Neural Dynamics of Cognitive Control over Working Memory Capture of Attention

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Abstract

The contents of working memory (WM) guide visual attention towards matching features, with visual search being faster when the target and a feature of an item held in WM spatially overlap (validly cued) than when they occur at different locations (invalidly cued). Recent behavioral studies have indicated that attentional capture by WM content can be modulated by cognitive control: when WM cues are reliably helpful to visual search (predictably valid), capture is enhanced, but when reliably detrimental (predictably invalid), capture is attenuated. The neural mechanisms underlying this effect are not well understood, however. Here we leveraged the high temporal resolution of event-related-potentials (ERPs) time-locked to the onset of the search display to determine how and at what processing stage cognitive control modulates the search process. We manipulated predictability by grouping trials into unpredictable (50% valid/invalid) and predictable (100% valid, 100% invalid) blocks. Behavioral results confirmed that predictability reduced WM-related capture. Comparison of ERPs to the search arrays showed that the N2pc, a posteriorly distributed signature of initial attentional orienting towards a lateralized target, was not impacted by target-validity predictability. However, a longer-latency, more anterior, lateralized effect – here termed the contralateral attention-related negativity (CARN) – was reduced under predictable conditions. This reduction interacted with validity, with substantially greater reduction for invalid than valid trials. These data suggest cognitive control over attentional capture by WM content does not affect the initial attentional-orienting process, but can reduce the need to marshal later control mechanisms for processing relevant items in the visual world.

Introduction

We continually maintain internal thoughts while simultaneously attending to the external world around us. The biased-competition model of attention (Desimone & Duncan, 1995) posits that attending to internally maintained items – conceptualized as working memory

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(WM) – guides external attentional selection to similar or matching items. This occurs even when we are not currently searching for those items, as documented in experiments where participants are asked to hold an item in WM (maintain an internal thought) while completing an unrelated visual search task (attend to the external world) containing that item. In particular, when that item happens to appear in the same spatial location as a search target (a validly cued trials), visual search is speeded, but when it appears in the same location as a search distracter (invalidly cued trials), search is slowed, compared to the case when no WM-matching item appears in the search display (Olivers, Peters, Houtkamp, & Roelfsema, 2011; Soto, Hodsoll, Rotshtein, & Humphreys, 2008).

This attentional capture by WM content was originally thought to be obligatory (Olivers, Meijer, & Theeuwes, 2006; Soto, Heinke, Humphreys, & Blanco, 2005; Soto, Humphreys, & Heinke, 2006), which is supported by the fact that visual WM contents bias even rapidly generated saccades, within 150ms of target onset (Hollingworth, Matsukura, & Luck, 2013). More recent behavioral work, however, has shown that this effect can be modulated by the predictability of the spatial relationship between the visual search target and a WM-matching distractor in the search display. In particular, knowing that the WM item will reliably aid (predictably valid trials) versus reliably impair (predictably invalid trials) visual search results in enhanced search performance, suggesting cognitive control can strategically enhance or reduce the effects of WM-driven attentional capture (Kiyonaga, Egner, & Soto, 2012). The goal of the present study was to understand the nature and neural dynamics of this cognitive control process specifically whether control underlying this effect is accomplished through directly affecting the initial attentional orienting processes to a search target, or whether cognitive control might instead be recruited in service of continued attentional processing stages once a target is selected.

Previous literature has indicated that attention capture by items in WM is reflected in underlying neural markers of attention during visual search (Kumar, Soto, & Humphreys, 2009). In particular, the amplitude of the N2pc – a lateralized ERP marker of attention processes – has shown to be reduced when WM items appear in different locations than search targets, indicating that WM items may function as distractors during search, capturing attention. In addition, previous fMRI work has indicated that prior to onset of visual search, the posterior parietal cortex is more activated under high-predictability conditions, suggesting a possible role in proactive control processes (Soto, Greene, Kiyonaga, Rosenthal, & Egner, 2012). However, the precise manner by which control with respect to WM contents occurs during the subsequent attentional selection processes in a visual search task has not yet been addressed. In particular, it is not known whether predictability-derived cognitive control may influence the initial attentional orienting to relevant target stimuli versus the subsequent feature processing of those stimuli.

To resolve this question, we leveraged the high temporal resolution and stimulus-location sensitivity of the N2pc, a lateralized event-related potential (ERP) component that has been found to reflect attentional orienting processes to a relevant target stimulus (S. J. Luck & Hillyard, 1994). Specifically, the N2pc is characterized by a greater negative-polarity deflection in the ERP over posterior scalp electrodes contralateral, versus ipsilateral, to a target item in a search array, a hallmark effect elicited ~200–300ms after array onset.

Importantly, the onset of the N2pc has been interpreted as marking the onset of orienting to, or selection of, targets in a visual search task (Hickey, Di Lollo, & McDonald, 2009; Steven J. Luck & Kappenman, 2011). Additionally, increased difficulty in attentional selection due to competition from more distracters has been shown to result in greater N2pc amplitude, which has been taken to reflect an increased need for the reactive attentional processing of target features (Kiss, Van Velzen, & Eimer, 2008; S. J. Luck & Hillyard, 1994; Mazza, Turatto, & Caramazza, 2009). Accordingly, the N2pc has been shown to be sensitive to the effects of WM guidance on attentional selection (Kumar et al., 2009), varying as a function of the presence of WM-matching distractors during visual search.

We contrasted possible effects of validity-predictability on initial attentional selection, indexed by the "early" posterior N2pc, while also examining possible modulation of subsequent processing stages by analyzing later contralateral, attention-related ERP components. Our reasoning for this examination was driven by other studies of attentional allocation, specifically studies of cued spatial attentional orienting, where longer-latency and more anterior lateralized effects (e.g., central and frontal -central scalp locations) have also been associated with attentional control processes(Eimer, 1993; Nobre, Sebestyen, & Miniussi, 2000; Hopf & Mangun, 2000; Kiss et al., 2008; Seiss, Gherri, Eardley, & Eimer, 2007). Specifically, an increased anterior negativity occurring contralateral to a cued target location has been argued to reflect the engagement of control processes over attentional shifts prior to onset of a target (Hopf & Mangun, 2000; Kiss et al., 2008; Nobre et al., 2000), as well as during target processing itself (Eimer, Velzen, & Driver, 2002). Of most relevance to the present task protocol, is that an enhanced lateralized negativity in more anterior electrodes has been suggested to reflect increased attentional control resources directed to the processing of targets, temporally distinct from the N2pc onset-index of reactive initial orienting to targets (Hopf & Mangun, 2000; see also Eimer, 1996, 1994a, 1994b). This parallels findings from N2pc research, in which the N2pc has been decomposed in certain circumstance into a rapid, partially overlapping cascade of two components, one representing the allocation of attention to targets and the other the suppression of distractors (N_t and P_d, respectively; see Hickey et al., 2009).

Thus, here we investigated for possible effects of predictability on both the initial attentional orienting to the target, as reflected in the posterior N2pc, and on later, potentially more anterior, contralateral activity reflecting potential longer-latency control processes subsequent to the initial target selection. If higher predictability reduces WM-induced attentional capture by modulating control over the initial attentional orienting process, it would lead to an amplitude change or onset shift of the posterior contralateral activity reflected by the N2pc. That is, with higher predictability, there would be less need for control over the initial attentional orienting process toward the relevant target, and thus there would be a smaller N2pc difference between valid and invalid trials during search. By contrast, if control over WM-driven attentional capture was implemented over processing stages subsequent to the initial attentional orienting, such as over additional control processes from the superior frontal-parietal attentional control network, this may be reflected in a later contralateral effect during unpredictable versus predictable conditions. Further, we hypothesized that such a longer-latency effect invoked under more unpredictable

conditions would be manifested at more anterior sites than the classic posterior N2pc, due to contribution from the frontal-parietal attention control network under such conditions.

Materials and Methods

Participants.

Twenty-seven healthy subjects between the ages of 18 – 35 (11 males, 16 females) and with normal or corrected-to-normal visual acuity were recruited through the Duke University Psychology Subject Pool or the Duke Interdisciplinary Behavioral Research Center. One subject was excluded from analysis due to having chance-level behavioral responses. Informed consent was obtained from all subjects for their credited or paid participation in accordance with a protocol approved by the Duke University Medical Center Institutional Review Board. The study required approximately 90 minutes to complete, preceded by one hour of preparation.

Experimental Design and Statistical Analysis

Stimuli and procedure.—Our paradigm was modeled after Kiyonaga et al.'s behavioral study (Kiyonaga, Egner, & Soto, 2012; Figure 1). All instructions were given on-screen, prior to the start of the experimental session, and clarified by the experimenter as necessary. At the beginning of each trial, a color WM cue was presented for 250 ms, with the task to hold the color of this item in working memory. After an inter-stimulus interval (ISI) of 1500 ms (jittered between 1400ms and 1600ms), either a visual search task (75% of trials) or a WM probe was presented (25% of trials). These two trial-sequence types were randomly intermixed, such that participants needed to always maintain the color cue in WM, as they could not predict on any trial whether a search display or a WM probe would follow. The search array for the visual search trials – presented for 100ms – was composed of single line segments embedded in three different colored circles (Figure 1). Two of the lines were vertical while the third line – the search target – was tilted to either the left or right. Participants' task was to find the tilted target line and identify the direction of its tilt via a button response. Each target location and direction occurred in randomized order and equally often. The visual search task contained two different trial types - *valid* and *invalid*. In *valid* trials the tilted target line appeared inside an outlined circled of the WM-matching color, whereas in *invalid* trials the tilted line did not appear within a WM-matching color. The WM probe trials – presented for 1500ms (jittered between 1400ms and 1600ms) – required participants to indicate whether the presented color was identical or different to the color of the WM cue. In both tasks – visual search and WM probe – participants were given an average of 1000ms (jittered between 900ms and 1100ms) to respond. An inter-trial interval (ITI) averaging 500ms (jittered between 400ms and 600ms) separated each trial, and a white fixation point remained on the screen throughout the duration of the experiment.

Critically, there was a block-wise predictability manipulation of visual search validity in order to manipulate the engagement of cognitive control. Half of the experimental blocks were predictable, split evenly between blocks in which search trials were predictably 100% valid or predictability 100% invalid. The other 50% of blocks were unpredictable (i.e. visual search trials in those blocks were randomly mixed 50% valid and 50% invalid trials).

Participants were explicitly informed about this predictability manipulation before each block. After each block, participants were provided feedback on their WM probe and visual search accuracy.

The total experiment included 1024 trials spread across 16 blocks of 64 trials. Participants were given a short break following each block. Participants completed practice blocks (each lasting 64 trials) prior to the start of the experiment until they were able to perform both the visual search and WM probe tasks with 80% accuracy. Presentation of the stimuli was controlled using Presentation 16.1 software (Neurobehavioral Systems, Inc., Albany, CA). Participants responded using a Logitech gamepad held by both hands. In the visual search trials, participants used their two index fingers to indicate a left or right tilt of the target line by pressing either the left or right upper trigger buttons, respectively. In the WM probe trials, participants used their two middle fingers to press the left or right lower trigger buttons to indicate whether the probe color was the same or different as the WM cue, respectively.

Behavioral Data and Analysis.—Our hypothesis centered on performance in the visual search trials. To assess how the factors of predictability and validity affected behavior we employed a 2×2 [(Predictability: Predictable vs. Unpredictable) $\times$ (Validity: valid vs. invalid)] repeated-measures analysis of variance (rmANOVA) on response times (RTs). Before the RT analysis, trials with incorrect responses were excluded, as were trials with RTs shorter than 200ms or longer than 1500ms (Hommel, 1994).

We also analyzed WM probe performance using an rmANOVA on RTs with the three levels of block condition (unpredictable, predictable valid, predictable invalid) and used a separate rmANOVA with the same conditions on accuracy. As in the analysis of the visual search data, before the WM probe RT analysis, errors and trials with responses faster than 200ms or slower than 1500ms were excluded.

EEG Data Acquisition.—Participants were seated approximately 39 inches from a 24-inch presentation monitor in a dimly lit, electrically shielded room. Online EEG data were recorded from a 64-channel custom, extended-coverage cap (Woldorff et al., 2002) using active electrodes (actiCAP, Brain Products GmbH, Gilching, Germany), an online right-mastoid reference, a 500 Hz sampling rate, and a three-stage cascaded integrator-comb anti-aliasing filter with a corner frequency of 130 Hz (actiCHamp, Brain Vision LLC, Cary, NC, USA). To monitor for blinks and horizontal eye movements, we used one channel below the left eye for the vertical EOG (VEOG) and computed two HEOG electrodes (near the left and right outer canthi) to monitor for blinks and horizontal eye movements.

Offline, the EEG data were bandpass filtered between .05 and 30 Hz using a causal finite infinite response filter, downsampled to 250 Hz, and re-referenced to the algebraic average of the left and right mastoid electrodes. Excessively noisy channels were interpolated using a spherical spline interpolation (Perrin, Pernier, Bertrand, & Echallier, 1989). A copy of the EEG data filtered between 1 and 30 Hz were then submitted to an infomax independent component analysis (ICA), and the resulting weights transferred back to the original dataset. Ocular components of the ICA were identified via the consensus of independent visual inspection performed by two researchers, and then removed from the data. Data were then

epoched from ─200 to 1000ms relative to presentation of the visual search stimuli, and baseline-corrected based on the ─200 to 0ms pre-stimulus period.

Three additional data-cleaning procedures were also performed before time-locked averaging. First, to identify excess electrical noise, a 60ms wide window moving in increments of 20ms across the epoch, to detect peak-to-peak voltage differences exceeding 100μV across any channel (excluding the VEOG and computed HEOG channels) was used. If five or fewer electrodes exceeded this threshold, each of these electrodes were replaced using the spherical-spline interpolation approach for that trial. Otherwise, if more than 5 electrodes exceeded this threshold, the epoch was rejected. Data were then submitted to an algorithm to detect horizontal eye-movements. In particular, a moving window 200ms wide, moving in 10ms steps from ─50 to 300ms of the epoch, between voltages at the two VEOG channel, was used to detect and reject epochs with peak-to-peak voltage difference exceeding 12μV. Finally, data were also submitted to an algorithm to detect horizontal eye movements, using a moving window 400ms wide, moving in steps of 10ms from 200 to 800ms across the epoch (a time window picked to encompass the *a priori* defined time region of the N2pc) to detect and reject epochs with peak-to-peak voltage differences exceeding 16uV in the HEOG channels (corresponding to approximately 1 degrees of horizontal eye movement). In total, these artifact-detection procedures resulted in the exclusion of ~8% of trials (range: 0.1% to 35.7%).

Data were pre-processed and analyzed in MATLAB, using a combination of the EEGLAB (Delorme & Makeig, 2004) and ERPLAB (Lopez-Calderon & Luck, 2014) toolboxes. Before each analysis, the appropriate trials were selectively averaged together to create event-related potentials (ERPs) time-lock-averaged to the onset of the visual search stimuli as a function of the different conditions.

EEG Data Analysis.—The lateralized ERP activity associated with attentional stimulus selection and processing was computed as the difference between activity in electrodes contralateral to a target stimulus minus electrodes ipsilateral to the same target stimulus, with this subtraction yielding the *contra-ipsi* difference wave of the N2pc over posterior scalp (S. J. Luck & Hillyard, 1994). Midline electrodes are excluded from this analysis, as they are neither contralateral nor ipsilateral to a target, and these contrasts only used trials in which there was a lateralized target (i.e., trials in which the target was in the midline were excluded).

For each resulting difference-wave contrast, non-parametric cluster-corrected permutation tests were conducted across the time window of 0ms to 1000ms, across all electrodes, to determine clusters of significant differences. Explicitly, a difference score between the lateralized activity from each contrast condition (i.e. valid versus invalid) was computed for each subject. Following this, a null distribution was computed through a 10,000-permutation random subtraction of the conditions (i.e. randomly shuffling the subtraction order of contralateral and ipsilateral conditions). To determine significance, the true difference score of the lateralized activity between the conditions was compared using t-statistics to the null distribution at each time point to determine which time points the difference-wave signal

was above the 97.5th percentile or below the 2.5th percentile (i.e., differing at an alpha level of .05).

Significant time points were further temporally cluster corrected according to the procedure outlined in (Maris & Oostenveld, 2007) to correct for multiple comparisons. Clusters were defined as temporally adjacent t-statistics with alpha levels under 0.05. The sums of the test-statistics within each significant cluster were computed, and the cluster with the maximum sum was taken as the significant time-region. For the lateralized effects derived from the array-triggered lateralized attentional orienting, visual examination of the scalp topography, guided by previous findings of lateralized effects during cued orienting of attention (Eimer, 1993; Hopf & Mangun, 2000), led to the selection of the electrode site of maximal difference for statistical interpretation for posterior (i.e. N2pc) and anterior scalp locations that were observed to have clear lateralized effects. All statistical analysis were done in Matlab, using custom-curated code (available at https://osf.io/78hba/).

Results

Behavioral

Visual Search Performance—There was a significant main effect of validity on the visual search RT, with valid trials being faster than invalid trials (Figure 2; Table 1; Table 2), replicating the classic attentional capture due to WM content (Soto et al., 2005). Critically, there was also a significant main effect of predictability, such that search trials in the predictable blocks were characterized by faster target detection than trials in the unpredictable blocks (Table 1; Table 2), thus replicating the findings from the Kiyonaga et al. (2012) behavioral study. There was also a significant interaction effect between compatibility and predictability, such that the RT validity effect (invalid – valid trials) in the unpredictable blocks was larger (48ms) than for the predictable block (37ms), also consistent with Kiyonaga et al. (2012; Experiment 2). These effects demonstrate that our predictability manipulation was successful in modulating the effect of attentional capture by WM content. That is, predictability of the search validity conditions allowed participants to enhance the beneficial effects and reduce the detrimental effects of attentional capture by WM-matching items.

Working Memory Probe Performance—In regards to the WM probe performance, neither the RT nor the accuracy rmANOVAs showed an effect of block condition (unpredictable; predictable – valid; predictable – invalid; Table 3). This pattern of results for the WM probe trials mirrored the results of Experiment 1 in Kiyonaga et al., (2012), in which the percentage of WM probe trials (20%) was close to that in our task-design (25%).

Neural Processes (Event-Related Potentials)

Attentional Target Selection as a function of Validity—Orienting-related neural activity evoked during visual search differed significantly as a function of validity (Figure 3a). Examination of the scalp topography revealed that this lateralized difference, time-locked to presentation of the visual search stimuli, was maximal at the posterior electrode sites in our montage closest to standard 10–20 sites P3/P4, consistent with the N2pc

(posterior contralateral N2) effect. Significant amplitude differences between the N2pc for valid ($-1.520\mu V$) versus invalid ($-0.33\mu V$) trials occurred between 188 – 284ms (Figure 3a; $p_{corr} < .05$) and appeared to be driven by an earlier onset of the N2pc in valid trials as compared to invalid trials. This difference was also seen more broadly in surrounding electrodes (Figure 3b). In conjunction with the significant behavioral effect between valid and invalid trials, this finding suggests that attentional capture differed as a result of the biases exerted by WM content in valid vs. invalid trials. More specifically, on valid trials, attentional capture (and initial attentional orienting) was guided by WM to the spatial location of the search target, due to the spatial overlap between the target (i.e., the tilted line) and the WM-matching colored circle. This configuration on valid trials thus appeared to allow for an earlier engagement of attentional selection neural processes towards the relevant target relative to its engagement in invalid trials. In contrast, on invalid trials, the WM content biased attentional capture towards the spatial location of a distracter, thereby delaying the onset of attentional selection and orienting processes towards the target stimulus.

Attentional Target Selection as a function of Predictability—Differences during visual search as a function of the block-wise predictability manipulation occurred at a somewhat longer latency and at more anterior sites (over contralateral central scalp in particular) than the standard N2pc (Figure 4). In order to distinguish this more anterior effect from that of the traditional, posterior N2pc, we have termed this lateralized ERP activity as the contralateral attention-related negativity (CARN) component. This later, more anterior effect appears to overlap with some effects seen in the previous literature on cognitive control of attentional orienting processes in response to informational cues (Eimer, 1993; Eimer et al., 2002; Hopf & Mangun, 2000; Kiss et al., 2008; Nobre et al., 2000).

Examination of the scalp topography revealed that this CARN difference, time-locked to presentation of the visual search stimuli, was maximal at the electrode sites C3/C4 over central scalp. Here, we saw significant amplitude difference between the CARN for predictable blocks (100% valid, 100% invalid) vs. unpredictable blocks (50% valid/invalid) during the time window between 344 – 464ms (Figure 3a; $p_{corr} < .05$). During this time window, the average amplitude for the CARN in predictable blocks (─0.77μV) was significantly smaller than for the CARN in unpredictable blocks (─1.22μV) (Figure 4a). A similar difference was seen also in surrounding electrodes (Figure 4b).

These results indicate that attentional target processing was modulated by predictability, but that this modulation affects processes subsequent to the initial attentional orienting process itself. In particular, when the relationship between the WM-item and search target could be anticipated, strategic (and presumably proactive) control appeared to attenuate the need for post-stimulus, reactive target enhancement processes during the visual search.

Differential effects of Predictability as a function of Validity—We next examined the CARN for valid trials and invalid trials as a function of the block-wise predictability manipulation, time-locked to the visual-search stimulus presentation (Figure 5). For both valid and invalid trials, visual examination of the scalp topography revealed that this CARN difference was maximal at the electrode sites closest to C3/C4; however, we used the

surrounding significant electrodes of the previous predictability contrast as a spatial ROI, averaging over three electrodes on each side: C3/C4, CP1/CP2, and CP5/CP6. This allowed our exploratory analysis to be consistent with our earlier described results from the main effect of predictability on visual search, as well as by prior work on attentional control during cued spatial orienting (Eimer, 1993; Hopf & Mangun, 2000; Kiss et al., 2008; Nobre et al., 2000).

These analyses revealed an interaction effect, showing that there was a greater difference between the predictable-unpredictable contrast for invalid trials ($-0.58\mu V$) as compared to valid trials ($-0.03\mu V$), occurring between 368 – 380ms (Figure 5c; $p_{corr} < .05$). In follow-up analyses to this interaction, the significant amplitude difference in the CARN for valid trials occurred in predictable ($-0.35\mu V$) versus unpredictable ($-0.78\mu V$) blocks at a latency after the maximal amplitude of the lateralized CARN wave, between 396 – 432ms (Figure 5a; $p_{corr} < .05$). Importantly, there was a significant difference in the CARN for invalid trials occurring in predictable ($-0.88\mu V$) versus unpredictable ($-1.35\mu V$) blocks in a latency window that encompassed the maximal amplitude of the lateralized CARN effect, between 328 – 424ms (Figure 5b; $p_{corr} < .05$). This indicates that the CARN maximal amplitude effect between predictable and unpredictable conditions was mainly driven by invalid trials (cf. Figure 4). This suggests that when trials are predictably invalid, cognitive control mechanisms reduce the attentional capture exerted by the contents of WM, which in turn modulates attentional selection processes when orienting to targets by reducing the need to reactively increase processing of the target item.

Discussion

In this study we aimed to investigate the mechanisms by which cognitive control modulates the influence of WM content on attentional selection and processing during visual search. To accomplish this, we focused our investigation on the effects of predictability and WM memory content on the contralateral attention-related activity elicited by a search-array target. In particular, we examined contralateral activity that included the N2pc ERP component, a posterior contralateral component reflecting the initial attentional orienting toward the relevant target item. Additionally, we also examined a later and more anterior contralateral effect, termed CARN here, which we postulate may reflect the recruitment of subsequent attentional control processes or sustained target enhancement activity following the initial orienting process (cf. Kiss et al., 2008; Hopf & Mangun, 2000).

More specifically, we modeled our paradigm after the behavioral study by Kiyonaga, et al. (2012), manipulating in a block-wise fashion the predictability of the spatial relationship – either predictable or unpredictable – between the target of the visual search task and the occurrence of a WM-matching distractor. Replicating prior behavioral results, we found that knowing whether WM cues would be reliably beneficial or reliably detrimental to visual search allowed participants to strategically enhance (in reliably valid conditions) or attenuate (in reliably invalid conditions) the capture effect. In investigating the underlying neural processes, we sought to distinguish between two possible mechanisms by which the implementation of control could lead to a reduction of WM-capture during attentional selection. (1) If predictability-based control over WM content were implemented over the

initial attentional orienting toward the target item, then we would expect to see a change in the posterior N2pc component, either in its amplitude on onset, during visual search as a function of predictability. However, (2) if the predictability-driven control over WM content were implemented over cognitive-control or target-enhancement processes after the initial attentional orienting, we would expect to see a change in the amplitude of the longer-latency CARN component as a function of predictability, with increased predictability leading to a decrease in the need to recruit less of such processing resources after the initial attentional orienting. Our results provide robust evidence for the latter, showing a reduced CARN effect in predictable blocks, compared to unpredictable blocks, with this effect being largely driven by invalid visual-search trials.

In addition to the key effect on the CARN, we also observed a difference in the onset of the N2pc as a function of validity, but no such change in amplitude or time-course for the posterior N2pc as a function of predictability. This effect was due to a delay of the N2pc onset, such that for a valid trial the N2pc towards the target occurred earlier than for an invalid trial (Figure 3). These electrophysiological results parallel the behavioral results (Figure 2), and previous behavioral findings (Kiyonaga et al., 2012) that demonstrated response times for invalid trials are slower than for valid trials. Importantly, this demonstrates that the contents of WM modulate attention during the initial stages of orienting, replicating conclusions drawn from prior WM-attention EEG studies (Kumar et al., 2009) and eye-tracking data (Hollingworth et al., 2013). Moreover, visual inspection of these data revealed a small positive deflection in the invalid trials (Figure 3), suggesting some partial attentional orienting the wrong direction (i.e., towards the WM-matching distractor) just prior to the onset of the N2pc contralateral to the target. This clarifies the cascade of attentional selection processes that occur in invalid trials in the absence of control – where attention is first captured by the WM-matching distractor (on the incorrect side) before the instantiation of the goal-directed attention-orienting towards the correct target.

As noted above, subsequent to the N2pc effect, we observed the longer-latency, more anterior, lateralized effect here, namely the CARN effect, in unpredictable versus predictable blocks (Figure 4). This difference was also reflected in our behavioral results (Figure 2), where predictable trials were faster than unpredictable trials, replicating prior behavioral findings (Kiyonaga et al., 2012). The reduction of the CARN amplitude for visual search trials in predictable blocks indicates reduced longer-latency processing during attentional selection of the target, likely as a product of the implementation of predictability-derived control processes over the item in WM prior to the onset of the visual search array. Furthermore, we examined this main effect of predictability as a function of trial type validity, and demonstrated that the decrease in the amplitude for predictable versus unpredictable trials was driven primarily by invalid trials (Figure 5), with little effect seen for valid trials. This closely paralleled our behavioral results, which showed a substantial behavioral improvement for invalid trials as a function of predictability, but none for valid trials (Figure 2).

Interestingly, the ERP differences between predictable versus unpredictable blocks were mainly seen over somewhat more anterior scalp locations than canonical N2pc effects (Figure 3; Figure 4; Figure 5). This speaks to the nature of the reduction we see later control

processing indexed by CARN amplitude, as this spatial distribution could reflect contributions from superior frontal-parietal attentional control regions. Alternatively, this longer-latency lateralized attention effect could reflect a cognitive control modulation directed at sustained target feature processing, which has been previously reported to occur in more anterior sites, such as those we found here characterized by the CARN (Kiss et al., 2008; Velzen & Eimer, 2003). Regardless, when faced with increased competition for attention by the WM-matching distractor (i.e. during unpredictable blocks) the engagement of the CARN component suggests an increased contribution from frontal (or fronto-parietal) regions. Conversely, when there is a predictable relationship between targets and WM-matching distractors, the overall distribution of activity demonstrates a more typical posterior topographic distribution, characteristic of the N2pc, suggesting less need to engage frontal or fronto-parietal control processes.

The relative lack of modulation in the maximal amplitude of the CARN for valid trials as a function of predictability could be due to the adaptive role WM-guidance plays in valid trials. Guidance by WM representations (see P. E. Downing, 2000; Hollingworth & Luck, 2009; Kumar et al., 2009; Olivers et al., 2006; Soto et al., 2005, 2006) is behaviorally advantageous for valid trials. That is, there is presumably no need to control the influence of the WM item in predictably valid blocks. This would suggest that there is a consistent engagement of cognitive control, potentially in service of continued feature enhancement processes post-orienting, during attentional selection in valid trials, regardless of the block-wise predictability manipulation. Conversely, on invalid trials, the influence of WM content on attentional selection is maladaptive to target selection during visual search, as the WM-matching item on such trials effectively acts as a distractor. Prior work has shown that, as the number of distractors in visual search tasks decreases, the need for engagement of feature enhancement processes to select a target – indexed by the N2pc – also decreases (Mazza et al., 2009). We see similar results in the current study, in that as the distractor influence decreased, the cognitive control activity reflected by the CARN also decreased. Therefore, the reduction in CARN amplitude for predictable versus unpredictable invalid trials in the current data likely reflects a reduction in the need for reactive engagement of cognitive control processes in order to maintain sustained enhancement of the processing of the target features. This adds to the argument that proactive control mechanisms were serving to attenuate the influence a WM item exerts prior to visual search, as a function of the predictability manipulation.

Together, this set of findings provides evidence that event-type predictability enables control over the influence of WM content, thereby reducing the need for increased control for ensuring continued target processing during the visual search task. The alternative possibility, in which the predictability manipulation between WM-matching distractors and targets in the visual search task would lead to a modulation of early target orienting processes, would have been expected to lead to a difference in the onset or amplitude of the initial posterior N2pc between predictable versus unpredictable trials, which was not observed here.

A caveat to the present interpretation is that the degree of generalizability of these results to the wide range of visual search tasks used within the literature is presently unknown.

Diverse visual search tasks have produced mixed findings as to the degree items in WM capture attention (Downing & Dodds, 2004; Houtkamp & Roelfsema, 2006; Peters, Roelfsema, & Goebel, 2012). Accordingly, the degree and manner in which control may modulate the influence of WM content on search may also vary as a function of the specific protocol. Thus, determining the precise boundary conditions for imposing control over WM-based capture of attention remain a question for future research. In addition, the current paradigm was not specifically designed to test potential mechanisms for the suppression of WM content, such as might be reflected by the P_d wave; the ERP marker of distractor suppression during visual search (Hickey et al., 2009). Our present design was sub-optimal in this regard largely due to the way in which a P_d wave is calculated, namely as the difference between the contralateral and ipsilateral neural response relative to a laterally presented distractor with a centrally presented target (Hickey et al., 2009). Given that our design utilized three potential target and distractor locations, with distractor presentation equally probable for each location, an analysis of a P_d wave would exclude at least two thirds of the current data. In an exploratory analysis, we nevertheless tested for this component, but only observed a small, insignificant P_d wave and no sign of a modulation by cognitive control factors. These inconclusive findings likely stem from the low trial count and high noise for this contrast in the current paradigm. However, future work investigating whether the suppression of WM content is differentially impacted by cognitive control in a design optimized for this type of analysis could be interesting to pursue.

In sum, prior work has shown behaviorally that the contents of WM guide visual attention towards matching features, speeding reaction times during visual search for valid versus invalid trials, and that cognitive control can modulate this attentional capture by the contents of WM. The nature of the underlying control mechanisms, however, has remained unknown. Using the N2pc and CARN as markers of attentional orienting to targets, and cognitive control directed towards continued feature enhancement of targets during attentional selection, respectively, we showed that the onset of the N2pc differed between valid and invalid trials, but did not differ as a function of predictability. However, the longer-latency, more anterior CARN activity was reduced under predictable conditions. Furthermore, this effect interacted with validity, such that the CARN reduction for invalid trials between predictable and unpredictable conditions was significantly greater than for valid trials. Together, these results suggest that predictability-driven control can be invoked to attenuate the need for reactive target enhancement processes during attentional capture by WM items in visual search.

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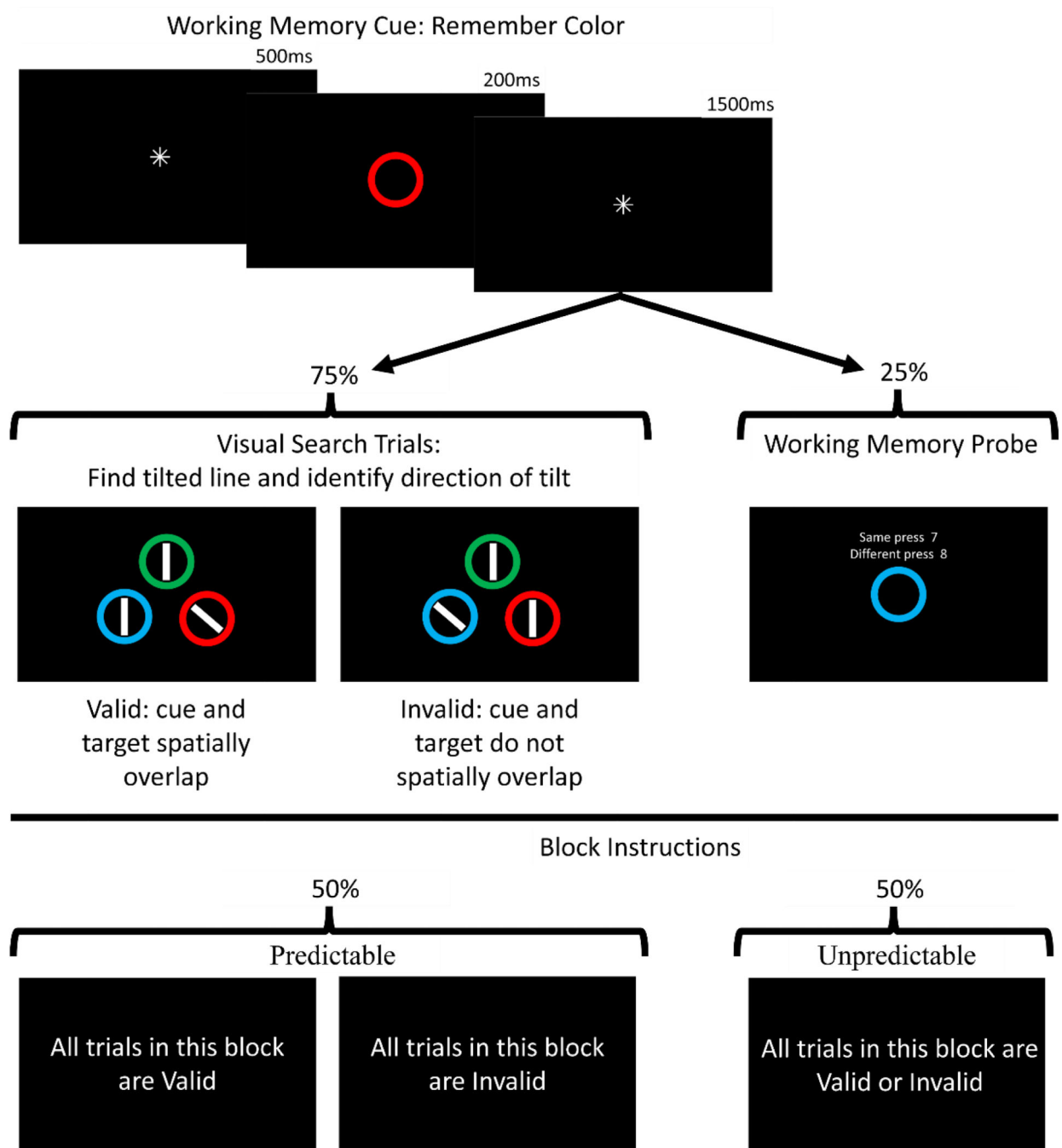
Figure 1.
Example trial sequence. Participants were asked to remember a colored circle, which was followed by a delay period. They were then either presented with a visual search trial (75% of the time) or a working memory probe trial (25% of the time). In the visual search trials, participants had to locate a slanted line and then indicate the direction of tilt. In the working memory probe trials, participants were given a recognition test (i.e. 'same' vs. 'different') for the original colored circle cue. Additionally, at the beginning of every block, participants

received instructions on whether the trials in the block were entirely valid (i.e. predictable), entirely invalid (i.e. predictable), or were both invalid and valid (i.e. unpredictable).
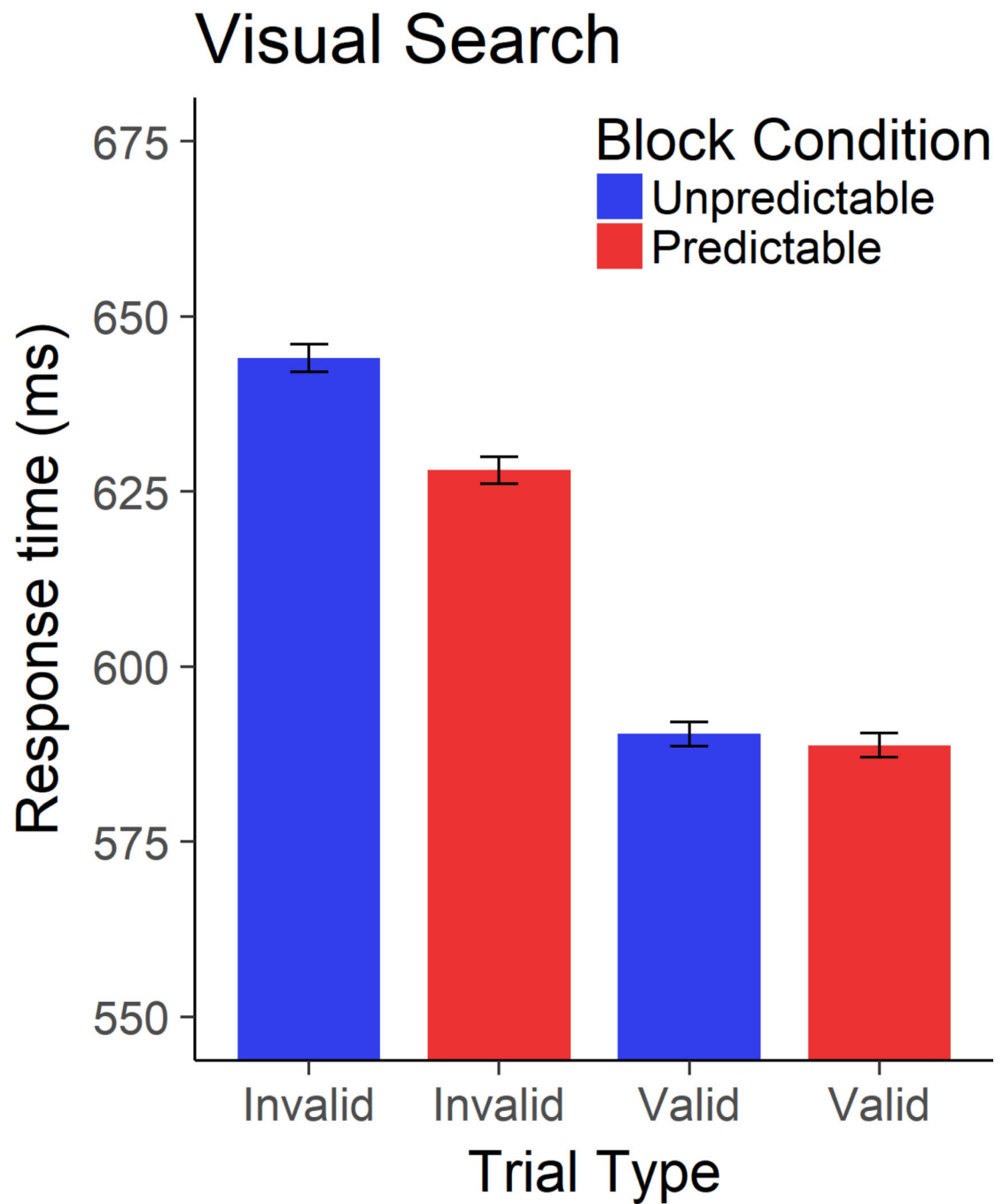
Figure 2.
Behavioral results for the visual search trials. Mean response times (ms ± standard error) for visual search trials are plotted as a function of the validity and block conditions.
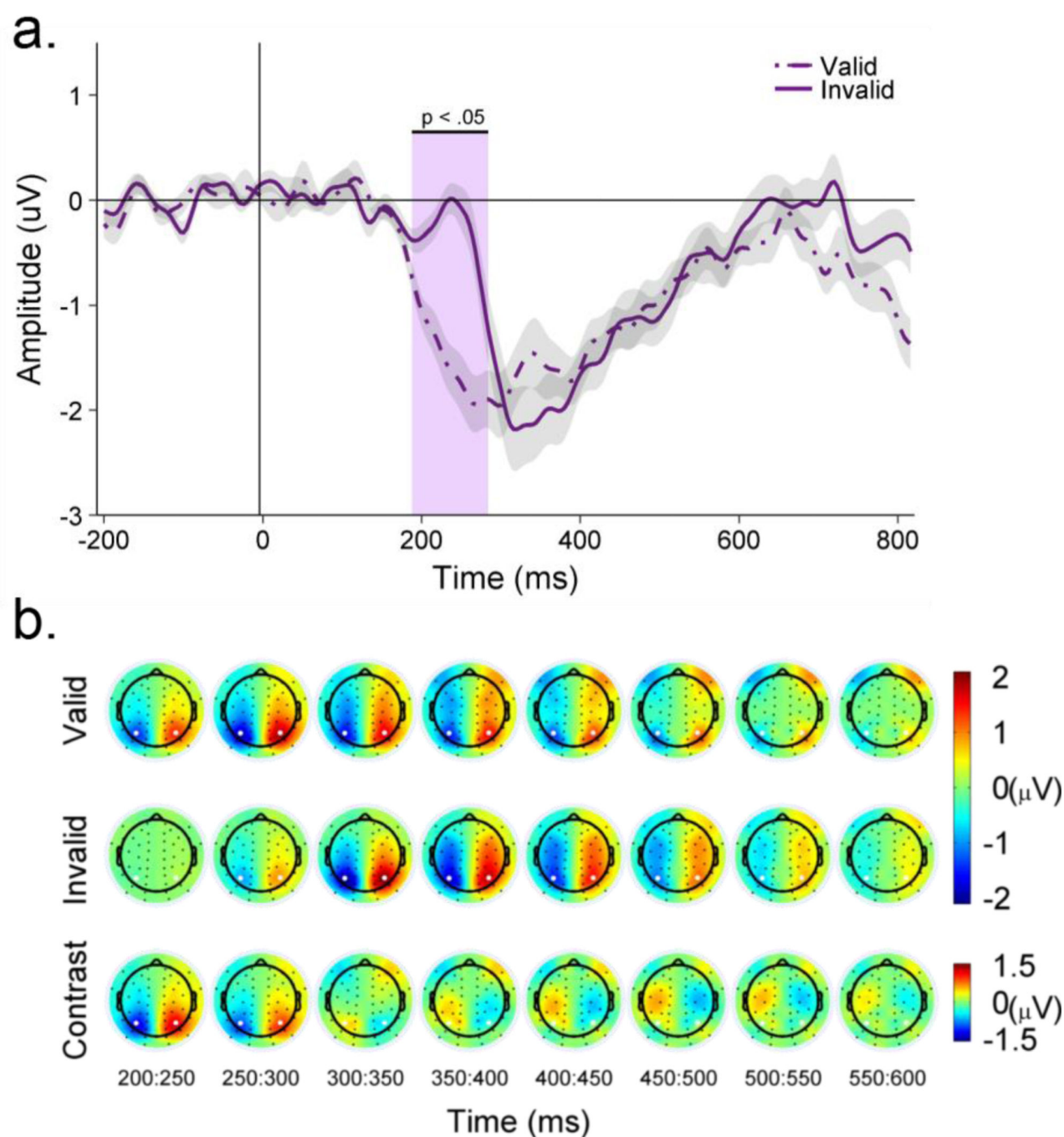
Figure 3.
The N2pc as a function of validity, irrespective of the predictability block in which the trial occurred. (a) The N2pc difference ERPs to the target (contralateral to the target – ipsilateral to the target) for valid and invalid visual search trials (electrode 55/56 or P3/P4). The vertical purple shaded area indicates the region of significant amplitude difference between N2pc ERPs for the time-window 188 – 284ms (p < .05) based on cluster corrected permutation testing. Shaded area around each N2pc difference ERP is the across subjects standard error. (b) Scalp topographies illustrating the valid N2pc difference, invalid N2pc

difference, and the contrast between them (invalid minus valid). The white electrodes indicate channel locations plotted above. Midline electrode locations are not visualized as they are computationally zero for lateralized ERP components.
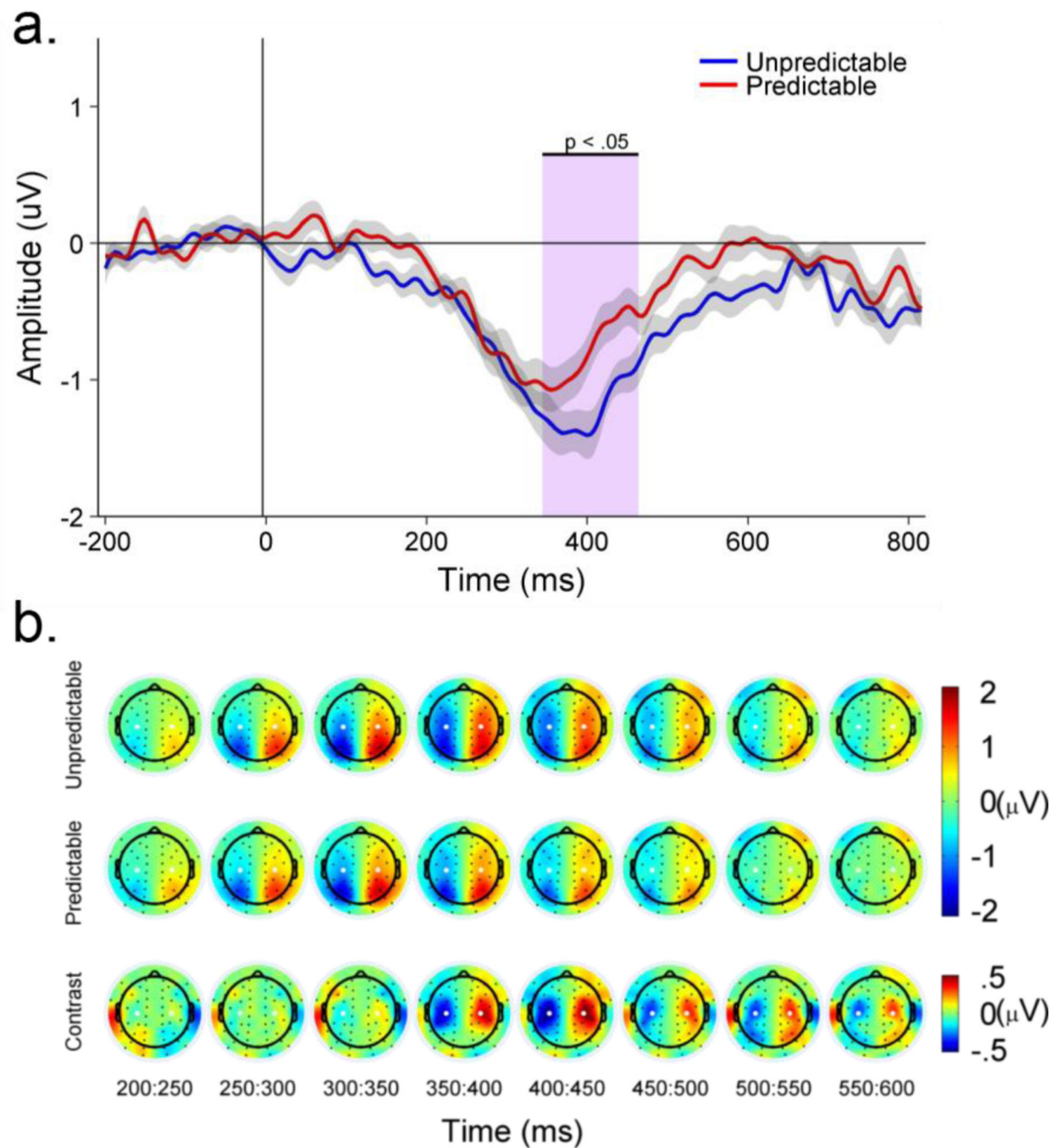
Figure 4.
The CARN as a function of predictability, irrespective of the validity of the trial. (a) The CARN difference ERPs to the target (contralateral to the target – ipsilateral to the target) for unpredictable and predictable blocks (electrode 59/60 or C3/C4). The vertical purple shaded area indicates the region of significant amplitude difference between CARN ERPs for the time-window 344 – 464ms (p < .05) based on cluster corrected permutation testing. Shaded area around each CARN difference ERP is the across subjects standard error. (b) Scalp topographies illustrating the unpredictable CARN difference, predictable CARN difference,

and the contrast them (unpredictable minus predictable). The white electrodes indicate channel locations plotted above. Midline electrode locations are not visualized as they are computationally zero for lateralized ERP components.
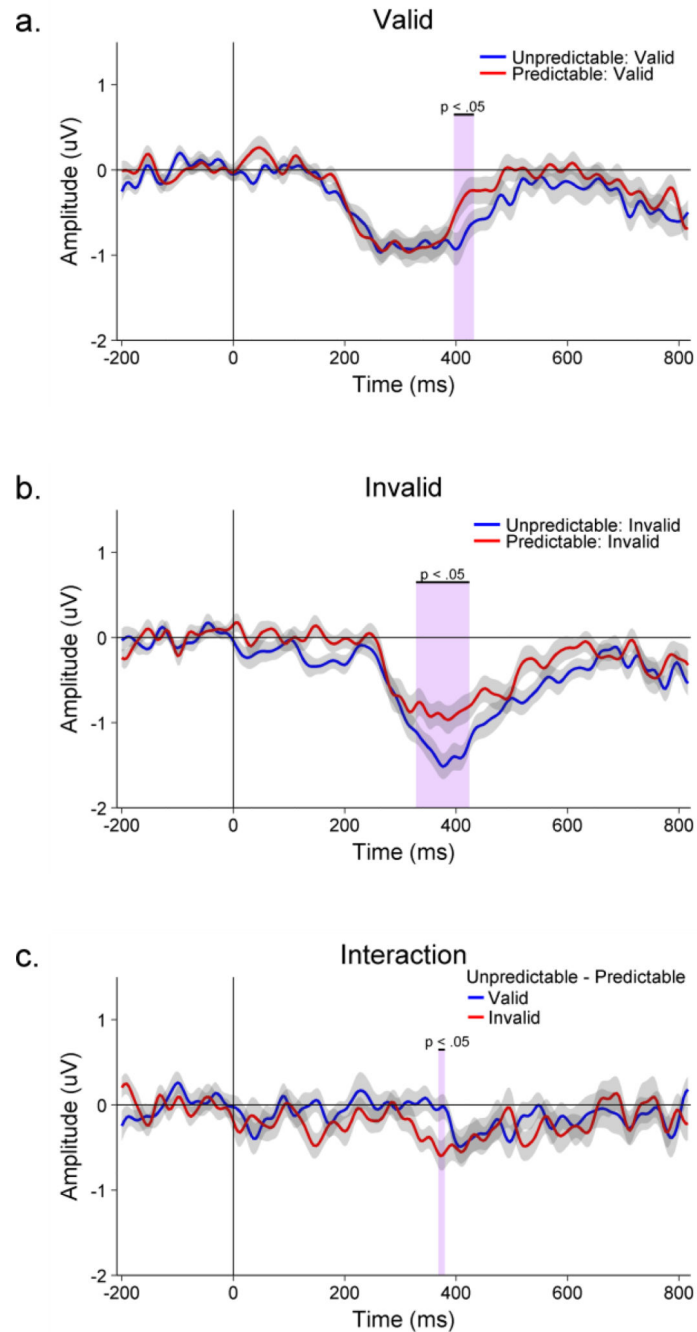
Figure 5.
The lateralized, CARN difference ERPs to the target (average of electrodes 59/60, 63/64, and 49/50 or C3/C4, CP1/CP2, and CP5/CP6) for (a) valid trials and (b) invalid trials occurring in unpredictable vs. predictable blocks (contralateral to the target – ipsilateral to the target), and (c) the interaction between valid vs. invalid lateralized contrasts (unpredictable – predictable). The vertical purple shaded area indicates the region of significant amplitude difference for the ERPs between 396 – 432ms (valid; $p < .05$), 328 –

424ms (invalid; p < .05), and 368 – 380ms (interaction; p < .05), based on cluster corrected permutation testing.

Table 1.

Visual Search Trials:

Mean and Standard Deviation for Response times (ms) by Validity and Predictability

	Validity	
Predictability	**Invalid**	**Valid**
Unpredictable	633 (121)	585 (113)
Predictable	620 (120)	583 (111)

Table 2.

Visual Search Trials:

Results from 2 (Predictability: Predictable vs. Unpredictable) × 2 (Validity: valid vs. invalid) Repeated Measures Analysis of Variance on response times in milliseconds

	F	*df*	*p*	η_p^2
Predictability	11.49	1, 26	.002	.298
Validity	94.62	1, 26	<.001	.778
Validity x Predictability	15.02	1, 26	<.001	.357

Table 3.

Working Memory Probe Trials:

Mean and Standard Deviation for Response times (ms) and Accuracy (% error) by block condition

Block Condition	Response times (ms)	Accuracy (% error)
Unpredictable	723 (123)	7.68 (26.62)
Predictably Valid	722 (118)	7.09 (25.68)
Predictably Invalid	721 (120)	8.43 (27.79)