# Neural Signatures of Competition between Voluntary and Involuntary Influences over the Focus of Attention in Visual Working Memory

**Yun Ding**[1], **Bradley R. Postle**[1], **and Freek van Ede**[2]

## Abstract

■ Adaptive behavior relies on the selection and prioritization of relevant sensory inputs from the external environment as well as from among internal sensory representations held in working memory. Recent behavioral evidence suggests that the classic distinction between voluntary (goal-driven) and involuntary (stimulus-driven) influences over attentional allocation also applies to the selection of internal representations held in working memory. In the current EEG study, we set out to investigate the neural dynamics associated with the competition between voluntary and involuntary control over the focus of attention in visual working memory. We show that when voluntary and involuntary factors compete for the internal focus of attention, prioritization of the appropriate item is delayed—as reflected both in delayed gaze biases that track internal selection and in delayed neural beta (15–25 Hz) dynamics that track the planning for the upcoming memory-guided manual action. We further show how this competition is paralleled—possibly resolved—by an increase in frontal midline theta (4–8 Hz) activity that, moreover, predicts the speed of ensuing memory-guided behavior. Finally, because theta increased following retrocues that effectively reduced working-memory load, our data unveil how frontal theta activity during internal attentional focusing tracks demands on cognitive control over and above working-memory load. Together, these data yield new insight into the neural dynamics that govern the focus of attention in visual working memory, and disentangle the contributions of frontal midline theta activity to the processes of control versus retention in working memory. ■

## INTRODUCTION

Working memory refers to the ability to maintain and manipulate relevant information for the guidance of perception, thought, and action (D'Esposito & Postle, 2015; Baddeley, 1992). Previous studies suggest that working memory and attention interact to guide ensuing memory-guided behavior (Ding, Paffen, Naber, & Van der Stigchel, 2019; Woodman, Carlisle, & Reinhart, 2013; Theeuwes, Belopolsky, & Olivers, 2009; Olivers, Meijer, & Theeuwes, 2006; for reviews, see van Ede & Nobre, 2023; Olivers, Peters, Houtkamp, & Roelfsema, 2011). For example, one influential line of work has demonstrated that information held in working memory can capture attention in a manner similar to the involuntary capture of attention by distracting visual stimuli (Bahle, Beck, & Hollingworth, 2018; Olivers et al., 2006; Soto, Heinke, Humphreys, & Blanco, 2005; for a review, see Soto, Hodsoll, Rotshtein, & Humphreys, 2008). A complementary line of research has focused on the role of attention in selecting and prioritizing the contents of mind themselves (Griffin & Nobre, 2003; see van Ede & Nobre, 2023; Souza & Oberauer, 2016, for reviews). In a recent study, van Ede, Board, and Nobre (2020) used eye-tracking to demonstrate that the selection and prioritization of one from among multiple items in visual working memory can be driven not only by voluntary but also involuntary factors (paralleling the classic distinction between voluntary and involuntary influences over externally directed selective attention, cf. Posner, 2016; Dalvit & Eimer, 2011; Corbetta & Shulman, 2002; Yantis & Jonides, 1990). In the present study, we replicated the procedures of van Ede and colleagues (2020) while additionally recording the EEG. This enabled us to assess the dynamic neural bases of voluntary and involuntary influences over the focus of attention inside visual working memory—as well as of the neural processes involved in ensuring appropriate attentional allocation when voluntary and involuntary influence compete for the internal focus of attention.

In the study that motivated this one (van Ede et al., 2020), participants encoded the orientation of two bars, one presented on each side of fixation and each in a different color. During the working-memory delay, the central fixation cross flashed briefly in one of the two colors serving as a retrocue (van Ede & Nobre, 2023; Souza & Oberauer, 2016; Griffin & Nobre, 2003). During "procue" blocks, this retrocue color indicated (with 100% validity) the item that would be tested, whereas during "anticue" blocks it indicated (with 100% validity) that the other item

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would be tested. In "null-cue" blocks, as a control condition, the retrocue did not predict which item would be tested (50% validity). Thus, both the pro- and anti-retrocues were informative, allowing for internal selection of one of the two items, and a concomitant decrease of working-memory load. Null-retrocues, in contrast, were non-informative and did not change working-memory load. Results from critical anticue blocks showed a delayed gaze bias—as an index of internal attentional allocation (Liu, Nobre, & van Ede, 2022; van Ede, Chekroud, & Nobre, 2019)—toward the cued (but color-incongruent) item, suggesting that an initial involuntary shift of attention (toward the color-congruent item) was overcome by a later-developing voluntary deployment to the contextually appropriate memory item.

In the present experiment, we took this task to EEG to address several open questions regarding the neural dynamics supporting selective attentional prioritization of working-memory content in the presence of both voluntary and involuntary factors. As a sanity check, we first inspected early visually ERPs time-locked to the retrocue to confirm that informative retrocues are processed differently than uninformative retrocues. Next, we investigated spectral dynamics in central motor electrodes to assess the time course of motor preparatory activity that has been reported to occur alongside visual retention in working-memory tasks (Nasrawi, Boettcher, & van Ede, 2023; Nasrawi & van Ede, 2022; Rösner, Sabo, Klatt, Wascher, & Schneider, 2022; Boettcher, Gresch, Nobre, & van Ede, 2021; van Ede, Chekroud, Stokes, & Nobre, 2019; Schneider, Barth, & Wascher, 2017) and that some hold to be a fundamental contributor to visual working memory (e.g., Postle & Hamidi, 2007; Postle, 2006; Postle, Idzikowski, Della Sala, Logie, & Baddeley, 2006). Such motor preparation signals are expected to follow, and hence index, the time course of item prioritization within working memory. Like what was previously observed for gaze, we hypothesized that such motor preparation signals would also be delayed following anti- compared with pro-retrocues, consistent with first needing to overcome the competition between involuntary and voluntary factors following anti-, but not pro-retrocues. Finally, of particular interest was oscillatory power in the theta-band (approximately 4–8 Hz) at frontal midline electrodes ("frontal-midline theta," hereafter FMT), which has been linked to two aspects of working memory that we could isolate in this study: cognitive control and working memory load.

With regard to control, FMT is known to covary with demands on control (e.g., Cavanagh & Frank, 2014; Hsieh & Ranganath, 2014), such as with the requirement to reorganize the contents of working memory into a canonical order (Griesmayr, Gruber, Klimesch, & Sauseng, 2010). Raghavachari and colleagues (2001) observed that the power of FMT increases at the beginning of a working memory trial, is sustained at an elevated level through the retention period, and then falls off precipitously at the end of the trial, a pattern interpreted as evidence for a role in "cognitive gating." In addition, however, FMT has also been seen to covary with working-memory load, consistent with a role in representation/retention per se. For example, Gevins, Smith, McEvoy, and Yu (1997) observed that FMT power was parametrically modulated by the number of items held in working memory (replicated by, e.g.: van Ede, Jensen, & Maris, 2017; Zakrzewska & Brzezicka, 2014; Meltzer et al., 2008; Jensen & Tesche, 2002). Consistently, brain stimulation (via transcranial magnetic stimulation or transcranial alternating-current stimulation) delivered in theta range to frontal midline cortex has been shown to improve working-memory performance (Riddle, Scimeca, Cellier, Dhanani, & D'Esposito, 2020; Reinhart & Nguyen, 2019; Zakrzewska & Brzezicka, 2014). Although these two functions—control and retention—need not be mutually exclusive, in our design, they can be dissociated: whereas anti-retrocue trials require control of the conflict between involuntarily and voluntarily triggered attention (relative to pro-retrocue trials), null-retrocue trials require the retention of more items (relative to pro- and anti-retrocue trials). Thus, our experiment enabled us to disentangle the involvement of FMT in these theoretically distinct functions.

## METHODS

The experimental procedures were reviewed and approved by the ethics committee of the Faculty of Behavioral and Movement sciences Vrije Universiteit Amsterdam.

### Participants

Twenty-seven participants (ranged 20–30 years; all right-handed) were recruited to achieve the predetermined sample size of 25, which was selected to match the sample size in van Ede and colleagues (2020). One participant was replaced because the participant did not complete the experimental session, and a second because of excessive movement-related artifacts in the EEG data. All participants provided written informed consent before participation and reported normal or corrected-to-normal vision and no history of neurological disorder.

### Setup

The experiment was run on a PC (with a 1920 × 1080 pixel LCD monitor with a 240-Hz refresh rate) in a dimly lit room, and the task was programmed in Presentation. A chin rest was used to maintain a viewing distance of approximately 75 cm. Gaze position was tracked and recorded at a sampling rate of 1000 Hz with an Eyelink 1000 eye tracker (SR Research Ltd.). The eye tracker was calibrated and validated for each participant before the experiment using a built-in 9-point calibration routine. Manual responses were made via computer mouse.

EEG signals were recorded with a 64-channel Biosemi system (1024 rate), with active electrodes distributed across the scalp using the International 10–20 positioning system. The left mastoid was used as the online reference, and the right mastoid was used to derive an average mastoid reference offline. Two EOG electrodes were placed below and to the right of the right eye to monitor for eye movements and blinks.

## Task and Procedure

The current experiment directly built on the task and procedure from van Ede and colleagues (2020) and thus had nearly identical procedures. In comparison to the original study, we made three adaptations. First and foremost, we here included neural EEG measurements. Second, to help disambiguate the retrocue from the memory probe, we adapted the retrocue to take the form of a color patch presented behind the fixation cross rather than a change in the color of the fixation cross itself (as we had used in the original study). Finally, to boost trial numbers in the most relevant conditions, we no longer included trials with gray neutral retrocues that we had included in the original study.

Each trial began with the brief simultaneous presentation of two visual stimuli of different color and orientation. The stimuli were rectangular bars (approximately 5.7° visual angle in height and 0.8° in width), and appeared centered at a distance of approximately 5.7° visual angle to the left or right of fixation. On each trial, one bar was colored purple and one green (location randomized across trials) and each appeared at an orientation that could vary between 1° and 180°. First, 750 msec after sample offset, a retrocue (a disc colored purple or green, with a radius of approximately 0.2°) appeared behind the fixation cross for 250 msec. Then, 1750 msec after retrocue offset, the fixation cross changed color to purple or green, prompting recall of the sample matching that color. Participants were instructed to maintain central fixation and hold the computer mouse stationary until they were ready to initiate their orientation recall response. Movement of the mouse triggered the onset of the response dial, which appeared displaying a randomly selected orientation, and participants adjusted the orientation of the dial to indicate their recall of the orientation of the probed sample, confirming their response by clicking the left button on the mouse. The response dial was a circle (radius of 5.7°) centered on the fixation symbol with two smaller circles centered on its circumference and separated by 180° (like handles on a steering wheel to indicate the current adjusting orientation; see Figure 1). The dial was operated by dragging the computer mouse in the angle of the to-be-reported orientation. The mouse position was continuously polled and its projected angle through the center of the screen determined the displayed orientation of the response dial. Participants were trained that the imaginary diameter connecting the two "handles" corresponded to the recalled orientation. Participants had an unlimited amount of time to initiate their response and then 2.5 sec to complete it. Upon mouse click (or timeout), participants received feedback about the accuracy of their response (200 msec; a digit ranging from 1 to 100, with "1" reflecting the maximum possible error of 90° and "100" reflecting a perfect report), followed by an intertrial interval that varied randomly between 500 and 800 msec.

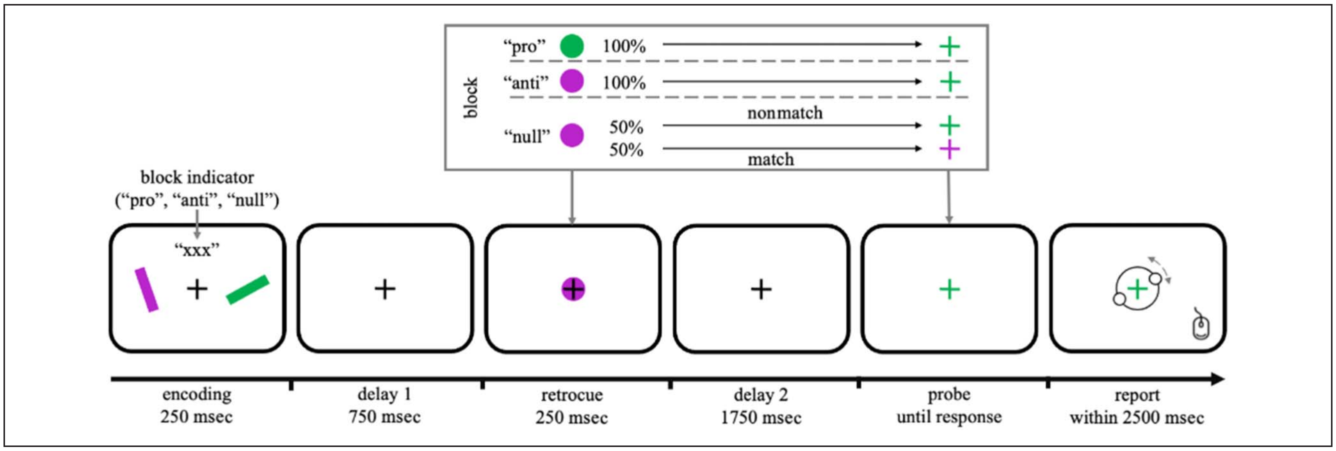

**Figure 1.** Visual working memory task with informative (pro, anti) and uninformative (null) retrocues. Participants encoded two visual tilted bars to reproduce the orientation of the probed memory item at the trial end. A dot colored with one of the memory colors was presented transiently at the fixation after the delay following the encoding, serving as the retrocue. After another delay, the central fixation cross was colored by one of the memory colors, serving as the probe for participants to report the matching item's orientation. In the informative retrocue blocks, pro- and anti-retrocues were each 100% predictive of the to-be-probed memory item but differed in whether their color also matched the probed item (pro) or matched the other item (anti). Null-retrocues were uninformative by matching the probed color or the other memory color for 50% of trials, respectively.

The central manipulation was that we included three types of retrocue trials that were blocked by category: "pro-retrocue," "anti-retrocue," and "null-retrocue." On pro-, anti-, and null-retrocue trials, the color of the retrocue predicted that the to-be-recalled memory item would be the color-matching memory item with 100%, 0%, and 50% validity, respectively (i.e., in anti-retrocue blocks, the cue predicted with 100% validity that the other, non-color-matching, memory item would be probed). The experiment comprised 16 pro-, 16 anti-, and 16 null-retrocue blocks, administered in clusters of three (one block of each condition, randomly determined order), with 16 trials per block. During the entirety of each block, the word "pro," "anti," or "null" was displayed at the top of the screen, so that participants could always remind themselves of how to use the cue. Participants initiated each block by pressing the enter key on the keyboard. Between each cluster of blocks, the eye tracker was recalibrated. Before data collection, each participant practiced one pro-block, followed by one anti-block, and then one null-block.

## Analysis of Behavioral (Manual Response) Data

Behavioral data were analyzed with two measures: RTs and reproduction errors. RTs were defined as the duration from probe onset to response initiation (i.e., initial movement of the cursor). Reproduction errors were defined as the absolute angular difference between the probed memory orientation and the reproduced one. Then, we used a one-way, repeated-measures ANOVA with factors retrocue informativeness (i.e., pro, anti, and null) and follow-up paired-samples *t* tests with these two dependent variables.

## Analysis of Eye-tracking Data

Eye-tracking data were converted from their original .edf format to .asc format using the EDF2ASC application, which is bundled with Eyelink. Subsequent processing was carried out with custom code in MATLAB (MathWorks). The data were cleaned of blink-related artifacts by removing signal ±120 msec around each blink. As in previous studies (van Ede et al., 2020; van Ede et al., 2019), biases in gaze following informative pro- and anti-retrocues were quantified using a measure of "towardness": capturing the bias in horizontal gaze position as a function of the cued items location at encoding. For both pro- and anti-retrocue trials, positive values were assigned to bias in the direction of the to-be-attended memory item (i.e., for anticue trials, this was always the item whose color did not match the cue). After towardness was calculated per time point, for visualization, trial-average gaze-position time courses were smoothed by a moving averaging kernel with five samples, at a sampling rate of 1000 Hz.

## Analysis of EEG Data

### *Preprocessing*

EEG data were processed and analyzed in MATLAB with FieldTrip (Oostenveld, Fries, Maris, & Schoffelen, 2011). During preprocessing, the data were epoched from 500 msec before memory array onset to 1000 msec after probe onset (using *ft_definetrial*). The epoched data were rereferenced to the average of both mastoids (using *ft_preprocessing*). Bad channels were interpolated with the two lateral neighboring electrodes. Next, eye-related artifacts were detected using independent component analysis (ICA; using *ft_componentanalysis*) with the FastICA algorithm (Hyvärinen, 1999). ICA components corresponding to artifacts, identified via correlation with the EOG signal and assessment of their topography, were removed from the data. To exclude all trials in which blinks may have interfered with processing retrocues, we removed trials in which the VEOG contained samples with amplitude higher than 2000 uV. Finally, we visually detected and discarded trials with obviously high variance by utilizing *ft_rejectvisual* function with the "summary" method. To increase topographical specificity, we conducted a surface Laplacian transform (using *ft_scalpcurrentdensity*) on the preprocessed data.

### *Electrode and Frequency-band Selection*

Channel and frequency-band selections for all presented time–frequency analyses were predetermined as follows. To explore manual response preparation, we focused on dynamics in the beta-band (15–25 Hz) at electrode C3, which in our study was always contralateral to the right hand that was used for responding, irrespective of whether participants were cued to attend to the left or the right memory item. The attenuation of beta activity contralateral to the response hand is a well-established neural marker of manual action planning (e.g., van Wijk, Daffertshofer, Roach, & Praamstra, 2009; Baker, 2007; Neuper et al., 2006; Mcfarland, Miner, Vaughan, & Wolpaw, 2000; Salmelin & Hari, 1994). To explore control-related demands of our task, power of frontal midline theta-band oscillations (Sauseng, Griesmayr, Freunberger, & Klimesch, 2010; Jensen & Tesche, 2002) was measured from 4 to 8 Hz at electrode AFz. Statistical analyses were done across the full time–frequency axes at the selected electrodes. In addition, we visualized topographies for which responses were averaged for the above predetermined frequency bands.

### *Time–frequency Analysis*

Time–frequency responses from 2 to 40 Hz were obtained in steps of 1 Hz using a short-time Fourier transform. Data were Hanning-tapered with a sliding time window of 300 msec, progressing in steps of 10 msec. To compare time–frequency responses of different conditions (say, conditions a and b), we normalized the power difference as percentage changes: ((a − b)/(a + b)) × 100. We focused on the period around retrocue onset (−500 to 2000 msec) to study retrocue-induced neural modulations.

### Statistical Evaluation

Statistical evaluation of all the gaze-position and spectral EEG data was performed with cluster-based permutation testing (Maris & Oostenveld, 2007). We permuted the conditions (i.e., the trial-average condition-specific responses) within participants and used the maxSumT as the cluster size. These analyses were conducted on the time-courses by considering clusters in time and on the time–frequency responses by considering clusters in both time and frequency, using 1000 permutations and an alpha level of .025.

## RESULTS

### Behavior: Informative Cues Enhance Performance

Patterns in response-onset times (RTs) and reproduction errors (Figure 2A) confirmed that participants used informative retrocues to internally select and prioritize the appropriate memory item following both pro- and anti-retrocues. As anticipated, responses were initiated most quickly on pro-trials ($M = 343$ msec), followed by anti- ($M = 417$ msec) and null-retrocue trials, $M = 642$ msec; $F(2, 48) = 68.66$, $p < .001$; pro vs. null, $t(24) = -11.94$, $p < .001$, d = 2.58; anti vs. null, $t(24) = -7.28$, $p < .001$, d = 1.70; pro vs. anti $t(24) = -3.19$, $p = .004$, $d = 0.64$ (Figure 2A, left). Consistent with the RT data, reproduction errors were smallest for pro-retrocue trials ($M = 9.26°$), followed by anti- ($M = 9.96°$) and null-retrocue trials, $M = 10.40°$, $F(2, 48) = 5.92$, $p = .005$; pro vs. null, $t(24) = -3.36$, $p = .003$, $d = 0.64$; anti vs. null, $t(24) = -1.19$, $p = .25$, $d = 0.18$; pro vs. anti, $t(24) = -2.44$, $p = .02$, $d = 0.38$ (Figure 2A, right).

### Eye Tracking: Gaze-bias Signatures of Selection and Competition

Spatial biases in gaze following the retrocue (Figure 2B) revealed signatures of selection in visual working memory following informative retrocues, in both the pro- and anti-retrocue conditions. In addition, gaze data confirmed competition between voluntary and involuntary factors revealed by the difference in selection dynamics following pro- and anti-retrocues.

In both conditions with informative retrocues, deviations of gaze from fixation could be observed beginning approximately 350 msec after retrocue onset, although the pattern differed markedly between the two. On pro-retrocue trials, beginning at around 350 msec, gaze bias shifted toward the location that had been occupied by the cued memory item, quickly differing from anti-retrocue trials (cluster $p = .007$) and (with a slightly longer latency) from baseline (cluster $p = .012$). This deviation reached its peak at approximately 650 msec after retrocue onset before reversing and becoming statistically indistinguishable from precue fixation at approximately 1000 msec after retrocue onset. On anti-retrocue trials, in contrast, the early deviation of gaze was noisier and initially took on numerically (although not significantly) negative values before subsequently shifting toward the location of the appropriate item. That is, on anticue trials, gaze bias initially trended toward the location of the sample whose color matched the retrocue, before subsequently

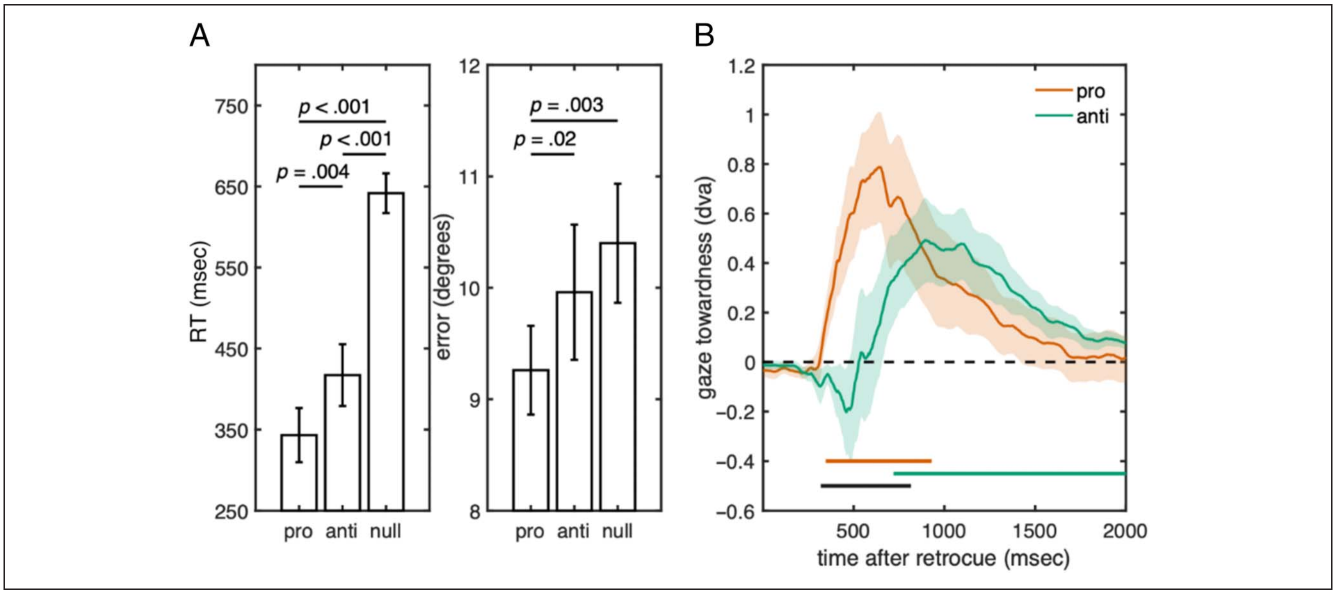

**Figure 2.** Behavioral performance and gaze biases of internal selective attention following pro- and anti-retrocues. (A) Behavioral performance as a function of retrocues for internal selection. Error bars represent ±1 standard error. (B) Pro- and anti-retrocues bias horizontal gaze toward memorized item locations. The red, green, and black horizontal lines indicate significant clusters for pro, anti, and the difference between them, respectively. The light shading around the time-courses in B indicate ±1 standard error.

shifting toward the memorized location of the relevant memory item. On anti-retrocue trials, the (positively valued) gaze bias cluster was observed approximately 700 msec after cue onset (cluster $p < .001$), flattened out approximately 300 msec later, but extended for the remainder of the delay period.

The observed delay in gaze bias to the appropriate memory item following anti- compared with pro-retrocues is consistent with a competition between involuntary (color-driven) and voluntary (goal-driven) factors over the focus of internal selective attention—a competition that needs to be resolved following anti-, but not pro-, retrocues (as also reported in van Ede et al., 2020). These findings replicate our earlier work and form the basis for the EEG results that were not available in our original study and that thus form the key advances of the current work.

## EEG

### *Cue-evoked Activity: Informative Retrocues Modulate the Cue-evoked Sensory Response*

In van Ede and colleagues (2020) and in this study (Figure 2B), the eye tracking data suggest that informative retrocues prompt the internal selection of the to-be-recalled memory item. On the basis of this, one might expect that the retrocue receives differential processing when it is informative (in the pro- and anti-retrocue conditions relative to the null-cue condition). To examine this possibility, we calculated the cue-locked ERPs of two bilateral posterior electrodes (i.e., P7/8) and focused on components P1 and N1 (Eason, Harter, & White, 1969; Mangun & Hillyard, 1991). As depicted in Figure 3, we observed significant effects of retrocue conditions in both the P1 and N1 components, $F(2, 48) = 4.07, p = .023$; $F(2, 48) = 8.48, p < .001$, respectively. The follow-up tests showed that the ERP for pro- and anticues became more negative than for the null-cue soon after cue onset, a difference that persisted during the initial positive-going deflection at around 70–130 msec ($p = .030$ and $p = .013$, respectively) and the first negative-going deflection that peaked around 130–200 msec ($p = .002$ and $p = .011$, respectively; Figure 3).

### *Contralateral Sensorimotor Beta: Informative Retrocues Induce Action Preparation, and This Is Delayed following Anti-retrocues*

To investigate activity associated with action preparation, we assessed sensorimotor beta activity at electrode

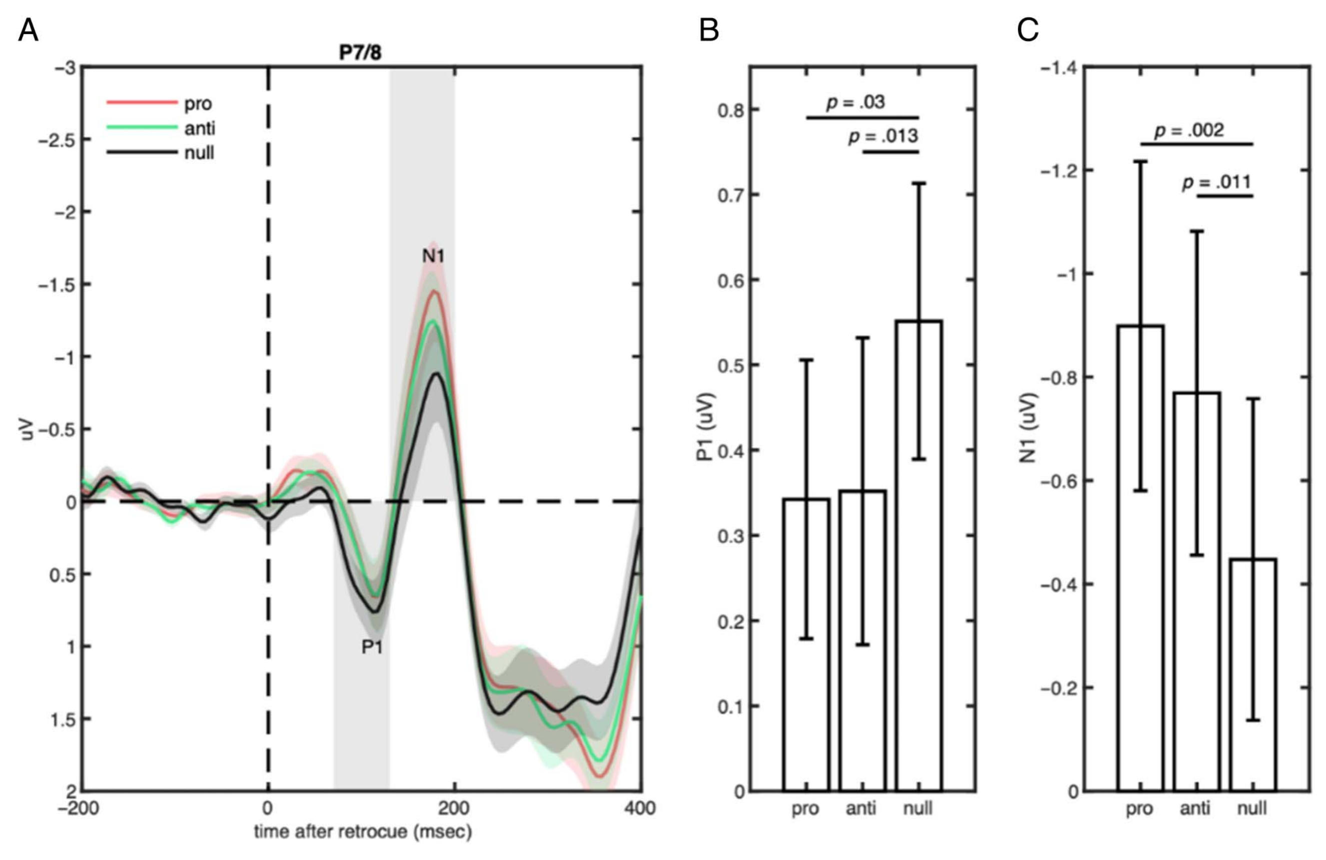

**Figure 3.** Cue-locked ERPs distinguish informative from uninformative retrocues. (A) ERPs recorded from electrodes P7/8 indicate differential processing of informative retrocues. Shading represents ±1 *SEM*. Vertical gray areas indicate time windows of interest to compare ERP components across conditions. (B) Mean ERP value of P1. (C) Mean value of N1. Note how for the P1 we plotted positive upward, whereas for the N1 we plotted negative upward, such that a larger P1 or N1 response is associated with higher bars in both graphs. Error bars denote ±1 *SEM* across observers.

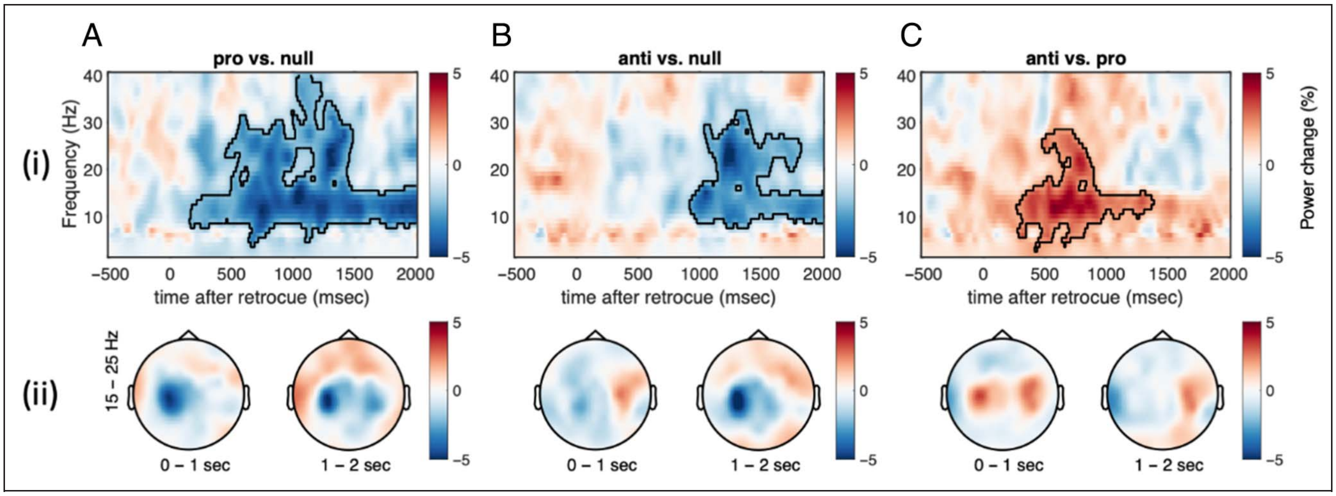

**Figure 4.** Informative retrocues initiate anticipatory action preparation that is delayed following anti-retrocues. (i) Comparison of time–frequency representations of oscillatory power, at electrode C3, for (A) pro- versus null-retrocues, (B) anti- versus null-retrocues, and (C) anti- versus proretrocues. (ii) Topographies of the comparisons from row (i), restricted to the beta band (15–25 Hz) for two different time windows after retrocue onset. Colors indicate percentage differences between conditions; black cluster outlines indicate significant differences from a cluster-based permutation test.

C3 (Figure 4), which would emphasize activity related to the upcoming response hand (which was always the right hand in the current experiment). Compared with the null-cue condition, postcue power in a frequency band spanning from approximately 9–15 Hz at C3 was decreased following pro-retrocues beginning approximately 100 msec after cue onset (cluster $p < .001$; Figure 4A, i), and on anticue trials beginning approximately 1000 msec after retrocue onset (cluster $p = .007$; Figure 4B, i). In both conditions, this relative power attenuation persisted for the remainder of the second delay and eventually incorporated a frequency band spanning approximately 8–30 Hz. The difference in the timing of these effects was confirmed by a significant difference between pro- and anticue trials during an epoch spanning from approximately 300–1300 msec after probe onset (cluster $p = .014$; Figure 4C, i) and is consistent with the delay in the gaze bias following anti- compared with pro-retrocues. These action-preparation signals were most prominent over electrode C3 (Figure 4, ii) consistent with an anticipated orientation-recall report with the right hand—a manual report that could be prepared for, at an abstract level, as soon as the appropriate item had been selected from working memory. Note that these results also provide indirect neural evidence for the assumption that working memory load drops following pro-retrocues and anti-retrocues.

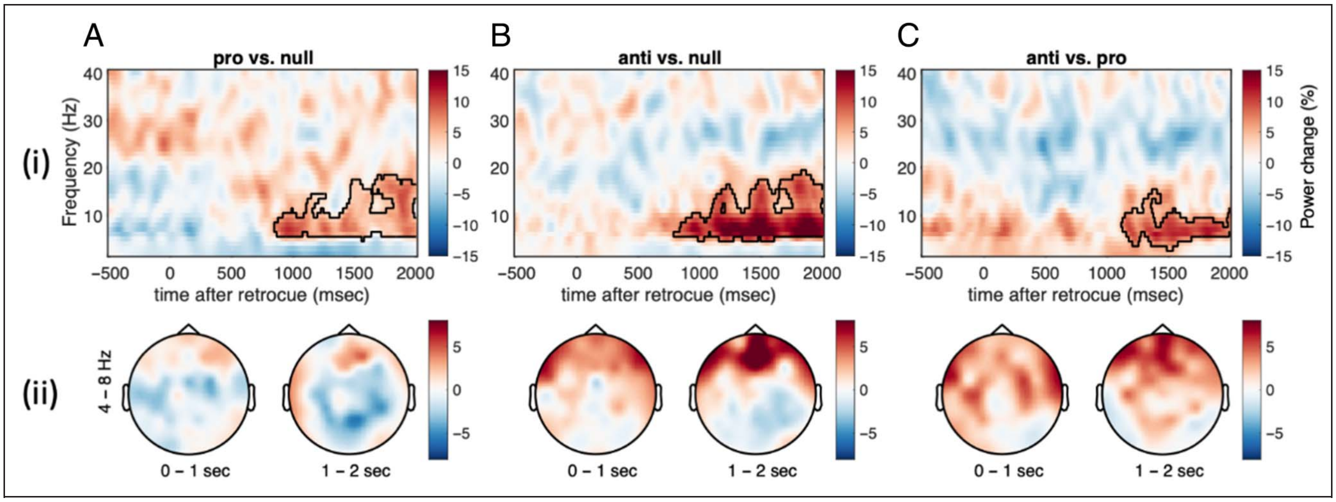

**Figure 5.** Frontal midline theta activity indexes demands on cognitive control. (i) Comparison of time–frequency representations of oscillatory power, at electrode AFz, for (A) pro- versus null-retrocues, (B) anti- versus null-retrocues, and (C) anti- versus proretrocues, aligned to retrocue onset. (ii) Topographies of the comparisons from row (i), restricted to the theta band (4–8 Hz), for two different time windows relative to retrocue onset. Colors indicate percentage differences between conditions; black cluster outlines indicate significant differences from a cluster-based permutation test.

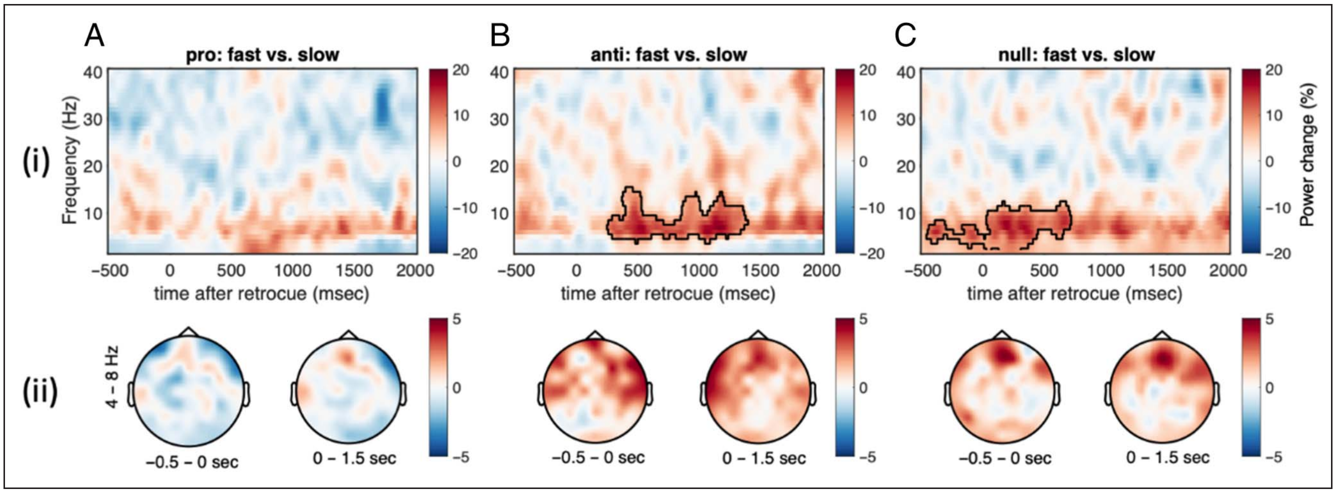

**Figure 6.** Frontal midline theta power predicts the response-initiation latency of ensuing working-memory-guided behavior. (i) Comparison of time–frequency representations of oscillatory power, on fast versus slow trials (median split), at electrode AFz, for (A) pro-, (B) anti-, and (C) null-retrocue trials, aligned to retrocue onset. (ii) Topographies of the comparisons from row (i), restricted to the theta-band (4–8 Hz), for two different time windows relative to retrocue onset. Colors indicate percentage differences between conditions; black cluster outlines indicate significant differences from a cluster-based permutation test.

### *Frontal Midline Theta: Tracking Demands on Cognitive Control over and above Working-memory Load*

We now turn to our analysis focusing on frontal midline theta activity that was of key interest in the current work for reasons outlined in our introduction. Figure 5 shows spectral modulations at the frontal-midline electrode AFz following pro- and anti-retrocues, relative to following null-retrocues that here served as the condition to which to compare the EEG signal. Oscillatory power at AFz became significantly elevated across a range spanning from roughly 4–10 Hz following both pro- (cluster $p$ = .004; Figure 5A) and anti-retrocues (cluster $p$ = .003; Figure 5B), beginning approximately 800 msec after cue onset and persisting for the remainder of the second delay period.

Note that, because the null-cue condition required the continued retention of two items while following the 100% informative retrocues load could be reduced to one item, these effects imply that the influence of selection demands on frontal midline theta may be greater than the influence of memory load.

In addition, when directly contrasting pro- and anti-retrocue conditions, we found larger theta modulations following anti-retrocues, consistent with larger demands on cognitive control following retrocues for which voluntary and involuntary factors compete for the focus of attention in working memory. This difference was most pronounced in the 4- to 10-Hz range from roughly 1100 msec after cue onset (cluster $p$ = .011; Figure 5C).

### *Frontal Midline Theta Predicts Ensuing Memory-guided Behavior*

Finally, to explore how the above-described theta modulations might relate to behavior, we used a median split analysis to investigate how postcue frontal midline theta-band power related to two aspects of behavior: response-initiation RT and recall precision. For response-initiation RT (Figure 6), after performing a median split, we observed that theta power at AFz was numerically higher on fast relative to slow trials for all three conditions. For RT, this effect reached significance on both anti-retrocue trials (with the cluster beginning approximately 250 msec after retrocue onset; cluster $p$ = .002; Figure 6B), and on null-retrocue trials (with the cluster beginning approximately 450 msec before retrocue onset and extending beyond cue processing; cluster $p$ < .001; Figure 6C).

For recall precision, after performing a median split, we also observed that delay-period oscillatory power at AFz was numerically higher on high- versus low-precision trials for all three conditions, although these effects did not survive statistical significance testing (for transparency, we present these results in Appendix Figure A1).

## DISCUSSION

Building on recent demonstration of joint voluntary and involuntary influences over the focus of attention inside visual working memory (van Ede et al., 2020), we set out to investigate the neural dynamics of such influences, and their competition. First, our results replicated the findings from van Ede and colleagues (2020) that performance improves with informative (pro- and anticue) relative to non-informative (null-cue) retrocues—confirming the successful manipulation of internal selective attention. We also replicated gaze biases associated with these internal attention shifts (cf. Liu et al., 2022; van Ede et al., 2020; van Ede et al., 2019), and the delayed allocation of attention to appropriate memory content when voluntary and involuntary factors competed (van Ede et al., 2020). The concurrently recorded EEG extended these original findings in several ways. First, retrocue-locked posterior ERP components were shifted negatively and the N1 component boosted following informative (pro- and anti-retrocues) relative to uninformative null retrocues. Second, at the central electrode overlaying the left motor cortex, power centered on the mu-alpha and beta bands—indexing preparation for the ensuing manual report—decreased soon following pro- relative to null-retrocues, and markedly later following anti- relative to null-retrocues—paralleling the delayed attentional allocation seen in gaze, but here extending it to action planning alongside visual retention. Finally, post-retrocue FMT activity was highest following anti-, then pro-, and then null-retrocues, despite informative retrocues (but not null retrocues) allowing to reduce memory load from two to one. We consider each of these electrophysiological findings in turn.

Memory report was fastest and most accurate for pro-retrocue trials, then anti-retrocue trials, relative to null-retrocue trials. Although this report could not begin until 1750 msec after cue onset, the cue-evoked ERPs suggest that the utilization of informative retrocues may have begun with enhanced perceptual processing of the cue itself, presumably because of enhanced (voluntary) attentional gain modulation of the initial sensory response to the cues (cf. Hillyard, Vogel, & Luck, 1998).

Subsequently, dynamics in the lower beta band at central electrodes indicated that quicker attentional allocation to the appropriate memory content afforded by pro-retrocues (as indexed by the quicker onset of gaze towardness) resulted in earlier engagement of anticipatory manual response preparation (cf. Nasrawi et al., 2023; Nasrawi & van Ede, 2022; Boettcher et al., 2021; van Ede, Chekroud, Stokes et al., 2019; Schneider et al., 2017). This shows that competition between voluntary and involuntary influences over the internal focus of attention results not only in delayed attentional allocation to appropriate memory content, but also in delayed initiation of preparation to act on this content (Rösner et al., 2022).

Turning to FMT, the findings are interesting from two perspectives: what they reveal about the control of competition for selection within visual working memory, and how they inform the interpretation of FMT dynamics as an index of working memory-related processing. Anti-retrocue trials were objectively more difficult than pro-retrocue trials. This was evidenced by RT and precision of recall, as well as by the delay in both the gaze bias (indexing attentional selection) and the central mu alpha/beta modulations (indexing action preparation). The dynamics of the gaze bias, in particular, suggest that anti-retrocues triggered an initial reflexive shift of attention toward the color-matching item, an operation that would need to be overridden by rule-guided (i.e., voluntary) control of behavior (i.e., select the color-nonmatching item). FMT has long been associated with cognitive control (e.g., Cavanagh & Frank, 2014; Hsieh & Ranganath, 2014; Sauseng et al., 2010) and the fact that postcue FMT was higher on anti- than pro-retrocue trials is consistent with a role in controlling the competition for selection (for a recent preprint that parallels this finding, see Ester & Nouri, 2022). Furthermore, the fact that postcue FMT was also higher on pro- than null-retrocue trials suggest a more general role in the control of selection within working memory. Indeed, in two of the three conditions in this experiment, we further observed that higher FMT following the cue predicted faster memory-guided behavior, suggesting a functional role for these theta modulations.

How do the present results inform our understanding of working-memory-related functions of FMT? Although to this point we have emphasized a role in indexing the need for control, it has also previously been reported that FMT power can track working-memory load (e.g., Zakrzewska & Brzezicka, 2014; Meltzer et al., 2008; Jensen & Tesche, 2002; Gevins et al., 1997). Our design effectively pits the factor of control-of-selection versus that of load, because, in contrast to the pro- and anti-retrocue conditions, in which load could be reduced to a single item, the null-retrocue condition required retention of the two memory items throughout the postcue delay. We observed higher FMT power following the retrocues that effectively triggered a reduction working-memory load. Consequently, our current results suggest that FMT cannot be interpreted as an index that is specific to working-memory load, per se. Instead, at a most general level, should be interpreted in the context of models of frontal midline systems (e.g., anterior cingulate cortex) involved in assessing the need for and regulation of the level of cognitive control (e.g., de Vries, Savran, van Driel, & Olivers, 2019; Fiebelkorn & Kastner, 2019; Helfrich et al., 2018; de Vries, van Driel, & Olivers, 2017; Sauseng, Hoppe, Klimesch, Gerloff, & Hummel, 2007; de Araújo et al., 2002; Gevins & Smith, 2000; Kahana, Sekuler, Caplan, Kirschen, & Madsen, 1999; Gevins et al., 1997; Pennekamp, Bösel, Mecklinger, & Ott, 1994).

One interesting observation with reference to our theta findings regard their timing. Although cluster statistics do not support inferences about the precise timing of events (Sassenhagen & Draschkow, 2019), it is nonetheless notable that the strongest most pronounced differences in FMT are in the period from 1000 to 2000 msec after retrocue onset, including the anti- versus pro-retrocue comparison (Figure 5). This is markedly later than the gaze and central beta effects that indicated that the competition between voluntary and involuntary factors was resolved mostly within the first second after the retrocue. Note how this difference in timing also rules out the possibility that the reported theta differences are a direct consequence of differences in gaze behavior. This opens the possibility that the pronounced FMT activity following anti-retrocues may not reflect the process of resolving competition per se, but rather the maintenance and/or consolidation of the postcue state. It is important to keep in mind, however, that a different analysis of the same data (the correlation of FMT power with RT) revealed a significant functional role for FMT during the earlier portion of the postcue delay in two conditions, and a trend in this direction for the third (Figure 6). This is consistent with an important role for FMT in the flexible control of the selection and processing of the response-critical information in working memory.

In summary, we have used EEG to investigate the neural dynamics associated with the competition between voluntary and involuntary control over the focus of attention in visual working memory. When voluntary and involuntary factors compete for the internal visual focus of attention, prioritization of the appropriate memory item is delayed. This is reflected both in gaze biases that track selection and in the neural dynamics of preparation for the appropriate upcoming manual action. We have further shown how this competition is paralleled—possibly followed—by frontal midline theta activity that influences memory-guided behavioral performance. Finally, our design uniquely enabled us to disentangle the processes of control versus retention in working memory, revealing how FMT tracks cognitive control demands over and above working memory load.

## APPENDIX

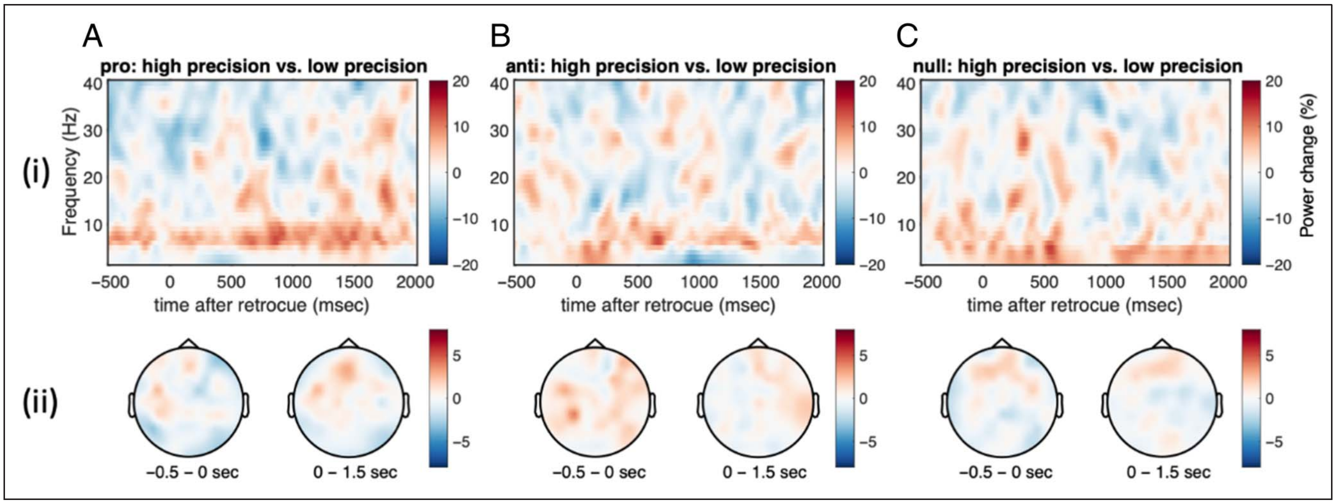

**Figure A1.** Comparison of neural activity between trials with high and low precision orientation reports separately for (A) pro, (B) anti, and (C) null retrocue trials. For each retrocue condition comparison: (i) difference in time–frequency response at AFz, aligned to retrocue onset. Colors indicate percentage differences between conditions. (ii) Topographies of theta (4–8 Hz) percentage difference between high precision and low precision trials, for each retrocue condition comparison, for two different time windows after retrocue onset.

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## Data Availability Statement

All data and code will be shared upon request.

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## Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .407, W(oman)/M = .32, M/W = .115, and W/W = .159, the comparable proportions for the articles that these authorship teams cited were M/M = .549, W/M = .257, M/W = .109, and W/W = .085 (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

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