10} = 1.83$. CDA amplitude in the 50% lateral condition

11   was numerically, but not significantly, smaller than in the 75% lateral condition, $t(19) = -1.92$, p

12   $= .069$, d = 0.43, $BF_{10} = 1.08$. Importantly, CDA amplitude was linearly related to the proportion

13   of lateral resources, adjusted-$R^2 = .91$, $RMSE = .10$, $t(19) = 3.4$, $p = .009$, such that amplitude

14   became more negative as the amount of resources increased (Fig. 5C). Together, these findings

15   suggest that even in the absence of prioritization cues, the CDA may reflect a combination of

16   memory load *and* the amount of attention/memory resources allocated toward these items.

Figure 5. A) Task schematic of Experiment 3. 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. C) Bar chart of mean CDA amplitudes in each condition. Error bars reflect within-subject 95% confidence intervals.

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

2   Across three experiments, the manipulation of resource allocation – whether by spatial

3 cues, feature-based cues, or memory load – affected the amplitude of the CDA. Although these

4 effects were sometimes small, they are consistent with previous behavioral findings (also

5 observed here) that the magnitude of the effect on memory performance depends on the

6 magnitude of the change in resource allocation. However, although small changes in resource

7 allocation may only produce small effects, these effects tend to follow a predictable pattern along

8 a continuous power-law in behavioral studies[18]. Thus, it is possible that the effect of resource

9 allocation on ERP measures of memory maintenance should similarly follow a continuous

10 pattern, wherein the amplitude of the CDA changes with the proportion of resources allocated to

11 laterally presented items. It is also possible that, although resource allocation is a better predictor

15

1   of memory performance than load alone, CDA amplitude may reflect a mixture of signals that

2   combine effects of load *and* resource allocation. To examine this prediction, we tested whether

3   the CDA amplitudes observed in Experiments 2 and 3 (which involved similar stimulus displays)

4   were best described by one of three models: one in which CDA amplitude was predicted by load

5   alone, another with resource allocation alone, and a model using a scaled combination of

6   memory load and resource allocation (see Methods).

7   When CDA amplitudes were compared to memory load alone (Fig. 6A), the model

8   accounted for 50% of the variance in the data, adjusted-R^2 = 0.50, $RMSE$ = 0.28, BIC = -17.52.

9   However, when examining the best-fit line, the direction of this function was in the opposite

10   direction to what was predicted, such that CDA amplitude appears not to saturate, but continues

11   to increase with increasing memory load. This suggests that a power function does not well

12   describe the data when fitting CDA amplitude with load, at least within the range of set sizes

13   tested here. CDA amplitudes were even less well fit with proportion of memory resources alone

14   (Fig. 6B), adjusted-R^2 = 0.33, $RMSE$ = 0.32, BIC = -15.62. However, when fitting CDA

15   amplitude to the weighted sum of both memory load and proportion memory resources, we

16   observed the best fit (Fig. 6C), adjusted-R^2 = 0.52, $RMSE$ = 0.27, BIC = -18.35. This

17   demonstrates that the amplitude of the CDA follows a predictable continuous function that is

18   affected both by the number of lateral items to be remembered, and by the proportion of total

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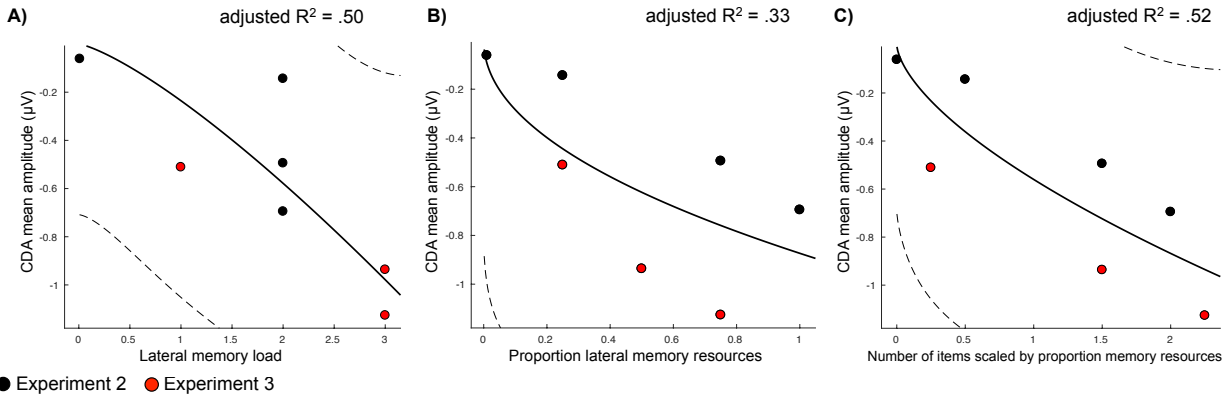
Figure 6. Power-law models and fits. Dotted lines represent 95% CIs of the model fit. Black dots represent condition means from Experiment 2 and red dots from Experiment 3. A) Fit between CDA mean amplitude and lateral memory load. B) Fit between CDA amplitude and proportion lateral memory resources.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

1   **General Discussion**

2   In this study, we sought to examine the effect of prioritization on ERP markers of

3   attentional enhancement, distractor suppression, and working memory maintenance, to better

4   understand flexible allocation of memory resources. In Experiment 1, we found that the CDA

5   was somewhat smaller when prioritizing one item over others than when all items were

6   prioritized equally. In Experiment 2, we implemented a stronger manipulation of resource

7   allocation using a systematic lateralization procedure[27,31], demonstrating that the CDA tracked

8   overall proportion of memory resources allotted laterally. We also found that the N2pc was

9   reflective of priority, providing evidence that the allocation of neural resources toward to-be

10 remembered items occurs via attentional enhancement. Moreover, both N2pc and CDA

11 amplitudes correlated with behavioral precision in this task. Finally, in Experiment 3 we

12 manipulated the proportion of memory resources that should be allocated to lateral items by

13 controlling the number of items presented laterally while manipulating overall load. Consistent

14 with the first two experiments, we found that CDA amplitude tracked the proportion of memory

15 resources allocated toward the lateral items in the memory array. When comparing across

17

1   Experiments 2 and 3, we also found that CDA amplitudes were best predicted by a weighted sum

2   of memory load and resources. This finding points to the CDA as a proxy of more than memory

3   load alone, suggesting that this component may also reflect the total amount of memory

4   resources allocated to lateral items.

5   One potential argument against the resource allocation interpretation is that instead of

6   flexibly distributing resources across all items in the display, individuals alternated strategies

7   *probabilistically* across trials: encoding higher probability items on most trials and lower

8   probability items less often. If items were being encoded probabilistically, then one might expect

9   that, on the majority of trials, participants would pay attention to and encode the higher

10   probability items first. This would result in an earlier N2pc, consistent with previous findings in

11   visual search tasks[32,33]. In contrast to this hypothesis, there was no difference in the timing of the

12   N2pc across conditions in Experiment 2, suggesting that all items were being attended to at the

13   same time, regardless of priority.

14   One interpretation of the probabilistic account is that participants alternate across trials

15   between encoding high or low probability items; however, this interpretation can be ruled out

16   based on the behavioral estimates of guess rates obtained from the two-component mixture

17   model[34] (see Supplementary Results). In Experiment 2, for example, if differences in CDA

18   amplitudes were due to participants probabilistically encoding items, then the number of encoded

19   items in the 75/25% condition should reflect this. That is to say, if participants encoded the two

20   higher priority items on 75% of trials, and the two lower priority items on 25% of trials, this

21   would lead to the same difference in CDA amplitude between conditions as was observed here,

22   but with a total estimated number of encoded items of 2. However, the total number of encoded

1   items in these conditions was 2.9, significantly greater than what would be predicted by the

2   probabilistic encoding account.

3   Even if participants weren't probabilistically encoding items, they may have been

4   selectively encoding the higher priority items on the majority of trials, which could affect the

5   CDA amplitude. However, this strategy cannot be ruled out based on estimates of the total

6   number of items encoded, as increased guessing can also result from low resource allocation[18,35].

7   Indeed fluctuations in CDA amplitude across trials is likely a feature of all CDA

8   measurements[36], as changes in the number of items and amount of information encoded have

9   been observed due to spontaneous fluctuations in attention[5,21,37,38], and top-down strategies[39,40].

10   Thus, although the experiments presented here may include some measure of strategic

11   differences in resource allocation across trials, resulting in some change in the number of stored

12   items, *spontaneous* changes in resource allocation across trials may be an additional source of

13   variance within past CDA studies that has been previously unidentified.

14   There are several implications that arise from these findings, such as the role of

15   attentional enhancement in prioritization. In Experiment 2 we found that the N2pc, but not the

16   P_D, tracked the priority of the lateralized items, while also predicting the precision of memory

17   report. This suggests that when using feature-based cues, participants relied on up-weighting

18   relevant information depending on their respective priorities, in comparison to down-weighting

19   irrelevant information using active suppression. This is consistent with previous findings, which

20   found that when given a pre-cue to up- or down-regulate memory encoding processes,

21   participants could only up-regulate processing to benefit performance[3]. Additionally, it has been

22   found that when using reward to prioritize items, only target selection is impacted and not

23   distractor suppression[41]. This speaks to the importance of attentionally selecting and enhancing

target information to VWM, instead of only inhibiting and filtering distractors. That is, although previous work has focused on the link between unnecessary memory storage of distractors and VWM capacity[42,43], 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 present results begin to point to potential mechanisms.

Finally, our results provide some information about the neuronal underpinnings of the CDA. The finding that the CDA follows a power-law when fit with a combination of 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 increasingly large, it produces a consequent smaller increment in neuronal activity, saturating at some maximum level[17]. Although the power-law examined here tests a similar pattern, the present 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.

Our results do suggest that it is possible that different types of information can independently affect the CDA. Consistent with this interpretation, there are a few studies that have found memory precision can modulate the CDA independent from memory load[44,45] (but see[46]). These previous findings support an account of VWM that encompasses both discrete item units, as well as continuous modulations in representational quality[47,48]. Consistent with this finding, a previous study observed independent effects of the number of items and complexity on the CDA at different channel pairs[49]. Thus, while the results of the experiments presented here cannot fully adjudicate between different models of VWM architecture (i.e., whether or not memory resources are tied to discrete units), they are consistent with the idea that how resources

1   are allocated should be considered in addition to overall load in neural and behavioral models of

2   VWM.

Methods

Participants

5   Informed, written consent was obtained from all participants. Procedures were approved

6   by and conducted in accordance with the Brock University Bioscience ethics review board. We

7   aimed for a sample size of 20 participants[15,16,50] (right handed, normal-color vision, no history of

8   mental illness). To reach these targets, a total of 30 participants were run in Experiment 1, 33 in

9   Experiment 2, and 28 in Experiment 3. Distinct samples (N = 20) were used for each experiment

10   (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} =

11   21.6, SD_{age} = 3.9, 3 male).

Stimuli and Procedures

13   All tasks were completed on a Windows PC with a 41-cm NEC MultiSync LCD

14   2090UXi computer monitor (1600 x 1200 pixels, 60 Hz refresh rate). Stimuli were rendered

15   using Psychopy v1.90.3 (Peirce, 2007) and presented on a grey background (RGB = 128 128

16   128) with a central fixation dot (radius of 0.3°). Viewing distance was approximately 57 cm. In

17   all experiments, participants first completed a standard change detection task[51]. These data are

18   not included.

19   The colors for the squares in the continuous report VWM tasks were chosen pseudo-

20   randomly from a 360-degree isoluminant color wheel (CIE L*a*b* color space, [L = 70, a = -6, b

21   = 14, radius = 49]), which was calibrated to the testing monitor. Memory stimuli colors were

22   separated by at least 30 degrees on the color wheel.

23   **Experiment 1.**

1   At the beginning of each block, participants were instructed on cue-validity, both with

2   on-screen and verbal instructions: In the 1-Cue/100%-Valid condition, the one cued item was

3   always probed; In the 4-Cues/100%-Valid condition, the probed item was randomly selected

4   from all four items; In the 1-Cue/50%-Valid condition, the cued item was probed on 50% of

5   trials, un-cued items were probed on the remaining trials. Each trial began with an arrow

6   indicating which side of the screen was task relevant (3° tall, 200 ms), followed by a jittered

7   fixation interval (200 – 500 ms). The memory array (150 ms) consisted of four squares on both

8   sides of the screen (1° x 1°, 4° from fixation) along with horizontal spatial line cues (2° long x 3

9   pixels wide, 2° from fixation). After a delay (900 ms), participants reported the color of the

10   bolded square (line width of 3 pixels vs. 1 pixel) from the color wheel (diameter of 7°) with the

11   mouse. There were 240 trials in both the 1-Cue/100%-Valid and 4-Cues/100%-Valid Conditions,

12   and 480 in the 1-Cue/50%-Valid condition, split equally between both sides of the screen (total

13   960). One participant's data consisted of only 840 trials due to a recording error.

14   **Experiment 2.**

15   In both Experiments 2 and 3 participants first completed a subjective luminance-

16   matching task, which was used to create the placeholder colors (see Supplementary Methods).

17   Each trial began with a feature-based cue (i.e. *100% Circle*; 1,000 ms, 1.5° tall) followed

18   by a jittered interval (500 – 1,000 ms). Next, eight shapes were presented in clusters of two at

19   each cardinal position 3° from fixation (to center of shape cluster) and 1.2° apart (vertical center

20   to center; 200 ms). There were always two colored squares (1° x 1°) and two colored circles

21   (diameter of 1°). The remaining four items were filled with the subjectively luminance-matched

22   grey and were always the un-cued shape. Shapes were presented in all possible position

23   configurations equally (16 unique positions). After a delay (900 ms), participants made a

1   response to the probed shape on the color wheel with the mouse (pseudo-randomly chosen from

2   top or bottom shape in cluster). There were a total of four conditions defined by the probability

3   that the lateral shapes would be probed: 100%, 75%, 25%, and 0%. Participants completed a

4   total of 816 trials (100% lateral: 200, 0% lateral: 200, 75% lateral: 208, 25% lateral: 208). One

5   participant completed 806 trials due to a programming error, and another completed 807 trials

6   due to an interruption to the recording session.

7   **Experiment 3.**

8   Participants were instructed that all items were equally likely to be probed. Each trial

9   began with a jittered ITI (500 – 1,500 ms) followed by the memory array (200 ms). Then, after a

10   delay (900 ms), participants made a response to the probed shape on the color wheel with the

11   mouse. There were three conditions: 1) Load 4 with three colored squares presented in a vertical

12   cluster to the left or right of fixation (1° x 1°, 1.2° apart center-to-center, 3° from fixation) and

13   one colored square presented vertically. 2) Load 4 with one square presented laterally and three

14   squares on the vertical. 3) Load 6 with three squares presented laterally and 3 vertically.

15   Participants were given feedback after their response (800 ms), where 'Correct' was considered

16   within 40° of the target color. Participants completed a total of 900 trials, 300 of each condition.

17   **EEG Recording and Pre-Processing**

18   All EEG pre-processing was done in MATLAB with the EEGLAB[52] (Version 14.0.0b),

19   and ERPLAB[53] (Version 6.1.2) toolboxes. EEG was DC recorded at a 512 Hz sampling rate from

20   a 64 Ag/AgCl electrode cap placed at the standard 10-20 sites[54]. The signal was online

21   referenced to the common mode sense (CMS) and the driven right leg (DRL) electrodes. Data

22   were re-referenced off-line to the average of the mastoids, baseline corrected to -200 ms before

23   memory array onset, and filtered with a 40-Hz low-pass and 0.1-Hz high-pass Butterworth filter

1 (slope: 12dB/octave). Data were epoched between -200 and 1,050 ms (Experiment 1) or -200 and

2 1,100 ms (Experiment 2), time-locked to the memory array.

3 **Artifact rejection.**

4 Horizontal electro-oculogram (HEOG) was recorded from bipolar external electrodes

5 placed laterally beside the eyes. Vertical electro-oculogram (VEOG) was recorded as the

6 difference between external electrodes placed below the eyes and FP1 or FP2. Trials with VEOG

7 activity $> \pm 80$ µV or HEOG activity $> \pm 32$ µV between stimuli onset and the end of the trial

8 were removed, as were trials in which the voltage over posterior channels (P1/2, P3/4, P5/6,

9 P7/8, P9/10, PO3/O4, PO8/O7, and O1/2) was $> \pm 100$ µV. Participants with more than 35% of

10 trials rejected were replaced. An average of 21.4% of trials were rejected in Experiment 1, ($SD =$

11 10.4%), 11.6% in Experiment 2 ($SD = 7.8\%$), and 13.3% in Experiment 3 ($SD = 10.1\%$). Across

12 studies, each participant had more than 100 trials in each condition bin.

13 In Experiments 2 and 3 we also replaced participants whose average residual HEOG

14 activity was greater than ± 4 µV between memory array onset and the end of the epoch.

15 Resulting in absolute residual HEOG values of 1.61 µV ($SD = 1.02$ µV) in Experiment 2 and

16 1.61 µV ($SD = 1.00$ µV) in Experiment 3. The total number of replaced participants was 10 in

17 Experiment 1, 12 in Experiment 2, and 8 in Experiment 3.

18 **Data Analysis**

19 **Behavioral data.**

20 Performance was assessed using the trial-by-trial raw response error (i.e., the difference

21 in degrees between the color of the probed item and the participant's response). Lower values

22 reflect more precise responding. Data from all experiments were fit to a power-law function:

23 $$y \propto ax^{-k}$$

1   Bayesian information criterion (BIC) values were computed to compare model fits. Raw

2   error values were calculated using custom scripts in MATLAB. Goodness of fit was computed

3   using nonlinear least squares regression in MATLAB's Curve-Fitting Toolbox using a bisquare

4   robust fitting procedure with the group data averaged across conditions.

5   **ERP data.**

6   Difference waves were calculated at electrode pairs: P3/4, P7/8, PO7/O8, PO3/O4, and

7   O1/2[55]. Across all experiments, there was no significant Condition x Channel interaction for any

8   of the ERP components (Fs < 2.24, ps > .055, η^2_ps < .11). Therefore, we averaged activity across

9   these electrode sites for all ERP measurements.

10   Repeated-measures ANOVAs were used along with follow-up linear contrasts and fits

11   where reported. Where violations of sphericity exist, Greenhouse-Geisser corrected degrees of

12   freedom and p values are reported. Two-tailed t-tests were Bonferroni-corrected only where a

13   priori hypotheses were not present. Bayesian repeated-measures ANOVAs and post-hoc tests are

14   reported where applicable (r scale prior width of 0.5, default Cauchy prior centered on 0, 10,000

15   Monte Carlo samples). Statistical analyses were completed using JASP Version 0.8.4[56] and

16   MATLAB R2017a.

17   In all experiments, the CDA was measured as the mean amplitude during the delay period

18   from 400 ms post-stimuli offset to the end of the trial[36,57]. An N2pc was only observed in

19   Experiment 2 and was measured as the mean amplitude from 200 – 300 ms post-stimuli

20   onset[32,58–60]. We also measured the negative 50% fractional peak latency of the N2pc between

21   200 – 300 ms[61]. In Experiment 2, we measured the P_D as the positively signed area from 250 –

22   400 ms[62,63]. We used a nonparametric permutation approach to determine the presence of the P_D.

1   The p values for the permutation tests were estimated using the following formula with

2   1,000 permutations[64]:

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

4   **Modelling CDA data.**

5   In Experiments 2 and 3, we fitted the CDA amplitudes to a power-law model. The

6   weighted-product values were calculated by the following formula:

7   % of lateral resources × number of lateral items

8   Model fits were completed using the Curve Fitting Toolbox in MATLAB and custom

9   MATLAB scripts to calculate BIC values to compare model fits.

10 **Data Availability:** The datasets generated or analysed during the present study are unavailable

11 due to the absence of consent.

12 **Code Availability:** Psychopy task scripts, R code, and MATLAB code used to pre-process EEG

13 data as well as to fit models are available online at: https://osf.io/r73c5/

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Additional Information

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