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Active Working Memory and Simple Cognitive Operations

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Abstract

Working memory is thought to serve as a buffer for ongoing cognitive operations, even in tasks that have no obvious memory requirements. This conceptualization has been supported by dual-task experiments, in which interference is observed between a primary task involving short-term memory storage and a secondary task that presumably requires the same buffer as the primary task. Little or no interference is typically observed when the secondary task is very simple. Here, we test the hypothesis that even very simple tasks require the working memory buffer, but interference can be minimized by using *activity-silent* representations to store the information from the primary task. We tested this hypothesis using dual-task paradigm in which a simple discrimination task was interposed in the retention interval of a change detection task. We used contralateral delay activity (CDA) to track the active maintenance of information for the change detection task. We found that the CDA was massively disrupted following the interposed task. Despite this disruption of active maintenance, we found that performance in the change detection task was only slightly impaired, suggesting that activity-silent representations were used to retain the information for the change detection task. A second experiment replicated this result and also showed that automated discriminations could be performed without producing a large CDA disruption. Together, these results suggest that simple but non-automated discrimination tasks require the same processes that underlie active maintenance of information in working memory.

Keywords: ERP, CDA, activity-silent memory, dual task

Working memory was originally conceived as a buffer that could serve the temporary storage needs of a broad range of cognitive tasks that are not themselves memory tasks per se, such as language comprehension and reasoning (Baddeley & Hitch, 1974). However, most working memory research focuses on explicit memory tasks and on correlations with other abilities, with much less research directly addressing how ongoing cognitive tasks make use of the working memory buffer. Even in *complex span* tasks that combine a processing task and a memory task (Bayliss et al., 2005; Daneman & Carpenter, 1980; Hudjetz & Oberauer, 2007; Turner & Engle, 1989), relatively little work has focused on exactly how the processing task makes use of the memory buffer. Research on the neurobiology of working memory has also focused primarily on the mechanisms that actively maintain information across brief delays in memory tasks rather than asking how working memory is used in the service of other cognitive tasks (Ester et al., 2015; Goldman-Rakic, 1995; Lundqvist et al., 2016; Vogel & Machizawa, 2004; Woloszyn & Sheinberg, 2009).

The smaller number of studies that have directly examined how working memory is used in the service of other cognitive tasks have primarily used dual-task paradigms. In these paradigms, a primary task involves the temporary storage of one set of information (to “fill the buffer”) and a secondary task involves some cognitive operation hypothesized to require the buffer (Bae & Luck, 2019; Cocchini et al., 2002; Saults & Cowan, 2007). Some combinations of primary and secondary tasks lead to substantial interference, which is taken to indicate that the secondary task requires the same buffer used by the primary task. Other combinations lead to minimal interference, which is taken to mean that the secondary task either does not require working memory or makes use of a different buffer than the primary task. Indeed, this pattern of results was the impetus for the influential Baddeley and Hitch (1974) model of working memory.

Outside the working memory literature, a largely independent line of dual-task research has shown that two tasks can interfere with each other even if they use very simple tasks with no obvious memory requirements (Pashler, 1994). Most of this research has used variations on the *psychological refractory period* (PRP) task, in which two stimuli are presented in close temporal succession, each of which requires an independent motor response. The PRP paradigm has been used to show that, for example, it is difficult to perform a visual letter discrimination task using a manual response and an auditory pitch discrimination task using a vocal response if the letter and the pitch are presented within a few hundred milliseconds of each other (Pashler, 1991). This may reflect the general problem faced by the human brain of being able to route virtually any discriminable stimulus to virtually any motor response depending on the current task instructions. Many researchers have proposed that a *central attention* mechanism is needed to perform this routing process (Johnston et al., 1995; Lien et al., 2008; Lien & Proctor, 2002; O'Malley et al., 2008), and this attention mechanism cannot easily route two different stimuli to two different responses at the same time[1].

Here, we test the hypothesis that the sorts of simple stimulus-response tasks that have been shown to involve central attention in the PRP literature require storing information in the memory buffer that has been studied in the working memory literature. Although we are unaware of previous research explicitly linking the PRP and working memory literatures in this way, the idea that performing a controlled task on a simple stimulus requires storing that stimulus in some

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[1] Researchers have vigorously debated whether this mechanism is strictly serial or can operate in parallel under some conditions (e.g. Fischer et al., 2014; Halvorson & Hazeltine, 2015; Pashler, 1994), but nearly all agree that substantial interference is present when response selection must be performed concurrently for two independent stimuli.

kind of short-term buffer has been raised in previous theories, such as those of Duncan (1980) and Bundesen (1990).

However, previous empirical research suggests that simple tasks do not require the working memory buffer. Specifically, there are conditions in which little or no interference is observed between a primary working memory task and a simple secondary task that is interposed during the delay period (Fougnie & Marois, 2006; Hollingworth & Maxcey-Richard, 2012; Hyun & Luck, 2007; Woodman et al., 2001; Woodman & Luck, 2004), and this has been taken as evidence that the specific secondary task does not require the buffer used by the working memory task. For example, if a visual search array is presented during the delay interval of a color change detection task, requiring a speeded discrimination, the interposed visual search task has minimal impact on change detection performance (Woodman et al., 2001).

Recent research on the neurobiology of working memory suggests an alternative explanation for such cases of minimal interference. Traditionally, working memory was thought to involve sustained activity in the cerebral cortex during the delay interval (Funahashi & Bruce, 1989; Major & Tank, 2004; Wang, 2001; Wei et al., 2012). If this were the sole mechanism of working memory maintenance (i.e., a *single-state* model), then a secondary task should cause significant disruption of performance in the primary task if the two tasks require using the same working memory buffer. However, a growing body of research supports the idea of a second state of working memory, often called *activity-silent memory*[2] (Lewis-Peacock et al., 2012; Myers et al., 2017; Rose et al., 2016; Stokes, 2015). When information is immediately relevant, it is maintained using sustained firing; however, information that is not immediately relevant to

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[2] Behavioral studies often refer to the same phenomenon as "memory outside the focus of attention" (Cowan, 2011; Lewis-Peacock et al., 2012). However, the equivalence of activity-silent memory and memory outside the focus of attention is not universally accepted. Here we use the less controversial (and more descriptive) term of "activity-silent memory" while remaining agnostic about the relationship to attention.

the present task—but might be useful later—is maintained with minimal neural activity. We call this the *multiple-state* class of working memory models (see review by Nee & Jonides, 2013). In dual-task experiments, multiple-state models would allow information from the primary task to be maintained in activity-silent memory during the brief portion of the delay period in which the secondary task is being performed. As a result, performance of the secondary task would lead to little or no reduction in accuracy for the primary memory task even if active memory for the primary task was disrupted.

Note that the exact nature of activity-silent memory is still unknown. In fact, the defining characteristic of activity-silent memory is that it is not visible using traditional neurophysiological markers of memory maintenance. Some theoretical mechanisms have been proposed. For example, Stokes et al. (2013) propose that information is stored through passively decaying synaptic weights. Others raise the possibility that this is not a separate memory system, but simply a special case of episodic memory (e.g., Beukers et al., 2021). For the purposes of the present paper, we remain agnostic about the specific mechanisms involved in activity-silent memory. However, the possibility of two separate states – an active maintenance state that is only able to store currently active representations, and a separate state of some sort that does not produce observable activity during the delay period – provides an interesting framework to describe how memory representations evolve when multiple tasks must be performed concurrently.

This multiple-state hypothesis leads to the prediction that performing a very simple secondary task during the delay period of a working memory task should reduce or eliminate the active maintenance of information for the working memory task, but with little or no reduction in behavioral performance for the working memory task itself. Such a result would call into question the conclusions of previous behavioral studies in which minimal interference was observed, including several from our own lab (Hyun & Luck, 2007; Woodman et al., 2001; Woodman & Luck, 2004). To test this hypothesis, the present study used an event-related potential (ERP) measure of active maintenance called *contralateral delay activity* (CDA).

As illustrated in Figure 1, Experiment 1 used a color change detection task (Leonard et al., 2013; Vogel & Machizawa, 2004) that was modified to add a foveal interposed stimulus (C or mirror-image C) on 50% of trials. In the dual-task condition, participants made a speeded discriminative response to the interposed stimulus in addition to performing the change detection task. In the single-task condition, the interposed stimulus was task-irrelevant. The change detection task used lateralized stimuli, making it possible to isolate the CDA, which consists of a negative voltage over the hemisphere contralateral to the to-be-remembered items during the delay period. The CDA is a well-validated correlate of working memory that is considered to reflect active maintenance (Adam et al., 2018; Hakim et al., 2019; Perez & Vogel, 2012).

The interposed task was chosen to be as simple as possible while still requiring non-automatic processing of the stimuli, as in typical PRP experiments. Crucially, the interposed task required an immediate response to the target without any explicit maintenance of target information[3]. This allowed us to test whether even simple cognitive operations create interference with the active maintenance of information about the primary task. In addition, the interposed stimuli did not resemble the stimuli for the memory task, minimizing the *contingent capture* of attention that may occur when a potentially distracting stimulus shares features with a target stimulus (Folk et al., 2002; Hakim et al., 2020).

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[3] The interposed task requires the maintenance of a *task set* (the rules for performing the task). However, any interference from the task set should be evident during the entire delay period of the change detection task rather than being triggered by the appearance of the target for the interposed task.

Several different patterns of results are plausible in this experiment. First, because the interposed task has no obvious memory requirements, the interposed stimulus might have little or no impact on the CDA for the change detection task (and therefore little or no impact on behavioral accuracy). However, if performing even a simple discriminative task requires the buffer provided by the active maintenance system (so that central attention can be used to link the stimulus to the appropriate motor response), then the interposed stimulus should reduce or eliminate active maintenance (as indexed by the CDA) in the dual-task condition. This reduction in active maintenance would then lead to impaired behavioral performance for the change detection task, but only if we assume a single-state model of working memory. Multiple-state models of working memory would instead posit that the stimuli for the change detection task could be stored in activity-silent memory, so disruption of active maintenance by the interposed stimulus would produce little or no impairment in change detection performance. Thus, the interposed stimulus might or might not disrupt the CDA in the dual-task condition (depending on whether the discrimination of this stimulus requires the working memory buffer), and disruption of the CDA might or might not be accompanied by impaired behavioral performance (depending on whether activity-silent memory is sufficient to perform the task).

It is also possible that the interposed stimulus would impact the CDA and change detection accuracy even in the single-task condition, when the interposed stimulus is task-irrelevant. That is, the sudden onset of a foveal stimulus should capture attention automatically, independent of its task relevance (Egeth & Yantis, 1997; Folk & Remington, 2015; Gaspelin et al., 2016). However, this would be a capture of *visuospatial attention*, which is very different from the *central attention* mechanism used for response selection in the PRP paradigm (Lee & Han, 2020; Pashler et al., 1993) and is also different from the kind of attention that some theorists have proposed is necessary for working memory maintenance (Cowan et al., 2005). Thus, it is unlikely that the interposed stimulus would disrupt either the CDA or behavioral performance in the single-task condition of the present study. Nonetheless, the single-task condition is important for demonstrating that any effects of the interposed stimulus in the dual-task condition are not simply a result of a redirection of visuospatial attention. That is, the interposed stimulus will certainly capture spatial attention whether it is task-relevant or task-irrelevant (Egeth & Yantis, 1997), so a lack of disruption by this stimulus in the single-task condition will indicate that any disruption in the dual-task condition is not a result of the allocation of visuospatial attention.

Note that our design also includes trials on which the interposed stimulus is absent. These trials allow us to separately assess the effects of preparing to perform the interposed task and the processes involved in actually performing the task. That is, if preparing for the interposed task impacts the CDA, then this could be observed by comparing the single- and dual-task conditions for trials on which the interposed stimulus is absent.

To preview the results, we found that the CDA was completely eliminated shortly after the presentation of the interposed stimulus in the dual-task condition (when the interposed stimulus was task-relevant), but not in the single-task condition (when the interposed stimulus was task-irrelevant). This suggest that even a very simple task requires at least some of the mechanisms that support active maintenance of information in working memory. We also found that behavioral accuracy for the change detection task was only slightly reduced by the performance of the interposed task, consistent with the use of activity-silent memory to maintain information for the change detection task.

We also conducted a second experiment that was designed to replicate the results of Experiment 1 and test a further hypothesis about what types of discriminations require the active maintenance buffer. Specifically, the brain performs many tasks automatically (e.g., the triggering of an eye movement to the location of a sudden movement), and these automatic responses do not appear to require central attention (Pashler et al., 1993). We therefore predicted that automatic discriminations could be performed during the delay period of a working memory task without disrupting the CDA.

Experiment 1

Method

Participants

The final sample consisted of 32 participants (23 female). Seven additional participants were tested but were excluded as described in the next section. The participants were between the ages of 18 and 30, with normal or corrected-to-normal visual acuity and no known neurological issues. Consent was obtained at the start of the experiment, and participants received monetary compensation. The protocol was approved by the University of California, Davis Institutional Review Board. We could not easily anticipate the effect size, so we could not use a formal a priori power analysis to determine the number of participants. The total number of participants was therefore chosen (a priori) to be on the upper end of the typical range found in experimental investigations of the CDA, which is generally 12-32 participants (e.g., Adam et al., 2018; Hakim et al., 2019, 2020; Pailian et al., 2017).

Exclusion Criteria

Participants were excluded if they met any of four exclusion criteria: 1) if they did not complete the recording session, either due to technical difficulties or because they opted to terminate the experiment early (2 participants); 2) if overall performance in the change detection task was too low (<55%; chance was 50%), indicating that the participant did not understand the task (0 participants); 3) if more than 25% of trials were rejected because of artifacts (5 participants); and 4) if there was excessive alpha (more than 5µV peak to peak for more than 1 cycle) during the pre-stimulus baseline of the averaged ERPs (0 participants).

Stimuli and Procedure

Stimuli were presented on a cathode ray tube monitor (refresh rate = 60 Hz) using PsychToolbox (Brainard, 1997; Pelli, 1997). The participants viewed the monitor from a distance of 75 cm in a dimly lit room. The monitor had a grey background and contained a white fixation cross that was visible at all times.

As illustrated in Figure 1, each trial started with a memory array, which was presented for 200 ms. The array consisted of 4 colored circles (diameter = 0.72°) presented on one side of the screen and 4 colored rectangles (0.32 × 0.92°) presented on the other, with the side chosen randomly on each trial. The colors of each individual shape were chosen randomly from a selection of 12 colors (red, green, blue, yellow, purple, cyan, pink, gray, black, white, orange, magenta) so that no color was repeated among the items of a given shape. Stimulus eccentricity varied randomly, but the stimuli were constrained to be centered at least 1.2° from the midline and no more than 3.2° from the fixation point. On each block, participants were instructed to attend to either the circles or the rectangles and to remember the colors of those shapes for the duration of the trial. The memory array was followed by a 350 ms delay period (*Delay 1*) in which only the fixation cross was present.

On 50% of the trials, Delay 1 was followed by a 200-ms interposed stimulus, which was a **C** or a mirror-reversed **C** (0.8° tall), centered at fixation. On the other 50% of trials, only the fixation cross was present during this 200-ms period. In both cases, this was followed by a 750 ms delay (*Delay 2*) during which only the fixation cross was visible. In dual-task trial blocks, participants were instructed to rapidly press a button on a gamepad if the interposed stimulus was a mirror-reversed C but to make no press if it was a normal C or if no interposed stimulus was present. In single-task trial blocks, the interposed stimulus was task-irrelevant and participants were told to ignore it. In those blocks, the C and mirror-reversed C were scrambled so they were not recognizable. This reduced the likelihood that participants would implicitly perform the discrimination task in the single-task blocks.

At the end of each trial, the change detection test array was presented for 2000 ms. The test array was identical to the memory array, except that on 50% of the trials (independent of the presence of the interposed stimulus) one of the to-be-remembered shapes changed to one of the colors that was not present in the sample array. The shapes on the other side never changed color. Participants were instructed to press a button on the gamepad to indicate if they detected a color change. An intertrial interval of 700–1000 ms (rectangular distribution) followed the test array.

The to-be-attended attended shape (color versus rectangle) and the task type (single-task versus dual-task) varied across blocks in a counterbalanced order. The interposed stimulus (C, mirror-image C, no C) and the side of the to-be-attended shape varied unpredictably from trial to trial within each block. Responses for the memory task (change vs no change) had to be made during the 2000 ms time duration of the test array. In the dual-task blocks, any response to the interposed stimuli had to occur during Delay 2. All responses were made using the participant's dominant hand.

EEG Recording and Analysis

EEG signals were recorded using a BioSemi ActiveTwo system (16 participants) or a Brain Products actiCHamp system (16 participants).

The Brain Products system had electrodes at 27 scalp locations (FP1, FP2, F3, F4, F7, F8, C3, C4, P3, P4, P5, P6, P7, P8, P9, P10, PO3, PO4, PO7, PO8, O1, O2, Fz, Cz, Pz, POz, Oz) as well as the left and right mastoids. The electrooculogram (EOG) was recorded simultaneously from an electrode placed 1 cm lateral to the outer canthus of each eye and from an electrode below the right eye. The data were recorded in single-ended mode and digitized at 500 Hz after application of an online cascaded integrator-comb anti-aliasing filter with a half-power cutoff at 260 Hz. Impedances were kept under 50 kΩ.

The BioSemi recordings were identical except that additional electrodes were placed at T7, T8, P1 , P2, and Iz, and the data were low-pass filtered with a fifth-order sinc filter (half-power cutoff at 208 Hz) online and digitized at 1024 Hz. Electrode offsets were kept below 40 mV.

Offline analysis was performed using the EEGLAB (Delorme & Makeig, 2004) and ERPLAB (Lopez-Calderon & Luck, 2014) open source Matlab packages. The recorded signals from both systems were down-sampled to 250 Hz after the application of an additional antialiasing filter at 100 Hz, and the additional channels from the BioSemi system were discarded. Then, a noncausal Butterworth high-pass filter was applied to the continuous EEG (half-amplitude cutoff = 0.01 Hz, slope = 12 dB/octave). The scalp EEG signals were referenced to the average of the left and right mastoids, and the EOG signals were referenced into bipolar horizontal EOG (right minus left outer canthus) and vertical EOG (below the right eye minus Fp2) derivations. Before artifact correction and segmentation, periods of EEG data that corresponded to breaks or contained extreme voltage deflections were removed to improve the artifact correction process that occurred next.

Artifact correction was performed using independent component analysis (ICA), and components corresponding to horizontal and vertical eye movements were identified on the basis of the correspondence of their shape, timing, and topography to the single-trial EOG signals. These components were then removed (typically 2-3 components per participant).

Artifact correction was supplemented with artifact rejection. We eliminated trials that contained large artifactual deflections in any channel following artifact correction (>250 µV at any point from -200 to 1500 ms relative to stimulus onset). We also removed trials on which the participants blinked or moved their eyes at a time that might impact the sensory input using a modified version of the technique described in Woodman and Luck (2003). Specifically, we applied a step-function algorithm (Luck, 2014) to the uncorrected vertical and horizontal bipolar EOG channels to identify trials containing eye blinks and eye movements from -200 to 200 ms relative to stimulus onset, and we then excluded those trials from the averaged ERPs. No more than 25% of total trials were rejected during the artifact rejection procedures for any participant. We then examined the residual HEOG activity (without artifact correction) in the averaged waveforms. The average deflection during that time-window was less than 3.2 µV for all participants, which would correspond to an average eye rotation of less than ±0.1° (on the basis of the normative values provided by Lins et al., 1993). Even without ICA correction, these eye movements would produce a voltage deflection of less than 0.1 µV at any of the electrodes used in our analyses.

Averaged ERPs were computed with an epoch of −200 to 1500 ms relative to stimulus onset and baselined to the pre-stimulus portion of the epoch. To isolate the CDA, we calculated a contralateral-minus-ipsilateral difference wave by subtracting the voltage in the electrodes over the hemisphere ipsilateral to the to-be-remembered items from the voltage in the electrodes over the contralateral hemisphere and then averaged across the left and right hemispheres. To simplify the analysis and reduce the potential for Type I errors (Luck & Gaspelin, 2017), statistical tests were limited to the P07 and P08 electrodes and the data were collapsed across attend-circle and attend-rectangle blocks. Statistical analysis was performed on the mean amplitude across two time periods: 350-550 ms and 1100-1500 ms after stimulus onset. These two time periods as well as the channel of interest were determined a priori using data from a pilot study with a similar paradigm. The two time periods were designed to measure the CDA before and after the time of the interposed stimulus.

Results

Behavioral results

Accuracy (percent correct) for the interposed discrimination task during the dual-task condition was near ceiling for all participants (M = 98.2%, SD = 1.8%). Thus, as intended, this task was trivially easy.

Accuracy (percent correct) for the change detection task is shown in Figure 1B. We found that presentation of the interposed stimulus produced only a small drop (1.1-1.5%) in memory, regardless of whether this stimulus was task-relevant. However, this small drop was statistically significant: a 2 (single task vs dual task) by 2 (interposed stimulus present vs absent) within subjects factorial ANOVA yielded a significant main effect of stimulus presence (F(1,31) = 5.88, p = 0.021), but no significant main effect of task (F(1,31) = 0.429, p = 0.517), and no significant interaction between the two (F(1,31) =0.159, p =0.693).

Because the task for the interposed stimulus required a response for one of the possible interposed stimuli (the “go” stimulus) but not the other (the “no-go” stimulus), we also looked for any difference in performance between the two. Change detection accuracy was similar on the “go” trials (mean = 80.3, SD = 8.29) and the “no-go” trials (mean = 81.1, SD = 7.15), and the small difference was not significant (t(31) = -1.49, p = 0.157).

Despite the small drop in performance when the interposed stimulus was presented, accuracy remained well above chance. Thus, although the interposed stimuli had a small negative effect on memory performance, participants were still able to access enough information to detect the change almost as accurately as they could when no interposed stimulus was present.

ERP results

Figure 2A shows the grand average contralateral-minus-ipsilateral difference waves for the dual-task condition. A contralateral negativity (CDA) appeared beginning approximately 200 ms after the onset of the sample array. The presentation of the interposed stimulus 550 ms after the onset of the sample array led to a brief sensory response that was superimposed on the CDA (see the Appendix for waveforms, analyses, and discussion). After that sensory response, the CDA dropped precipitously, with a voltage near zero during the 1100-1500 ms measurement window. By contrast, the CDA declined only slightly over the delay period when the interposed stimulus was absent.

The interposed stimulus produced a somewhat different sensory response in the single-task condition (Figure 2C, and it did not lead to a long-lasting disruption of the CDA relative to trials on which the interposed stimulus was absent.

To analyze these results statistically, we entered the mean voltage during the 1100-1500 ms measurement window into a 2-way ANOVA with factors of task type (single-task versus dual-task) and stimulus presence (interposed stimulus present versus absent). The drop in CDA amplitude produced by the interposed stimulus in the dual-task condition, but not in the single-task condition, led to a significant interaction between task type and stimulus presence ($F(1,31) = 10.98$, $p = 0.002$). This interaction was decomposed with pairwise comparisons, which indicated that the drop in amplitude on stimulus-present versus stimulus-absent trials was significant in the dual-task condition ($t(31) = 6.95$, $p < 0.001$) but not in the single-task condition ($t(31) = 1.74$, $p = 0.09$). Interestingly, when the interposed stimulus was present in the dual-task condition, the mean CDA amplitude during the measurement window was close to zero and actually slightly positive (mean = 0.29 µV, 95% CI = 0.05 - 0.52 µV), indicating that the CDA was largely eliminated in this condition. Table 1 shows t-tests against 0 for all conditions.

The task for the interposed stimulus was to make a response (“go”) for one shape and no response (“no-go”) for the other shape. We did not observe any differences in the CDA between the go and no-go trials, and the results shown in Figure 2A are collapsed across the go and no-go trials. The go and no-go data are presented separately in Figure 2B.

Because participants knew that a task-relevant interposed stimulus was likely in the dual-task condition, it is possible that they made less use of active maintenance even prior to the onset of the interposed stimulus in this condition. Such a strategy would have led to a reduced CDA amplitude in the dual-task condition relative to the single-task condition prior to the onset of the interposed stimulus. However, the CDA during this time period was nearly identical in the single-task and dual-task conditions. As a statistical test, we performed the same 2-way ANOVA on the data from 350-500 ms after the onset of the sample array (which was prior to the onset time of the interposed stimulus at 550 ms). The CDA amplitude during this period was not significantly affected by task (F(1,31) = 2.49, p = 0.125), stimulus presence (F(1,31) = 2.92, p = 0.097), nor their interaction (F(1,31) = 0.10 , p = 0.748).Thus, there was no evidence that different expectations during the single-task and dual-task conditions impacted the CDA. As a further test, we conducted a 3-way ANOVA with factors of time period (350-550 versus 1100-1500), task (single versus dual), and interposed stimulus (present versus absent). This ANOVA yielded a significant 3-way interaction (F(31) = 21.78, $p < 0.001$), indicating that the drop in CDA produced by the interposed stimulus was greater for the dual-task condition than for the single-task condition.

Discussion

Experiment 1 demonstrated that a trivially simple discrimination task performed during the delay interval of a working memory task can dramatically disrupt the active maintenance process reflected by the CDA. This finding is consistent with the hypothesis that the active maintenance system is used for any task that requires central attention, even something as simple as pressing a button for the letter C and not pressing for a mirror-image C. Interestingly, the CDA was not just reduced slightly but was essentially eliminated.

Because the CDA disruption was limited to the dual-task condition, it appears to reflect the allocation of central attention rather than the capture of visuospatial attention by the interposed stimulus. That is, the interposed stimulus disrupted the CDA only in the dual-task condition, even though it was a sudden-onset stimuli that would be expected to automatically capture visuospatial attention in both the single-task and dual-task conditions (Jonides & Yantis, 1988; Yantis & Jonides, 1984) . Thus, the disruption of the CDA appears to reflect the controlled allocation of central attention to the interposed stimulus rather than the automatic allocation of visuospatial attention.

The nearly complete elimination of the CDA by the interposed stimulus in the dual-task condition is especially remarkable given that behavioral accuracy for the memory task remained quite high. Behavioral performance was only slightly reduced when the interposed stimulus was present compared to when it was absent, and this reduction in accuracy was approximately equivalent whether the interposed stimulus was task-relevant or task-irrelevant. Previous research has demonstrated that sudden-onset stimuli tend to be encoded in working memory whether or not they are task-relevant (Schmidt et al., 2002). Thus, the small accuracy reduction observed in the present study likely reflects the automatic capture of attention by the sudden onset of the interposed stimulus as opposed to the controlled processing of this stimulus that was required in the dual-task condition.

The finding of high working memory accuracy in the absence of the CDA suggests that information about the sample stimuli was maintained in some kind of activity-silent memory. The present working memory task required detecting large, categorical changes in color, so this activity-silent memory did not necessary contain the same degree of precision that was available when the CDA was present. Indeed, previous research using a delayed estimation task shows that a simple interposed task causes working memory representations to become less precise and more categorical (Bae & Luck, 2019). However, the conclusion that the high accuracy in the working memory was due to activity-silent memory is based on an *absence* of observed delay-period activity, with no positive evidence for the use of another memory system. Thus, this conclusion is necessarily tentative.

Experiment 2

Experiment 2 was designed to replicate the results of Experiment 1 and test a further hypothesis about what types of discriminations require the active maintenance buffer.

Specifically, we wanted to better describe which processes lead to the disruption of the active maintenance buffer. The brain performs many tasks automatically (e.g., the triggering of an eye movement to the location of a sudden movement, the coding of orientation in primary visual cortex), and such tasks do not seem to require central attention (Pashler et al., 1993). Given how prevalent these processes are in the real world, it would be quite problematic if they disrupted active maintenance of information in working memory. In fact, work by Hakim et al. (2021) shows that when spatial attention alone (and not central attention) is captured by task-irrelevant interposed stimuli, working memory is largely unaffected. It seems likely that other automatic processes that do not require central attention similarly spare active maintenance, allowing items to be maintained efficiently even when competing task-irrelevant sensory information may be automatically parsed and processed.

For example, given how visually salient the task-irrelevant stimuli in Experiment 1 were, it is very likely that they captured spatial attention and received substantial automatic processing. This automatic processing did not require central attention, and which explains why the CDA was not disrupted. However, we have no means of assessing the extent to which the interposed stimuli were actually discriminated when they were task-irrelevant. Experiment 2 was designed to directly test the hypothesis that substantial automatic processing can occur without disrupting the active maintenance of information in working memory.

To test this hypothesis for a relatively high-level aspect of automatic processing, we focused on orthographic processing that is known to be automated in skilled readers (Carr, 1992;

Schaffer & Berge, 1979; Stroop, 1935; Taft et al., 2008). In particular, previous research has found that the brain automatically distinguishes between pseudowords (e.g. FOPTER) and consonant strings (e.g. FTPTXR), producing an N400-like ERP difference even when the items are task-irrelevant (Bentin et al., 1999). We predicted that this relatively high-level discriminative processing could proceed during the delay interval of our change detection task without disrupting active maintenance.

In Experiment 2, we used the same working memory task as in Experiment 1, but we used pseudowords and consonant strings as the interposed stimuli (see Figure 1C). In the single-task condition, in which these stimuli were task-irrelevant, we predicted that the brain would be automatically discriminate between the pseudowords and consonant strings, leading to differences in the ERPs. However, because we assume that the discrimination is automatic, we predicted that these stimuli would not disrupt the CDA. In the dual-task condition, by contrast, participants were required to press different buttons for the pseudowords and consonant strings, and the process of mapping these stimuli onto motor responses would require central attention. We therefore predicted that the CDA would be disrupted by the interposed stimuli in the dual-task condition, as in Experiment 1.

Note that this orthographic task is likely more complex and difficult than the task used in Experiment 1. The reason we chose this task was not to make the interposed stimuli simpler, but because pseudowords and consonant strings produce different ERPs when they are differentiated by the brain (as opposed to the C and mirror-image C stimuli used in Experiment 1). This difference can then be used to confirm that the stimuli were indeed automatically discriminated without disrupting the CDA. Furthermore, the use of more complex stimuli tests a stricter version of our hypothesis – namely that even relatively complex processing can spare active maintenance, as long as it is automatic.

Method

The method was identical to that of Experiment 1 except as noted.

The final sample again consisted of 32 participants (21 female) between the ages of 18 and 30 (mean = 20.5, SD = 2.03). An additional 13 participants were tested but were excluded (2 because of technical difficulties, 5 because of low performance, 1 because of excessive ocular artifacts, and 5 because of excessive alpha).

The stimuli were presented on a Hewlett-Packard ZR2440w LCD monitor rather than on a CRT. Because LCDs often produce a significant delay, a photosensor was used to measure the monitor delay (32 msec), and the event codes were shifted offline to be aligned with the actual stimulus presentation time.

The interposed stimuli were changed to be letter strings, either pronounceable pseudowords (e.g., FOPTER) or unpronounceable consonant strings (e.g., FTPTXR). On each trial with an interposed stimulus, one pseudoword or consonant string was chosen at random from a list of 50 pseudowords and 50 consonant strings ranging from 4-7 characters long. The same interposed stimuli were used in both the single-task and dual-task blocks. In the dual-task blocks, a 2-alternative forced-choice task was used for the interposed stimuli rather than a go/no-go task. Specifically, participants were asked to press one button (top right shoulder button) on a game pad if the interposed stimulus was a pseudoword and another (bottom right shoulder button) if it was a consonant string.

The EEG was recorded using the same Brain Products actiCHamp system used in Experiment 1.

Additional ERP analyses were performed to determine whether the pronounceable pseudowords elicited a different electrophysiological response than the consonant strings. Previous research found a broad central-parietal difference emerging ~320-450 ms from stimulus onset, with a more negative voltage for pseudowords than for consonant strings (Bentin et al., 1999). We measured the voltage during this same time window, time-locked to the letter strings, to determine whether the pseudowords and consonant strings were differentiated by the brain, even though they were task-irrelevant. Given the broad scalp distribution of the expected effect, the voltage was measured from a single electrode cluster created by averaging together all central and parietal channels (Cz,C3, C4, Pz, P3, P4, P5, P6, P7, P8, P9, P10, POz, PO3, PO4, PO7, PO8).

Results and Discussion

Behavioral results

Accuracy (percent correct) for the interposed discrimination task during the dual-task condition was relatively high but not at ceiling (M = 86.0%, SEM = 2.12), whereas it was near ceiling in Experiment 1. A two-sample *t* test (using the Welch formula to account for any difference in between-subjects variance across the two experiments) indicated that this difference was statistically significant ($t(31.253) = 289.08$, $p < 0.001$).

Accuracy (percent correct) for the change detection task is shown in Figure 1D. Interestingly, unlike Experiment 1, we found that the task relevancy of the interposed task had a large effect on performance. When the interposed stimuli were task-irrelevant (single-task condition), we found the presence of the interposed stimulus led to the same small drop in accuracy (1.1%) as in Experiment 1. However, when the interposed stimuli were task-relevant (dual-task condition), we found that the presence of this stimulus produced a much larger drop in performance (13.0%) than was observed in Experiment 1. This may be related to the finding that the interposed task in Experiment 2 was more difficult than the interposed task in Experiment 1. However, change detection performance remained well above chance.

We analyzed this difference in performance using a 2 (single-task vs dual-task) by 2 (interposed stimulus present vs absent) within-subjects ANOVA, which revealed a significant interaction between the stimulus presence and task relevance ($F(1,31) = 51.10$, $p <0.001$). Post hoc pairwise comparisons revealed that the difference in performance between stimulus-present and stimulus-absent trials was significant in the dual-task condition ($t(31) =10.61$, $p <0.001$) but not in the single-task condition ($t(31) =1.45$, $p = 0.158$).

Note that the key finding was that the interposed stimulus did not significantly disrupt memory performance in the single-task condition, when it was task-irrelevant. This makes it possible for us to ask whether the brain could discriminate whether the interposed stimulus was a consonant string or a pronounceable pseudoword in this condition, even though it did not draw enough processing resources to disrupt working memory performance.

ERP results

Processing of the interposed stimuli.

The addition of letter-string stimuli allowed us to more thoroughly examine the processing of interposed stimuli. Our main question for this analysis was whether the brain discriminated between the pseudowords and the consonant strings in the single-task condition, when these stimuli were task-irrelevant and produced minimal disruption of working memory accuracy. As in Experiment 1, the interposed stimuli led to a brief sensory response that was superimposed on the CDA (see the Appendix for waveforms, analyses, and discussion).

As shown in Figure 3, between 320 ms and 450 ms from the interposed stimulus onset (corresponding to 870 – 1000 ms from the onset of the memory array) pseudowords elicited a more negative voltage than consonant strings in the single-task condition—just as in the prior study of Bentin et al. (1999). This effect was statistically significant, as indicated by a one-sample t-test, $t(31) = -2.21$, $p = 0.035$.

Given the difference between the ERPs to consonant strings and pseudowords, we can conclude that the brain was able to discriminate between the two letter string types during this time period. Moreover, the next set of analyses will show that these stimuli produced little disruption of the CDA during this time period, consistent with the hypothesis that the brain can perform automated discriminations without involving the active maintenance system reflected by the CDA.

Note that the timing and broad central-parietal distribution of the effect is consistent with a larger N400 for the pseudowords than for the consonant strings. However, the N400 is not the only component that might produce such a pattern of results, and it is impossible to conclusively determine whether the observed effect consists of an N400 modulation. Fortunately, the question being asked in the present study is independent of any particular ERP component; any ERP difference between the pseudowords and consonant strings indicates that the two types of stimuli were differentially processed by the brain, regardless of the specific components that are involved. Moreover, the fact that the effect occurred after 300 ms indicates that it reflects a relatively late stage of processing rather than a difference in low-level visual features.

Figure 4 shows the corresponding waveforms from the dual-task condition, in which participants were actively discriminating between pseudowords and consonant strings. As in the single-task condition, the voltage was more negative following pseudowords than following consonant strings. This effect was not directly relevant for our hypotheses, and it likely reflects a combination of automatic and task-related processes, so these data were not analyzed further.

Contralateral delay activity. Figure 5 shows the average contralateral-minus-ipsilateral difference waves. The ERP results largely replicate those from Experiment 1, with a substantial drop in the CDA after a task-relevant interposed stimulus but not after a task-irrelevant interposed stimulus.

The key question was whether the CDA would be disrupted by the interposed stimulus in the single-task condition, in which the stimulus was task-irrelevant but was automatically discriminated, as indicated by the greater negativity observed when the interposed stimulus was a pseudoword than when it was a consonant string (Figure 3). Our first CDA analysis therefore focused on the time period when we can be certain that the interposed stimulus was being discriminated, namely the period in which the difference between the consonant strings and pseudowords was significant (320–450 ms from the onset of interposed stimulus, corresponding to 870–1000 ms relative to the onset of the sample array). We computed the CDA voltage over this time period from the contralateral-minus-ipsilateral difference waves (see the green shading in Figure 5) and entered this voltage into a 2-way ANOVA with factors of task type (single-task versus dual-task) and stimulus presence (interposed stimulus present versus absent). The drop in CDA amplitude produced by the interposed stimulus in the dual-task condition, but not in the single-task condition, led to a significant interaction between task type and stimulus presence ($F(1,31) = 26.13$, $p < 0.001$). These results are summarized in Figure 6A.

Post hoc pairwise comparisons indicated that there was no significant effect of stimulus presence on the CDA in the single-task condition ($t(31) = 0.548$, $p = 0.588$), but there was a significant disruption of the CDA (during the same time window) in the dual-task condition (t(31) = 7.01, $p < 0.001$. Because the absence of a significant effect is difficult to interpret, we also computed Bayes factors using the method of Rouder et al.(2009) with the default JZS scaling factor of 0.707. For the single-task condition, the resulting Bayes factor was 4.61 in favor of the null hypothesis, providing positive evidence that the interposed stimulus had no impact on the CDA in this condition. The Bayes factor was 203,513 in favor of an effect in the dual-task condition, confirming the presence of a very strong disruption of the CDA in this condition. Thus, automatic discriminative processing of a task-irrelevant interposed stimulus can occur without disrupting active maintenance (as indexed by the CDA), whereas controlled processing does disrupt active maintenance.

For the sake of completeness, we also analyzed the CDA with the same time window used in Experiment 1 (1100-1500 ms after the onset of the sample array). A 2 (single task vs dual task) by 2 (interposed stimulus present vs absent) within-subjects ANOVA yielded a significant interaction (F(1,31) = 13.68, $p < 0.001$). Thus, as in Experiment 1, the interposed stimulus disrupted the CDA during this time window more when it was task-relevant than when it was task-irrelevant. However, the task-irrelevant interposed stimulus did produce a small reduction in CDA in this late time window. This led to a small but significant effect of stimulus presence in the single-task condition (t(31) =2.33, $p = 0.027$). A significant effect of stimulus presence was also observed in the dual-task condition (t(31) =7.76, $p < 0.001$). These results are summarized in Figure 6B. Note that a small reduction in CDA amplitude was also observed following the task-irrelevant interposed stimulus in Experiment 1, but the effect did not reach significance in that experiment. This may be related to the small reduction in behavioral change detection accuracy that was produced by the task-irrelevant interposed stimulus in both experiments.

Furthermore, as in Experiment 1, the CDA in Experiment 2 was completely eliminated in the dual-task condition but not the single-task condition.

As in Experiment 1, we verified that the observed effect in Experiment 2 was not simply due to differing expectations about the interposed stimulus by performing the same 2 by 2 within-subjects ANOVA on an earlier time window (350-500 ms after stimulus onset) which fell before the presentation of the interposed stimulus. The mean amplitude of the contralateral-minus-ipsilateral difference wave during this period was not significantly affected by task (F(1,31) = 2.35, p = 0.135) nor by the interaction between task and stimulus presence (F(1,31) = 1.50 , p = 0.230). We did find a significant main effect of stimulus (F(1,31) = 9.02 , p = 0.005), with the voltage being slightly less negative for trials on which a stimulus was later presented (M = -1.27, SD = 0.85) compared to trials without an interposed stimulus (M = 1.44, SD = 0.72). However, because this time-window fell before the presentation time of the interposed stimulus, and the trials were identical up to that point, this effect of stimulus presence must have been spurious.

To verify that this spurious difference was not driving the effect we observed in the later time window, we conducted a 3-way ANOVA with factors of time window (early or late), task (single-task vs dual-task), and stimulus (interposed stimulus present vs absent). Crucially, the three-way interaction was significant (F(31) = 11.98, p = 0.002), demonstrating that the effects we found in the later time window were not (primarily) caused by the differences that were present in the early time window. This 3-way interaction was also significant (F(31) = 23.25, p < 0.001) when the early time window (350-500 ms) was compared with the time window where we found the significant difference between the consonant strings and pseudowords (870 – 1000 ms).

General Discussion

The goal of this study was to determine whether very simple cognitive operations—with no obvious need to store the target in memory—involve the active working memory buffer. Across two separate experiments, we observed that simple discrimination tasks produced a disruption of the CDA, a marker of working memory maintenance. Little or no disruption was observed when the interposed stimulus was absent or task-irrelevant. The virtually complete disruption of the CDA produced by the interposed stimulus when it was task-relevant is a very striking finding, especially given that behavioral performance for the working memory task remained well above chance. At a minimum, we can conclude that accurate change detection performance is possible even when the CDA—a widely used index of visual working memory maintenance—has been largely eliminated.

By the logic of prior dual-task studies of working memory (Baddeley & Hitch, 1974; Cocchini et al., 2002; Saults & Cowan, 2007), we can further conclude that the simple interposed tasks used in the present study must rely on the active working memory system that the CDA is widely thought to index. This is consistent with PRP studies indicating that simple tasks of this nature require central attention (Johnston et al., 1995; Lien & Proctor, 2002; O'Malley et al., 2008), which is also thought to be important for working memory (e.g., Souza & Oberauer, 2017). However, to our knowledge, the kind of central attention studied in the PRP paradigm has not previously been empirically linked with the kind of central attention thought to underly working memory maintenance.

These conclusions contrast with previous behavioral studies in which simple interposed tasks produce little or no effect on memory performance. Indeed, behavioral performance also remained high in all conditions of Experiment 1, even when the CDA was completely disrupted.

However, given the recent evidence for multiple states of working memory, it is plausible that a separate state of working memory, one which is not tracked by the CDA, is responsible for memory performance remaining relatively high in the absence of the active maintenance mechanism tracked by the CDA.

However, this is an indirect inference, and we cannot know whether the specific activity-silent memory mechanisms that have been identified in previous experiments were responsible for the above-chance memory performance we observed in the dual-task conditions of the present study. By definition, activity-silent memory cannot be seen in delay-period activity, so we have no direct evidence that activity-silent memory was used. It is possible, for example, that some kind of active maintenance was present but was invisible in the scalp ERP signal. However, the present results are at the very least consistent with several previous studies providing evidence for activity-silent maintenance of visual information (Lewis-Peacock et al., 2012; Myers et al., 2017; Rose et al., 2016; Stokes, 2015).

This set of findings reconcile the original formulation of working memory as a general buffer for cognitive operations with the traditional neurobiological approach of focusing on active maintenance. We found evidence that, as predicted by the original Baddeley and Hitch (1974) model, working memory is recruited when someone must perform a non-automatic cognitive operation. However, we also found evidence that is consistent with more recent findings indicating that working memory consists of multiple states, which vary in terms of their dependence on central attention.

It is important to note that the disruption of the CDA observed in the present study was a consequence of performing a controlled task and not a result of automatic processes. In both experiments, we found that the task-irrelevant interposed stimuli produced only a small reduction in CDA amplitude (compared to trials without an interposed stimulus). Thus, although the interposed stimulus would be expected to automatically attract visuospatial attention (Jonides & Yantis, 1988; Yantis & Jonides, 1984), it did not disrupt the CDA unless the subject performed a non-automated task using this stimulus. Moreover, in Experiment 2, we found direct evidence that the brain automatically discriminated between the pseudowords and the consonant strings, a fairly complex discrimination. Even so, we found no discernable drop in the CDA for these stimuli when they were task-irrelevant (during the time period when the brain was clearly making the discrimination). We did find a small drop in the CDA later in time (though nowhere near the complete disruption we observed for task-relevant stimuli). The cause of this small drop late in time is unclear. Perhaps the participants sometimes consciously tried to process the task-irrelevant interposed stimuli, or perhaps there was some carry-over effect from the condition in which these stimuli were relevant. Regardless of the reason for this late drop in CDA amplitude, it was clearly different from the more rapid and substantial disruption of the CDA that was observed when the stimuli were task-relevant.

Although the most parsimonious explanation of the present results is that the task-relevant interposed stimuli disrupted the active maintenance of the to-be-remembered colors, the nature of ERPs means that several alternative explanations for the apparent drop in CDA are possible. First, it is possible that the change in mean voltage following the interposed stimulus was not due to a decrease in the CDA, but was instead the result of the addition of another, unknown component of opposite polarity that canceled out the CDA. However, there is no reason to believe that the interposed stimulus would elicit a contralateral positivity of this nature, so this is not a very plausible explanation of the observed pattern of results.

Another alternative explanation is that the CDA was indeed disrupted, but this did not reflect a disruption of the actual maintenance of information in working memory. According to this argument, the CDA does not track working memory directly, but instead is a marker of some kind of secondary support process rather than being an index of the actual memory trace. Under this assumption, it is possible that during the interposed task, this secondary process (and thus the CDA) was disrupted but the primary processes associated with working memory remained intact. However, if the CDA reflects a support process that is important for working memory maintenance, then it seems implausible that the CDA could be disrupted without also disrupting the memory trace. Indeed, the CDA ordinarily tracks working memory quite closely. For example, previous research has shown that the CDA tracks the amount of information in working memory (e.g., Luria et al., 2016), and it has been shown that spatial attention alone cannot affect the CDA (Hakim et al., 2019). Thus, it seems most likely that the observed disruption of the CDA was accompanied by a disruption of active memory maintenance.

A related possibility is that working memory representations are stored in multiple areas, and only some of them exhibit disruption from a task-relevant interposed stimulus. For example, Miller et al. (1996) found that delay-period activity in inferotemporal cortex was disrupted by the presentation of a task-relevant distractor but no disruption was observed in prefrontal cortex. Thus, it is possible that the disruption of the CDA produced by task-relevant interposed stimuli in the present study reflects a disruption of active maintenance in some but not all relevant brain regions. In this case, the preserved performance for the color change detection task would be explained by the remaining active maintenance rather than by activity-silent representations. However, the existing evidence suggests that the CDA is not generated in inferotemporal cortex but instead arises from posterior parietal cortex (Becke et al., 2015; Robitaille et al., 2009) and/or prefrontal cortex (Reinhart et al., 2012).

Hakim et al. (2021) performed a complementary study in which the to-be-remembered stimuli were on the midline and the interposed stimuli were lateralized, making it possible to obtained lateralized measures of the processing of the interposed stimuli. They found that the lateralized interposed stimuli captured attention (indicated by the N2pc component) when they were task-relevant but were suppressed (indicated by the P_D component) when they were task-irrelevant. In addition, the interposed stimuli elicited a small CDA when they were task-relevant, even though the interposed task required an immediate shape discrimination without any explicit memory requirements. This is consistent with the evidence from the present study that task-relevant interposed stimuli require access to the working memory buffer. It should be noted that the interposed stimuli used by Hakim et al. (2021) were much more complex than those used in the present study. Thus, the combination of that study and the present study indicate that the discrimination of both simple and complex stimuli requires access to the working memory buffer.

In a second experiment, Hakim et al. (2021) used lateralized stimuli for the memory task and midline stimuli for the interposed task, as in the present study. As in the present study, they found that the CDA for the to-be-remembered stimuli was interrupted by task-relevant interposed stimuli. However, they found a similar interruption when the interposed stimuli were task-irrelevant. As they noted, this may be because the interposed stimuli were very similar to the to-be-remembered stimuli, so participants may have been unable to fully ignore them (i.e., contingent capture of attention, as in Folk et al., 2002). Similarly, Hakim et al. (2020) found that the CDA for the to-be-remembered stimuli was interrupted by task-irrelevant interposed stimuli that were similar to the to-be-remembered stimuli. This effect was stronger whether the interposed stimuli were rare, consistent with prior research showing that involuntary attentional capture is greater for rare than for frequent stimuli (Geyer et al., 2008). Thus, the lack of CDA produced by task-irrelevant stimuli in the present study likely reflects the fact that the interposed stimuli were dissimilar to the to-be-remembered stimuli, thus avoiding contingent capture of attention.

To summarize, the most parsimonious explanation of the present results is that active maintenance in working memory is recruited even for very simple non-automatic processes that require central attention, such as performing stimulus-response mappings. The present results are also consistent with the hypothesis of a parallel memory system (e.g., activity-silent synaptic storage) that allows some information to be retained when central attention must be momentarily directed to other tasks.

References

Adam, K. C. S., Robison, M. K., & Vogel, E. K. (2018). Contralateral Delay Activity Tracks Fluctuations in Working Memory Performance. *Journal of Cognitive Neuroscience*, *30*(9), 1229–1240. https://doi.org/10.1162/jocn_a_01233

Baddeley, A. D., & Hitch, G. (1974). Working Memory. In *ReCALL* (pp. 47–89). https://doi.org/10.1037/0033-295X.102.2.211

Bae, G. Y., & Luck, S. J. (2019). What happens to an individual visual working memory representation when it is interrupted? *British Journal of Psychology*, *110*(2), 268–287. https://doi.org/10.1111/bjop.12339

Bayliss, D. M., Jarrold, C., Baddeley, A. D., & Gunn, D. M. (2005). The relationship between short-term memory and working memory: Complex span made simple? *Memory*, *13*(3–4), 414–421. https://doi.org/10.1080/09658210344000332

Becke, A., Müller, N., Vellage, A., Schoenfeld, M. A., & Hopf, J.-M. (2015). Neural sources of visual working memory maintenance in human parietal and ventral extrastriate visual cortex. *NeuroImage*, *110*, 78–86. https://doi.org/10.1016/j.neuroimage.2015.01.059

Bentin, S., Mouchetant-Rostaing, Y., Giard, M. H., Echallier, J. F., & Pernier, J. (1999). ERP Manifestations of Processing Printed Words at Different Psycholinguistic Levels: Time Course and Scalp Distribution. *Journal of Cognitive Neuroscience*, *11*(3), 235–260. https://doi.org/10.1162/089892999563373

Beukers, A. O., Buschman, T. J., Cohen, J. D., & Norman, K. A. (2021). Is Activity Silent Working Memory Simply Episodic Memory? *Trends in Cognitive Sciences*, *25*(4), 284–293. https://doi.org/10.1016/j.tics.2021.01.003

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436. https://doi.org/10.1163/156856897X00357

Bundesen, C. (1990). A theory of visual attention. *Psychological Review*, *97*, 523–547.

Carr, T. H. (1992). Automaticity and cognitive anatomy: Is word recognition "automatic"? *The American Journal of Psychology*, *105*(2), 201–237. https://doi.org/10.2307/1423028

Cocchini, G., Logie, R. H., Della Sala, S., MacPherson, S. E., & Baddeley, A. D. (2002). Concurrent performance of two memory tasks: Evidence for domain-specific working memory systems. *Memory and Cognition*, *30*(7), 1086–1095. https://doi.org/10.3758/BF03194326

Cowan, N. (2011). The focus of attention as observed in visual working memory tasks: Making sense of competing claims. *Neuropsychologia*, *49*(6), 1401–1406. https://doi.org/10.1016/j.neuropsychologia.2011.01.035

Cowan, N., Elliott, E. M., Scott Saults, J., Morey, C. C., Mattox, S., Hismjatullina, A., & Conway, A. R. A. (2005). On the capacity of attention: Its estimation and its role in working memory and cognitive aptitudes. *Cognitive Psychology*, *51*(1), 42–100. https://doi.org/10.1016/j.cogpsych.2004.12.001

Daneman, M., & Carpenter, P. A. (1980). Individual Differences in Working Memory and Reading. *Journal of Verbal Learning and Verbal Behavior; New York*, *19*(4), 450–466. https://doi.org/10.1016/s0022-5371(80)90312-6

Duncan, J. (1980). The locus of interference in the perception of simultaneous stimuli. *Psychological Review*, *87*, 272–300.

Egeth, H. E., & Yantis, S. (1997). VISUAL ATTENTION: Control, Representation, and Time Course. *Annual Review of Psychology*, *48*(1), 269–297. https://doi.org/10.1146/annurev.psych.48.1.269

Ester, E. F., Sprague, T. C., & Serences, J. T. (2015). Parietal and Frontal Cortex Encode Stimulus-Specific Mnemonic Representations during Visual Working Memory. *Neuron*, *87*(4), 893–905. https://doi.org/10.1016/j.neuron.2015.07.013

Fischer, R., Gottschalk, C., & Dreisbach, G. (2014). Context-sensitive adjustment of cognitive control in dual-task performance. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *40*(2), 399–416. https://doi.org/10.1037/a0034310

Folk, C. L., Leber, A. B., & Egeth, H. E. (2002). Made you blink! Contingent attentional capture produces a spatial blink. *Perception & Psychophysics*, *64*(5), 741–753. https://doi.org/10.3758/BF03194741

Folk, C. L., & Remington, R. W. (2015). Unexpected abrupt onsets can override a top-down set for color. *Journal of Experimental Psychology: Human Perception and Performance*, *41*(4), 1153–1165. https://doi.org/10.1037/xhp0000084

Fougnie, D., & Marois, R. (2006). Distinct Capacity Limits for Attention and Working Memory: Evidence From Attentive Tracking and Visual Working Memory Paradigms. *Psychological Science*, *17*(6), 526–534. https://doi.org/10.1111/j.1467-9280.2006.01739.x

Funahashi, S., & Bruce, C. J. (1989). Mnemonic coding of visual space in the monkey ' s dorsolateral prefrontal cortex. *Journal of Neurophysiology*, *61*(2), 331–349. https://doi.org/10.1016/j.neuron.2012.12.039

Gaspelin, N., Ruthruff, E., & Lien, M.-C. (2016). The problem of latent attentional capture: Easy visual search conceals capture by task-irrelevant abrupt onsets. *Journal of Experimental Psychology: Human Perception and Performance*, *42*(8), 1104–1120. https://doi.org/10.1037/xhp0000214

Geyer, T., Müller, H. J., & Krummenacher, J. (2008). Expectancies modulate attentional capture by salient color singletons. *Vision Research*, *48*(11), 1315–1326. https://doi.org/10.1016/j.visres.2008.02.006

Goldman-Rakic, P. S. (1995). Cellular basis of working memory. *Neuron*, *14*(3), 477–485. https://doi.org/10.1016/0896-6273(95)90304-6

Hakim, N., Adam, K. C. S., Gunseli, E., Awh, E., & Vogel, E. K. (2019). Dissecting the Neural Focus of Attention Reveals Distinct Processes for Spatial Attention and Object-Based Storage in Visual Working Memory. *Psychological Science*, *30*(4), 526–540. https://doi.org/10.1177/0956797619830384

Hakim, N., Feldmann-Wüstefeld, T., Awh, E., & Vogel, E. K. (2020). Perturbing Neural Representations of Working Memory with Task-irrelevant Interruption. *Journal of Cognitive Neuroscience*, *32*(3), 558–569. https://doi.org/10.1162/jocn_a_01481

Hakim, N., Feldmann-Wüstefeld, T., Awh, E., & Vogel, E. K. (2021). Controlling the Flow of Distracting Information in Working Memory. *Cerebral Cortex*, *31*(7), 3323–3337. https://doi.org/10.1093/cercor/bhab013

Halvorson, K. M., & Hazeltine, E. (2015). Do small dual-task costs reflect ideomotor compatibility or the absence of crosstalk? *Psychonomic Bulletin & Review*, *22*(5), 1403–1409. https://doi.org/10.3758/s13423-015-0813-8

Hollingworth, A., & Maxcey-Richard, A. M. (2012). Selective maintenance in visual working memory does not require sustained visual attention. *Journal of Experimental Psychology: Human Perception and Performance*, *39*(4), 1047. https://doi.org/10.1037/a0030238

Hudjetz, A., & Oberauer, K. (2007). The effects of processing time and processing rate on forgetting in working memory: Testing four models of the complex span paradigm. *Memory & Cognition*, *35*(7), 1675–1684. https://doi.org/10.3758/BF03193501

Hyun, J.-S., & Luck, S. J. (2007). Visual working memory as the substrate for mental rotation. *Psychonomic Bulletin & Review*, *14*(1), 154–158. https://doi.org/10.3758/BF03194043

Johnston, J. C., McCann, R. S., & Remington, R. W. (1995). Chronometric Evidence for two Types of Attention. *Psychological Science*, *6*(6), 365–369. https://doi.org/10.1111/j.1467-9280.1995.tb00527.x

Jonides, J., & Yantis, S. (1988). Uniqueness of abrupt visual onset in capturing attention. *Perception & Psychophysics*, *43*(4), 346–354. https://doi.org/10.3758/BF03208805

Kappenman, E. S., & Luck, S. J. (2012). ERP components: The ups and downs of brainwave recordings. In S. J. Luck & E. S. Kappenman (Eds.), *The Oxford Handbook of ERP Components* (pp. 3–30). Oxford University Press.

Lee, J., & Han, S. W. (2020). Visual search proceeds concurrently during the attentional blink and response selection bottleneck. *Attention, Perception, & Psychophysics*, *82*(6), 2893–2908. https://doi.org/10.3758/s13414-020-02047-6

Leonard, C. J., Kaiser, S. T., Robinson, B. M., Kappenman, E. S., Hahn, B., Gold, J. M., & Luck, S. J. (2013). Toward the neural mechanisms of reduced working memory capacity in schizophrenia. *Cerebral Cortex*, *23*(7), 1582–1592. https://doi.org/10.1093/cercor/bhs148

Lewis-Peacock, J. A., Drysdale, A. T., Oberauer, K., & Postle, B. R. (2012). Neural evidence for a distinction between short-term memory and the focus of attention. *Journal of Cognitive Neuroscience*, *24*(1), 61–79. https://doi.org/10.1162/jocn_a_00140

Lien, M.-C., & Proctor, R. W. (2002). Stimulus-response compatibility and psychological refractory period effects: Implications for response selection. *Psychonomic Bulletin & Review*, *9*(2), 212–238. https://doi.org/10.3758/BF03196277

Lien, M.-C., Ruthruff, E., Cornett, L., Goodin, Z., & Allen, P. A. (2008). On the nonautomaticity of visual word processing: Electrophysiological evidence that word processing requires central attention. *Journal of Experimental Psychology: Human Perception and Performance*, *34*(3), 751–773. https://doi.org/10.1037/0096-1523.34.3.751

Lins, O. G., Picton, T. W., Berg, P., & Scherg, M. (1993). Ocular artifacts in EEG and event-related potentials I: Scalp topography. *Brain Topography*, *6*(1), 51–63. https://doi.org/10.1007/BF01234127

Lopez-Calderon, J., & Luck, S. J. (2014). ERPLAB: An open-source toolbox for the analysis of event-related potentials. *Frontiers in Human Neuroscience*, *8*. https://doi.org/10.3389/fnhum.2014.00213

Luck, S. J. (2014). An Introduction to the Event-Related Potential Technique, second edition. In *The MIT Press*. https://doi.org/10.1118/1.4736938

Luck, S. J., & Gaspelin, N. (2017). How to get statistically significant effects in any ERP experiment (and why you shouldn't). *Psychophysiology*, *54*(1), 146–157. https://doi.org/10.1111/psyp.12639

Lundqvist, M., Rose, J., Herman, P., Brincat, S. L., Buschman, T. J., & Miller, E. K. (2016). Gamma and Beta Bursts Underlie Working Memory. *Neuron*, *90*(1), 152–164. https://doi.org/10.1016/j.neuron.2016.02.028

Luria, R., Balaban, H., Awh, E., & Vogel, E. K. (2016). The contralateral delay activity as a neural measure of visual working memory. *Neuroscience and Biobehavioral Reviews*, *62*, 100–108. https://doi.org/10.1016/j.neubiorev.2016.01.003

Major, G., & Tank, D. (2004). Persistent neural activity: Prevalence and mechanisms. *Current Opinion in Neurobiology*, *14*(6), 675–684. https://doi.org/10.1016/j.conb.2004.10.017

Miller, E. K., Erickson, C. A., & Desimone, R. (1996). Neural mechanisms of visual working memory in prefrontal cortex of the macaque. *Journal of Neuroscience*, *16*, 5154–5167.

Myers, N. E., Stokes, M. G., & Nobre, A. C. (2017). Prioritizing Information during Working Memory: Beyond Sustained Internal Attention. *Trends in Cognitive Sciences*, *21*(6), 449–461. https://doi.org/10.1016/j.tics.2017.03.010

Nee, D. E., & Jonides, J. (2013). Trisecting representational states in short-term memory. *Frontiers in Human Neuroscience*, *7*(November), 796. https://doi.org/10.3389/fnhum.2013.00796

O'Malley, S., Reynolds, M. G., Stolz, J. A., & Besner, D. (2008). Reading aloud: Spelling-sound translation uses central attention. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *34*(2), 422. https://doi.org/10.1037/0278-7393.34.2.422

Pailian, H., Störmer, V., & Alvarez, G. (2017). Neurophysiological Marker of Visual Working Memory Manipulation. *Journal of Vision*, *17*(10), 1116–1116. https://doi.org/10.1167/17.10.1116

Pashler, H. (1991). Do response modality effects support multiprocessor models of divided attention? *Journal of Experimental Psychology: Human Perception and Performance*, *16*(4), 826. https://doi.org/10.1037/0096-1523.16.4.826

Pashler, H. (1994). Dual-task interference in simple tasks: Data and theory. *Psychological Bulletin*, *116*(2), 220–244. https://doi.org/10.1037/0033-2909.116.2.220

Pashler, H., Carrier, M., & Hoffman, J. (1993). Saccadic eye movements and dual-task interference. *The Quarterly Journal of Experimental Psychology Section A*, *46*(1), 51–82. https://doi.org/10.1080/14640749308401067

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*(4), 437–442. https://doi.org/10.1163/156856897X00366

Perez, V. B., & Vogel, E. K. (2012). What ERPs Can Tell Us aboutWorking Memory. In *The Oxford Handbook of Event-Related Potential Components* (pp. 1–664). https://doi.org/10.1093/oxfordhb/9780195374148.001.0001

Pratt, H. (2011). Sensory ERP components. *The Oxford Handbook of Event-Related Potential Components*, 89–114. https://doi.org/10.1093/oxfordhb/9780195374148.013.0050

Reinhart, R. M. G., Heitz, R. P., Purcell, B. A., Weigand, P. K., Schall, J. D., & Woodman, G. F. (2012). Homologous Mechanisms of Visuospatial Working Memory Maintenance in Macaque and Human: Properties and Sources. *Journal of Neuroscience*, *32*(22), 7711–7722. https://doi.org/10.1523/JNEUROSCI.0215-12.2012

Robitaille, N., Grimault, S., & Jolicoeur, P. (2009). Bilateral parietal and contralateral responses during maintenance of unilaterally-encoded objects in visual short-term memory: Evidence from magnetoencephalography. *Psychophysiology*, *46*, 1090–1099.

Rose, N. S., LaRocque, J. J., Riggall, A. C., Gosseries, O., Starrett, M. J., Meyering, E. E., & Postle, B. R. (2016). Reactivation of latent working memories with transcranial magnetic stimulation. *Science*, *354*(6316), 1136–1139. https://doi.org/10.1126/science.aah7011

Rossion, B., Joyce, C. A., Cottrell, G. W., & Tarr, M. J. (2003). Early lateralization and orientation tuning for face, word, and object processing in the visual cortex. *NeuroImage*, *20*(3), 1609–1624. https://doi.org/10.1016/j.neuroimage.2003.07.010

Rouder, J. N., Speckman, P. L., Sun, D., Morey, R. D., & Iverson, G. (2009). Bayesian t tests for accepting and rejecting the null hypothesis. *Psychonomic Bulletin & Review*, *16*(2), 225–237. https://doi.org/10.3758/PBR.16.2.225

Saults, J. S., & Cowan, N. (2007). A central capacity limit to the simultaneous storage of visual and auditory arrays in working memory. *Journal of Experimental Psychology: General*, *136*(4), 663–684. https://doi.org/10.1037/0096-3445.136.4.663

Schaffer, W. O., & Berge, D. L. (1979). Automatic Semantic Processing of Unattended Words. *Journal of Verbal Learning and Verbal Behavior; New York*, *18*(4), 413–426. https://doi.org/10.1016/s0022-5371(79)90228-7

Schmidt, B. K., Vogel, E. K., Woodman, G. F., & Luck, S. J. (2002). Voluntary and automatic attentional control of visual working memory. *Perception & Psychophysics*, *64*(5), 754–763. https://doi.org/10.3758/BF03194742

Souza, A. S., & Oberauer, K. (2017). The contributions of visual and central attention to visual working memory. *Attention, Perception, & Psychophysics*, *79*(7), 1897–1916. https://doi.org/10.3758/s13414-017-1357-y

Stokes, M. G. (2015). “Activity-silent” working memory in prefrontal cortex: A dynamic coding framework. *Trends in Cognitive Sciences*, *19*(7), 394–405. https://doi.org/10.1016/j.tics.2015.05.004

Stokes, M. G., Kusunoki, M., Sigala, N., Nili, H., Gaffan, D., & Duncan, J. (2013). Dynamic coding for cognitive control in prefrontal cortex. *Neuron*, *78*(2), 364–375. https://doi.org/10.1016/j.neuron.2013.01.039

Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*, *18*(6), 643–662. https://doi.org/10.1037/h0054651

Taft, M., Castles, A., Davis, C., Lazendic, G., & Nguyen-Hoan, M. (2008). Automatic activation of orthography in spoken word recognition: Pseudohomograph priming. *Journal of Memory and Language*, *58*(2), 366–379. https://doi.org/10.1016/j.jml.2007.11.002

Turner, M. L., & Engle, R. W. (1989). Is working memory capacity task dependent? *Journal of Memory and Language*, *28*(2), 127–154. https://doi.org/10.1016/0749-596X(89)90040-5

Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature*, *428*(6984), 748–751. https://doi.org/10.1038/nature02447

Wang, X. J. (2001). Synaptic reverberation underlying mnemonic persistent activity. *Trends in Neurosciences*, *24*(8), 455–463. https://doi.org/10.1016/S0166-2236(00)01868-3

Wei, Z., Wang, X. J., & Wang, D. H. (2012). From distributed resources to limited slots in multiple-item working memory: A spiking network model with normalization. *Journal of Neuroscience*, *32*(33), 11228–11240. https://doi.org/10.1523/JNEUROSCI.0735-12.2012

Woloszyn, L., & Sheinberg, D. L. (2009). Neural Dynamics in Inferior Temporal Cortex during a Visual Working Memory Task. *Journal of Neuroscience*, *29*(17), 5494–5507. https://doi.org/10.1523/JNEUROSCI.5785-08.2009

Woodman, G. F., & Luck, S. J. (2003). Serial deployment of attention during visual search. *Journal of Experimental Psychology: Human Perception and Performance*, *29*(1), 121–138. https://doi.org/10.1037/0096-1523.29.1.121

Woodman, G. F., & Luck, S. J. (2004). Visual search is slowed when visuospatial working memory is occupied. *Psychonomic Bulletin & Review*, *11*(2), 269–274. https://doi.org/10.3758/BF03196569

Woodman, G. F., Vogel, E. K., & Luck, S. J. (2001). Visual Search Remains Efficient when Visual Working Memory is Full. *Psychological Science*, *12*(3), 219–224. https://doi.org/10.1111/1467-9280.00339

Yantis, S., & Jonides, J. (1984). Abrupt visual onsets and selective attention: Evidence from visual search. *Journal of Experimental Psychology. Human Perception and Performance*. https://doi.org/10.1037/0096-1523.10.5.601

Appendix- Lateralized sensory processing of interposed stimuli

Although our experiments were designed to examine disruption of the CDA by interposed stimuli, we also found an unexpected secondary phenomenon – an apparent difference in the sensory processing of the central interposed stimuli as a function of which side of the memory array was maintained in working memory. This can be seen in Figures 2 and 5, where there is a large sensory response to the interposed stimuli in the contralateral-minus-ipsilateral difference waves (relative to the to-be-remembered side) even though the interposed stimuli were presented at the fixation point. In other words, the lateralization of working memory storage appeared to produce a lateralization in the sensory processing of the foveal interposed stimuli.

To isolate the sensory response elicited by the interposed stimuli and subtract out the activity related to the working memory task, we constructed present-minus-absent difference waves by subtracting the activity evoked on trials without an interposed stimulus from that evoked on trials where an interposed stimulus was present (separately for each task, and separately at electrodes contralateral vs ipsilateral to the to-be-remembered side of the sample array). The resultant difference waves for both experiments are shown in Figure A1.

Because the interposed stimulus was always central, and its identity and location were independent from the location of the to-be-remembered side of the sample array, we did not expect the activity elicited by the interposed stimuli to be lateralized with respect to the to-be-remembered side of the sample array. However, differences emerged in the P1 and N1 elicited by the interposed stimuli across the two hemispheres. The specific pattern of the difference depended on the nature of the interposed stimuli. For orthographic stimuli (i.e., the letter strings used in Experiment 2 and the C and reversed-C used in the dual-task condition of Experiment 1), we observed a robust visual evoked response in both hemispheres, but with a larger P1 and N1 in the hemisphere ipsilateral to the to-be-remembered array. For the scrambled letters used in the single-task condition of Experiment 1, we observed a much less defined visual evoked response, with a positivity emerging in the ipsilateral hemisphere.

To investigate this further, we performed a post-hoc statistical analysis of this effect. Using a collapsed localizer approach (Luck & Gaspelin, 2017), we determined the time windows and electrodes where the P1 and N1 components were the clearest (collapsing across all conditions). We found that both P1 and N1 were most clear in posterior occipital electrodes, so we focused our statistical analysis in PO8/PO7. The measurement windows were then defined as a 40-ms window centered on the peak of each component: For Experiment 1, the resulting windows were 130-170 ms for the P1 and 180 to 220 ms for the N1; for Experiment 2, the windows were 78 ms to 118 ms for the P1 and 154 ms to 194 ms for the N1.

Sensory processing of coherent, orthographic stimuli

The most consistent effect emerged for the orthographic stimuli. These stimuli produced a distinct visual evoked response in both hemispheres, including a clear P1 and N1. The P1 and N1 appeared to be larger in the ipsilateral hemisphere compared to the contralateral hemisphere (relative to the visual field of the stimuli being maintained in working memory).

To examine this effect statistically, we measured P1 and N1 amplitude from the interposed-present-minus-interposed-absent difference wave at P07/P08, comparing the contralateral and the ipsilateral hemispheres during the time window that emerged from the collapsed localizer analysis. For the dual-task condition in Experiment 1, a paired *t* test revealed a significantly larger amplitude for the ipsilateral hemisphere than for the contralateral hemisphere in both the P1 latency range (t(31) = 2.41, p=0.022) and the N1 latency range (t(31)

$= 8.45$, $p < 0.001$). Results from the scrambled stimuli used in the single-task condition of Experiment 1 are analyzed in the next section.

For Experiment 2, a 2 (single-task vs dual-task) by 2 (contralateral vs ipsilateral hemisphere) ANOVA revealed that P1 amplitude was significantly larger in the ipsilateral hemisphere than the contralateral hemisphere, $F(31) = 7.70$, $p = 0.009$, but we found no main effect of task, $F(31) = 1.19$, $p = 0.284$, or interaction between task and hemisphere, $F(31) = 1.04$, $p = 0.316$. Similarly, N1 amplitude was significantly more negative in the ipsilateral hemisphere compared to the contralateral hemisphere, $F(31) = 87.1$, $p < 0.001$. We found no main effect of task on N1 amplitude, $F(31) = 2.13$, $p = 0.154$, but we did find an interaction between task and hemisphere, $F(31) = 12.6$, $p = 0.001$. Pairwise comparisons revealed that the difference in amplitude was numerically larger in the dual-task condition (1.48 μV) than in the single-task condition (0.78 μV), although both conditions showed a significant difference in amplitude($t(31) = 8.73$, $p < 0.001$ for the dual-task condition; $t(31) = 5.53$, $p<0.001$ for the single-task condition). Thus, in all three of these cases, the P1 and N1 were substantially generally larger in the ipsilateral hemisphere compared to the contralateral hemisphere.

Because these components are associated with early sensory processing (Pratt, 2011), this pattern suggests that despite the stimuli being centrally presented, sensory processing was greater in the hemisphere that was less involved in the working memory task than in the hemisphere that was primarily involved in working memory maintenance. This difference in processing was independent of the task during the P1 latency range, but it was larger in the dual-task condition than in the single-task condition during the N1 latency range.

Given the fact that the observed lateralization of sensory processing was tied to the location of the memoranda and not the side of the eliciting stimulus, this effect may reflect an interaction between active working memory and low-level visual processing. In other words, these results suggest that sensory processing was generally decreased in the hemisphere that was “busy” maintaining the working memory representation (contralateral to the to-be-remembered side), so most visual processing occurred in the opposite hemisphere (ipsilateral to the to-be-remembered side).

However, it is important to note that this is purely post-hoc speculation. Moreover, we cannot rule out the possibility that this effect is a consequence of small deviations of eye position toward to the to-be-remembered side. For example, a small leftward deviation of the eyes when the left side of the sample display was task-relevant would have caused the interposed stimuli to be presented slightly to the right of the actual point of fixation, leading to a larger sensory response in the left hemisphere (the hemisphere ipsilateral to the to-be-remembered side). Thus, we present these findings merely as an interesting observation that might be worth future exploration, and we do not draw any strong conclusions about the underlying processes.

Sensory processing of scrambled stimuli

Although we found a consistent sensory effect for the orthographic stimuli across conditions, the scrambled stimuli used in the single-task condition of Experiment 1 exhibited a very different evoked response and were thus analyzed separately.

The scrambled stimuli had the same overall brightness as the C and reversed-C used in the dual-task condition of Experiment 1, but the shapes were broken up into non-coherent lines so that they no longer form a distinct, letter-like shape (see Figure A1). When we examined the visual evoked response to these stimuli, we did not see distinct P1 and N1 waves. Instead, the evoked response consisted of a broad positivity across the first 300 ms. This could reflect a weak N170 response, which is typically larger for word-like stimuli (Rossion et al., 2003). As a result, any differences between contralateral and ipsilateral electrodes are difficult to link to specific ERP components.

When we analyzed the data from these stimuli using the same time windows that we used for the orthographic stimuli, we found that the evoked activity was significantly more positive for the ipsilateral electrodes than for the contralateral electrodes during the P1 time window, $t(31) = 2.98$, $p = 0.005$. No significant difference was found during the N1 time window, $t(31) = 0.13$, $p = 0.901$.

Figure Captions

Table 1: Post-hoc t-tests against 0, showing whether the mean CDA amplitude was significantly different than 0 μV across the different conditions.

Figure 1: The task design for experiment 1 (A) and experiment 2 (C). Note that the stimuli are not to scale, though they are representative of the range of stimuli used. (B) and (D) show the overall accuracy for the memory task in the various conditions. Error bars represent within subjects 95% confidence intervals.

Figure 2: Contralateral-minus-ipsilateral difference waves for Experiment 1, plotted separately for the dual-task condition (A) and the single-task condition (C). The purple and orange bars on the x-axis denote the timing of the memory array and interposed stimulus respectively. (D) shows the mean amplitude of the CDA across the time-window of interest (1100-1500 ms from stimulus onset), denoting significant differences between interposed present and interposed absent trials across the two tasks. (B) shows the difference waves separately for trials with task-relevant stimuli that required a motor response (Go trials), and those with task-relevant stimuli that did not require a response (No-Go trials).

Figure 3: Pseudoword-minus-Consonant string difference wave (A) for the single task condition, showing the automatic orthographic processing of task-irrelevant letter strings. The area shaded in green shows the time-window of interest. The mean amplitude during that time-window was found to be significantly lower than 0 μV. The orange bar denotes the timing of the

interposed stimulus. (B) shows the scalp distribution of activity during the significant time-windows.

Figure 4: Pseudoword-minus-Consonant string difference wave (A) for the dual-task condition, showing the task-relevant differentiation between pseudowords and consonant strings. The area shaded in green shows the time-window of interest. The orange bar denotes the timing of the task-relevant interposed stimulus. (B) shows the scalp distribution of the difference wave during the time-window of interest.

Figure 5: Contralateral-minus-ipsilateral difference waves for experiment 2, split between the dual task condition (A) and the single task condition (B). The purple and orange bars on the x-axis denote the timing of the memory array and interposed stimulus respectively. The green boxes denote the time-window when a significant difference between pseudowords and consonant strings was observed, as shown in figure 3. The light grey box denotes the time-window of interest that was used in experiment 1.

Figure 6: Contralateral-minus-ipsilateral mean amplitude for all conditions across the two time-windows of interest – the time-window when a significant difference between the task-irrelevant letter stimuli was observed (A), and the time-window of interest from experiment 1 (B). Error bars represent within-subjects 95% confidence intervals. Significant markers denote significant differences between interposed-present and interposed-absent trials.

Figure A1: Interposed-present-minus-interposed-absent difference waves, showing activity related to the sensory processing of the central interposed stimulus. This activity is further broken down by its relation to the location of the to-be-remembered memory array, with activity shown separately for electrodes that lie contralateral and ipsilateral to the to-be-remembered side of the memory array (collapsing across trials where the ipsilateral hemisphere was on the left and on the right). Note that the waveforms are time-locked to the onset of the interposed stimulus, and thus have a different timing than the CDA figures above. That is, the 0 ms point in this figure corresponds to the 550 ms point in the Figure 2 and Figure 5 in the main paper. The dark square under the electrode label shows examples of stimuli used in each condition.

Experiment 1

1100-1500 ms

	Interposed-Absent		Interposed-Present	
	Single-task	**Dual-task**	**Single-task**	**Dual-task**
t(31)	-6.34	-4.73	-4.59	2.48
p	<0.001	<0.001	<0.001	0.018

Experiment 2

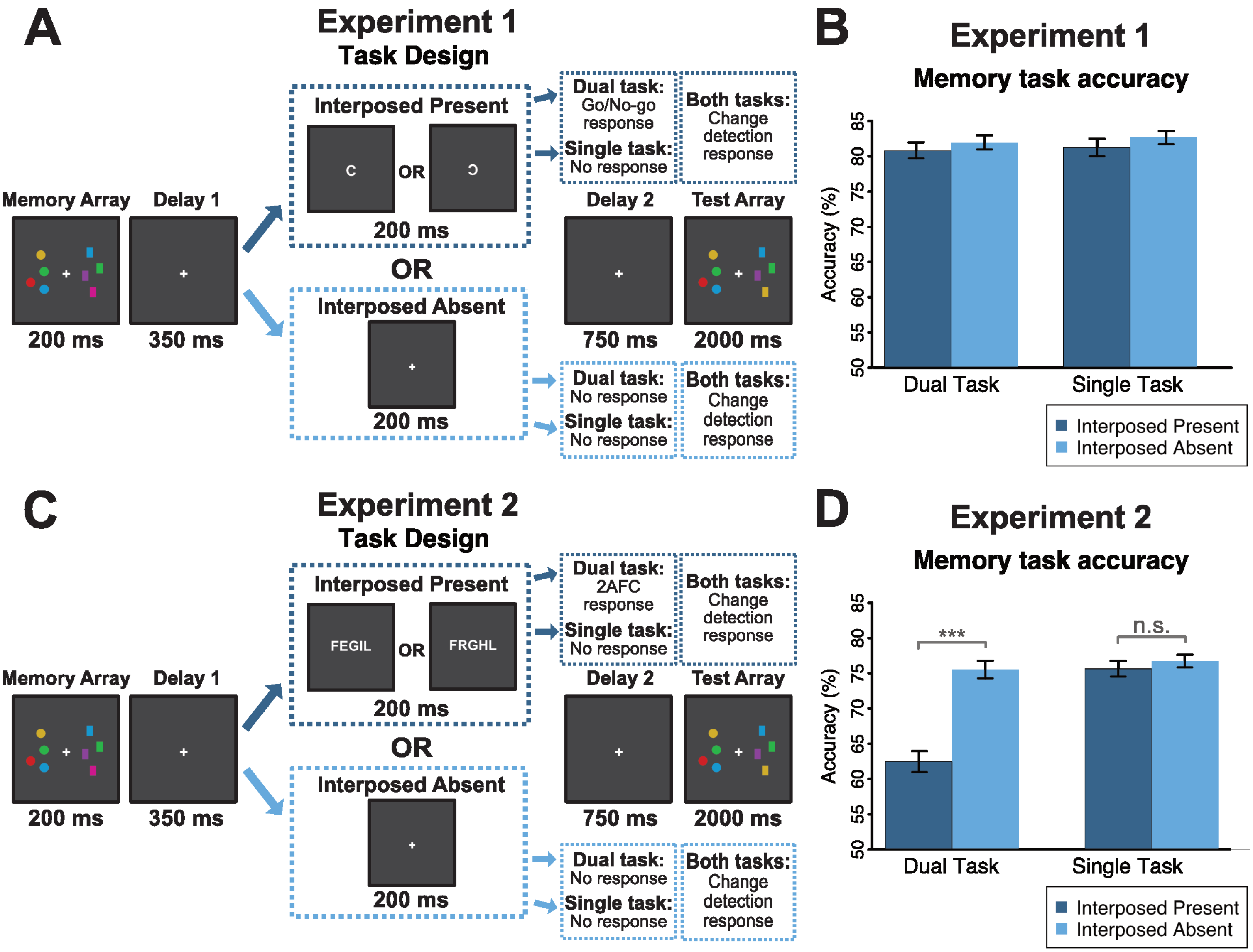
870-1000 ms

	Interposed-Absent		Interposed-Present	
	Single-task	**Dual-task**	**Single-task**	**Dual-task**
t(31)	-8.33	-9.46	-6.33	-1.24
p	<0.001	<0.001	<0.001	0.225

1100-1500 ms

	Interposed-Absent		Interposed-Present	
	Single-task	**Dual-task**	**Single-task**	**Dual-task**
t(31)	-5.28	-7.61	-2.23	3.95
p	<0.001	<0.001	0.033	<0.001

Table 1: Post-hoc t-tests against 0, showing whether the mean CDA amplitude was significantly different than 0 µV across the different conditions.



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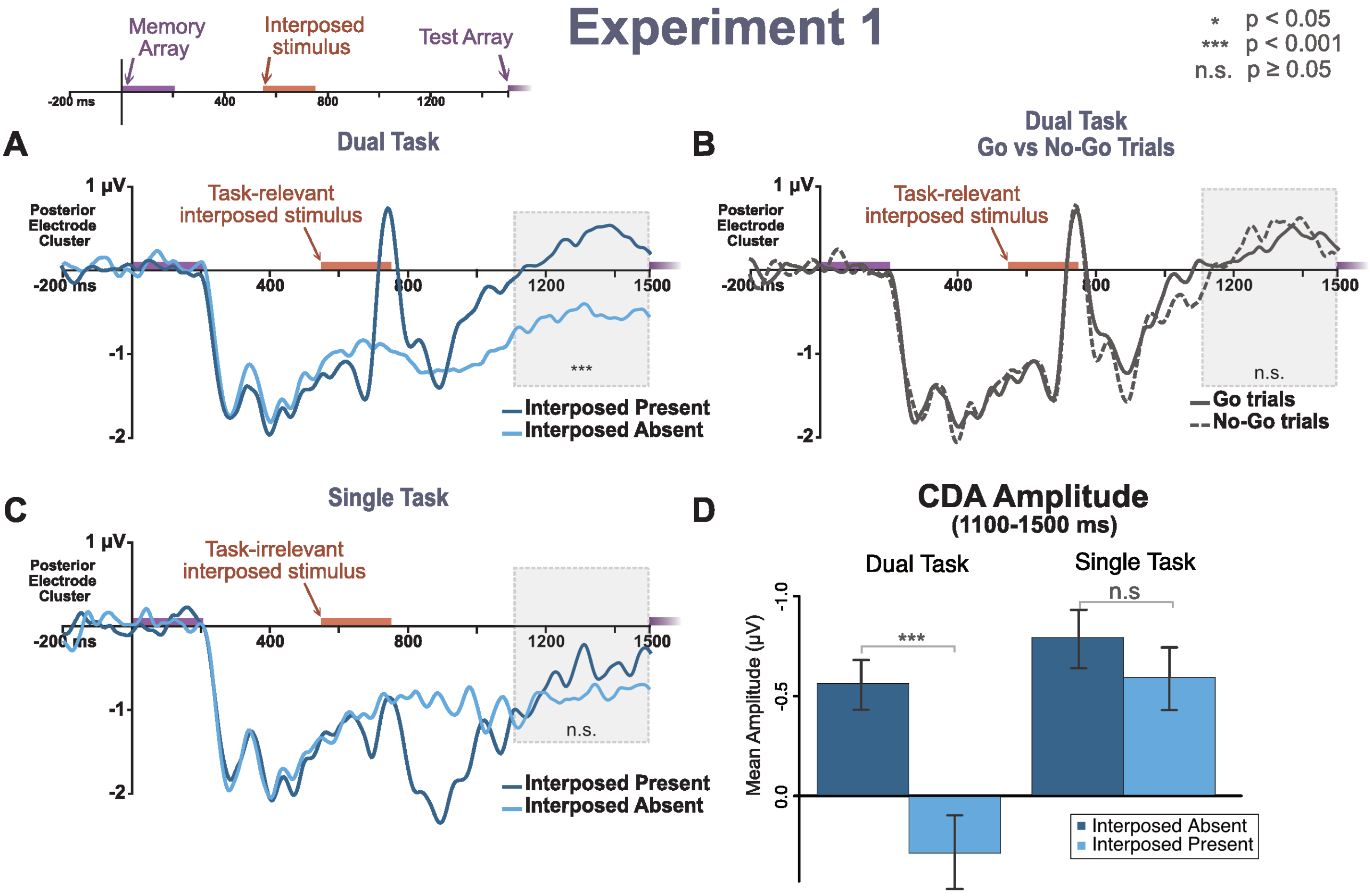
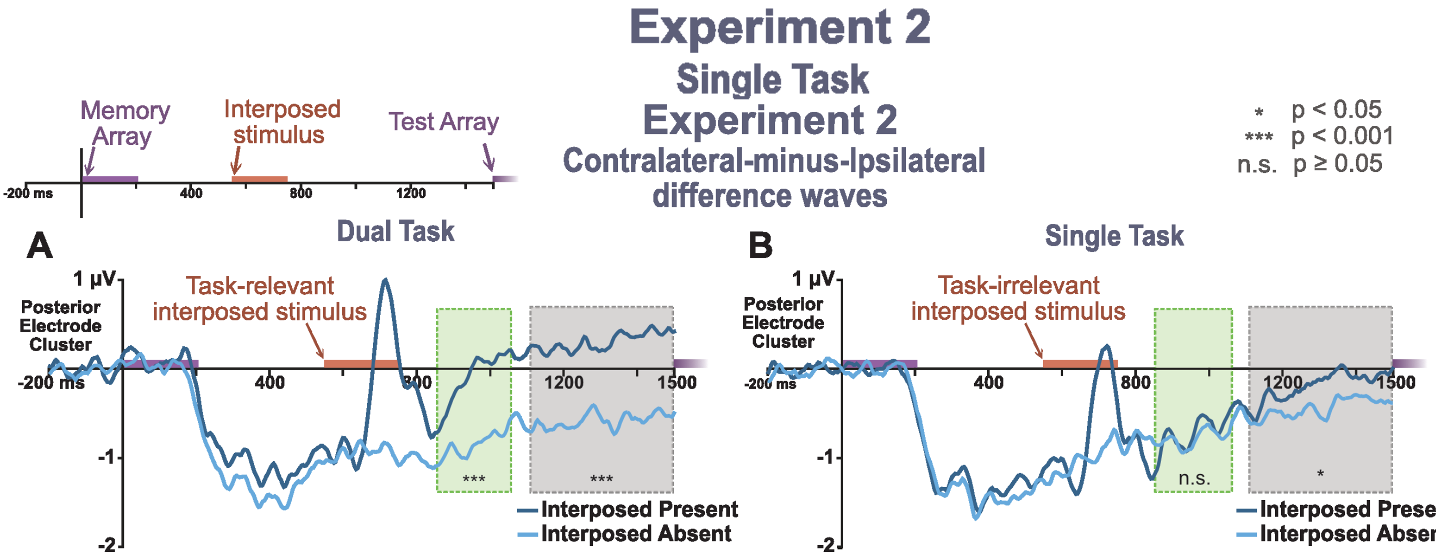


Figure 2: Contralateral-minus-ipsilateral difference waves for Experiment 1, plotted separately for the dual-task condition (A) and the single-task condition (C). The purple and orange bars on the x-axis denote the timing of the memory array and interposed stimulus respectively. (D) shows the mean amplitude of the CDA across the time-window of interest (1100-1500 ms from stimulus onset), denoting significant differences between interposed present and interposed absent trials across the two tasks. (B) shows the difference waves separately for trials with task-relevant stimuli that required a motor response (Go trials), and those with task-relevant stimuli that did not require a response (No-Go trials).



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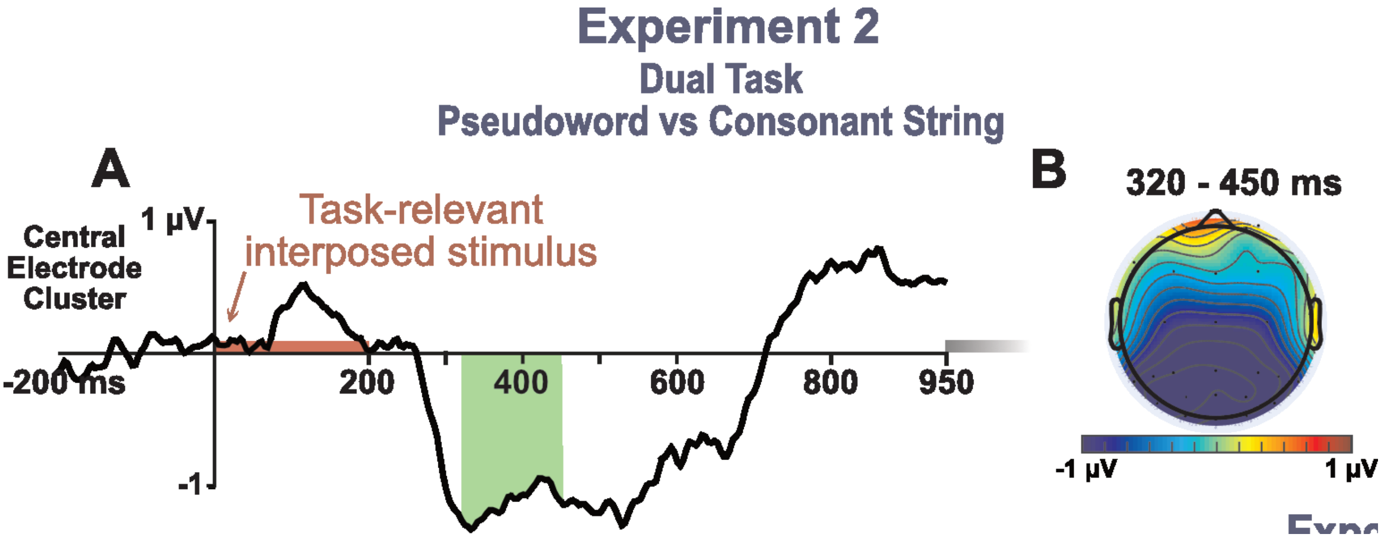

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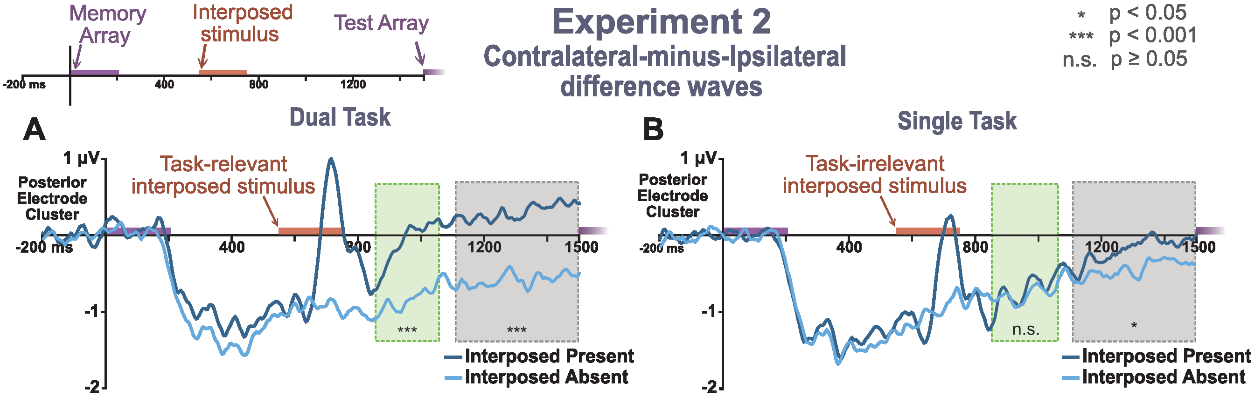
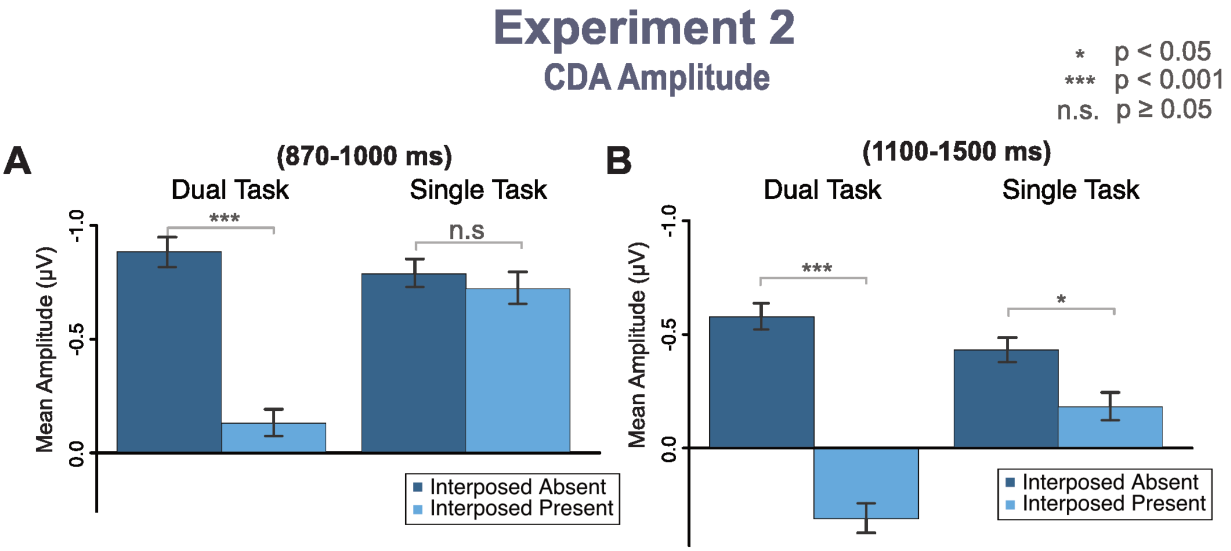


Figure 5: Contralateral-minus-ipsilateral difference waves for experiment 2, split between the dual task condition (A) and the single task condition (B). The purple and orange bars on the x-axis denote the timing of the memory array and interposed stimulus respectively. The green boxes denote the time-window when a significant difference between pseudowords and consonant strings was observed, as shown in figure 3. The light grey box denotes the time-window of interest that was used in experiment 1.



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Appendix- Lateralized sensory processing of interposed stimuli

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To isolate the sensory response elicited by the interposed stimuli and subtract out the activity related to the working memory task, we constructed present-minus-absent difference waves by subtracting the activity evoked on trials without an interposed stimulus from that evoked on trials where an interposed stimulus was present (separately for each task, and separately at electrodes contralateral vs ipsilateral to the to-be-remembered side of the sample array). The resultant difference waves for both experiments are shown in Figure A1.

Because the interposed stimulus was always central, and its identity and location were independent from the location of the to-be-remembered side of the sample array, we did not expect the activity elicited by the interposed stimuli to be lateralized with respect to the to-be-remembered side of the sample array. However, differences emerged in the P1 and N1 elicited by the interposed stimuli across the two hemispheres. The specific pattern of the difference depended on the nature of the interposed stimuli. For orthographic stimuli (i.e., the letter strings used in Experiment 2 and the C and reversed-C used in the dual-task condition of Experiment 1), we observed a robust visual evoked response in both hemispheres, but with a larger P1 and N1 in the hemisphere ipsilateral to the to-be-remembered array. For the scrambled letters used in the single-task condition of Experiment 1, we observed a much less defined visual evoked response, with a positivity emerging in the ipsilateral hemisphere.

To investigate this further, we performed a post-hoc statistical analysis of this effect. Using a collapsed localizer approach (Luck & Gaspelin, 2017), we determined the time windows and electrodes where the P1 and N1 components were the clearest (collapsing across all conditions). We found that both P1 and N1 were most clear in posterior occipital electrodes, so we focused our statistical analysis in PO8/PO7. The measurement windows were then defined as a 40-ms window centered on the peak of each component: For Experiment 1, the resulting windows were 130-170 ms for the P1 and 180 to 220 ms for the N1; for Experiment 2, the windows were 78 ms to 118 ms for the P1 and 154 ms to 194 ms for the N1.

Sensory processing of coherent, orthographic stimuli

The most consistent effect emerged for the orthographic stimuli. These stimuli produced a distinct visual evoked response in both hemispheres, including a clear P1 and N1. The P1 and N1 appeared to be larger in the ipsilateral hemisphere compared to the contralateral hemisphere (relative to the visual field of the stimuli being maintained in working memory).

To examine this effect statistically, we measured P1 and N1 amplitude from the interposed-present-minus-interposed-absent difference wave at P07/P08, comparing the contralateral and the ipsilateral hemispheres during the time window that emerged from the collapsed localizer analysis. For the dual-task condition in Experiment 1, a paired *t* test revealed a significantly larger amplitude for the ipsilateral hemisphere than for the contralateral hemisphere in both the P1 latency range (t(31) = 2.41, p=0.022) and the N1 latency range (t(31)

= 8.45, $p < 0.001$). Results from the scrambled stimuli used in the single-task condition of Experiment 1 are analyzed in the next section.

For Experiment 2, a 2 (single-task vs dual-task) by 2 (contralateral vs ipsilateral hemisphere) ANOVA revealed that P1 amplitude was significantly larger in the ipsilateral hemisphere than the contralateral hemisphere, F(31) = 7.70, p = 0.009, but we found no main effect of task, F(31) = 1.19, p = 0.284, or interaction between task and hemisphere, F(31) = 1.04, p = 0.316. Similarly, N1 amplitude was significantly more negative in the ipsilateral hemisphere compared to the contralateral hemisphere, F(31) = 87.1, $p < 0.001$. We found no main effect of task on N1 amplitude, F(31) = 2.13, p = 0.154, but we did find an interaction between task and hemisphere, F(31) = 12.6, p = 0.001. Pairwise comparisons revealed that the difference in amplitude was numerically larger in the dual-task condition (1.48 μV) than in the single-task condition (0.78 μV), although both conditions showed a significant difference in amplitude(t(31) = 8.73, $p < 0.001$ for the dual-task condition; t(31) = 5.53, $p<0.001$ for the single-task condition). Thus, in all three of these cases, the P1 and N1 were substantially generally larger in the ipsilateral hemisphere compared to the contralateral hemisphere.

Because these components are associated with early sensory processing (Pratt, 2011), this pattern suggests that despite the stimuli being centrally presented, sensory processing was greater in the hemisphere that was less involved in the working memory task than in the hemisphere that was primarily involved in working memory maintenance. This difference in processing was independent of the task during the P1 latency range, but it was larger in the dual-task condition than in the single-task condition during the N1 latency range.

Given the fact that the observed lateralization of sensory processing was tied to the location of the memoranda and not the side of the eliciting stimulus, this effect may reflect an interaction between active working memory and low-level visual processing. In other words, these results suggest that sensory processing was generally decreased in the hemisphere that was “busy” maintaining the working memory representation (contralateral to the to-be-remembered side), so most visual processing occurred in the opposite hemisphere (ipsilateral to the to-be-remembered side).

However, it is important to note that this is purely post-hoc speculation. Moreover, we cannot rule out the possibility that this effect is a consequence of small deviations of eye position toward to the to-be-remembered side. For example, a small leftward deviation of the eyes when the left side of the sample display was task-relevant would have caused the interposed stimuli to be presented slightly to the right of the actual point of fixation, leading to a larger sensory response in the left hemisphere (the hemisphere ipsilateral to the to-be-remembered side). Thus, we present these findings merely as an interesting observation that might be worth future exploration, and we do not draw any strong conclusions about the underlying processes.

Sensory processing of scrambled stimuli

Although we found a consistent sensory effect for the orthographic stimuli across conditions, the scrambled stimuli used in the single-task condition of Experiment 1 exhibited a very different evoked response and were thus analyzed separately.

The scrambled stimuli had the same overall brightness as the C and reversed-C used in the dual-task condition of Experiment 1, but the shapes were broken up into non-coherent lines so that they no longer form a distinct, letter-like shape (see Figure A1). When we examined the visual evoked response to these stimuli, we did not see distinct P1 and N1 waves. Instead, the evoked response consisted of a broad positivity across the first 300 ms. This could reflect a weak N170 response, which is typically larger for word-like stimuli (Rossion et al., 2003). As a result, any differences we between contralateral and ipsilateral electrodes are difficult to link to specific ERP components.

When we analyzed the data from these stimuli using the same time windows that we used for the orthographic stimuli, we found that the evoked activity was significantly more positive for the ipsilateral electrodes than for the contralateral electrodes during the P1 time window, t(31) = 2.98, p = 0.005. No significant difference was found during the N1 time window, t(31) = 0.13, p = 0.901.

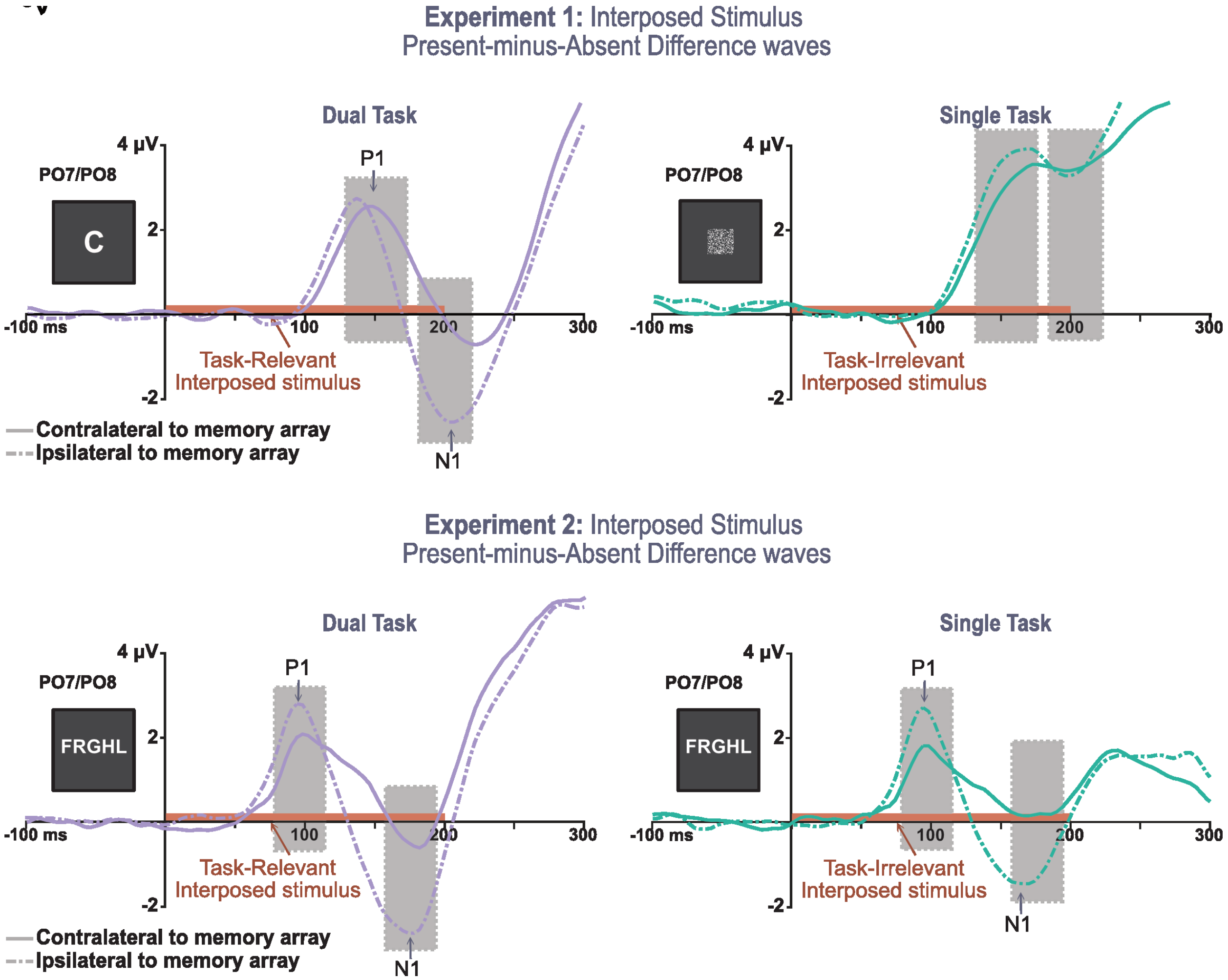

Figure A1: Interposed-present-minus-interposed-absent difference waves, showing activity related to the sensory processing of the central interposed stimulus. This activity is further broken down by its relation to the location of the to-be-remembered memory array, with activity shown separately for electrodes that lie contralateral and ipsilateral to the to-be-remembered side of the memory array (collapsing across trials where the ipsilateral hemisphere was on the left and on the right). Note that the waveforms are time-locked to the onset of the interposed stimulus, and thus have a different timing than the CDA figures above. That is, the 0 ms point in this figure corresponds to the 550 ms point in Figure 2 and Figure 5. The dark square under the electrode label shows examples of stimuli used in each condition.