# Distinct Cortical and Oculomotor Dynamics During Endogenous–Exogenous Competition in Working Memory

Dayana Valdez[1], Edward F. Ester[1-2]

[1]Department of Psychology, University of Nevada, Reno
[2]Institute for Neuroscience, University of Nevada, Reno

**Abstract**

Working memory (WM) enables the temporary maintenance of information for guiding thought and action, but its limited capacity requires internal selective attention mechanisms to prioritize goal-relevant representations. Like external attention, internal selection can be shaped by both endogenous (goal-driven) and exogenous (stimulus-driven) factors. Classic work by Charles Folk and Roger Remington demonstrated that such factors interact competitively during external attention, producing stimulus-driven capture under certain conditions. Whether similar competitive dynamics govern internal selection remains unclear. Here, we combined EEG and eye-tracking to examine how endogenous and exogenous influences interact during the selection of information held in working memory. Participants remembered two oriented bars and used either a pro-cue or an anti-cue to guide recall. Behavioral responses and lateralized alpha-band activity revealed robust delays in selecting task-relevant WM content under competition. In contrast, oculomotor biases toward memorized locations emerged with similar timing across pro- and anti-cue conditions, providing no evidence for retro-capture or delayed selection. These findings indicate that internal selection does not resolve competition via rapid capture, as in external attention, but through time-extended cortical processes. Our results highlight functional dissociations between cortical and oculomotor systems and offer new insight into how internal attention implements selection under competitive demands.

Efficient behavior requires mechanisms for selecting information that is relevant to current goals while suppressing competing inputs. Foundational work by Charles Folk and Roger Remington—whose influential ideas this special issue celebrates—demonstrated that external attention is shaped by the interplay of endogenous (goal-driven) and exogenous (stimulus-driven) factors. Their contingent involuntary orienting framework showed that stimulus-driven capture depends critically on the match between stimulus properties and an observer's attentional control settings, revealing that attentional competition unfolds through dynamic interactions between goals and salience rather than through purely bottom-up or top-down routes (Folk & Remington, 1998). This framework has profoundly shaped theories of attentional control and continues to inspire new lines of inquiry.

A central question in contemporary cognitive neuroscience is whether the same competitive principles govern selection within working memory (WM). Because WM is capacity-limited, internal attention must determine which representations gain privileged access to behavior and which are deprioritized or suppressed (Souza & Oberauer, 2016; Ester et al., 2018). Although internal attention shares functional similarities with external attention, it operates on stored rather than incoming information and may therefore rely on distinct neural mechanisms and computational constraints. Recent studies offer differing views on how endogenous and exogenous factors interact during internal selection. An eye-tracking study by van Ede et al. (2020) reported evidence for "retro-capture": salient retrocues biased gaze toward matching but task-irrelevant WM content, suggesting that involuntary influences can briefly dominate internal selection. In contrast, an EEG study using a similar pro-cue/anti-cue manipulation (Ester & Nouri, 2023) found no evidence for retro-capture. Instead, competition between endogenous and exogenous selection mechanisms delayed the endogenous selection of task-relevant WM content without producing erroneous prioritization of irrelevant representations. Together, these findings raise a critical unresolved question: Do different

physiological systems—such as cortical oscillations and oculomotor behavior—reflect the same or different internal selection dynamics under competitive demands?

To address this question, we recorded EEG and eye-tracking data while participants performed a retrospectively cued visuomotor WM task used in earlier work to demonstrate retro-capture (van Ede et al., 2020). As in that work, we manipulated whether retrocues matched task-relevant or task-irrelevant WM content, placing endogenous and exogenous selection mechanisms in alignment (pro-cue) or in competition (anti-cue). If competition is resolved uniformly across neural systems, both EEG and gaze measures should show parallel delays or capture. Alternatively, if distinct systems implement different stages or forms of internal selection, they may reveal dissociable patterns. By situating internal selection within the broader theoretical tradition shaped by Folk and Remington, our work asks not only whether endogenous and exogenous influences compete within WM, but also whether this competition engages shared or different selection mechanisms across physiological systems.

**Methods**

*Participants.* 35 human volunteers (both sexes) participated in this study. Volunteers aged 18-40 were recruited from the University of Nevada, Reno (UNR) community and completed a single 2.5-hour testing session in exchange for course credit or monetary compensation ($15/h). We had no a priori reason to expect that task performance would vary across sex, gender identity, race, ethnicity, handedness, or any other immutable characteristic. Thus, to better protect participants' privacy, we did not collect this information. All experimental procedures were approved by the UNR Institutional Review Board. Data from 5 participants were discarded due to technical issues, for example, hardware failures that prevented event markers from being sent from the stimulus presentation computer to the EEG recording computer. The data reported here reflects the remaining 30 participants.

*Testing Environment*. Participants were seated in a dimly lit room for the duration of testing. Visual displays were generated in MATLAB and rendered on a 27-in. LCD monitor (1920 × 1080 resolution) cycling at 240 Hz using Psychtoolbox-3 (Kleiner, Brainard, & Pelli, 2007). Participants were seated 85 cm from the display via a chin rest and responded using a standard U.S. computer keyboard synced to the monitor refresh rate.

*Visuomotor Memory Tasks*. Participants performed two variants of a visuomotor memory task used in prior research (van Ede et al., 2019; van Ede et al., 2020; Figure 1A). Each trial began with a 0.5 sec sample display containing colored bars (5.7° length x 0.8° height from a viewing distance of 85 cm) presented 5.7° to the left and right of a central fixation cross. The orientation of one bar was chosen from the interval -70°:1°:-20° (i.e., counterclockwise) and the orientation of the other bar was chosen from the interval 20°:1°:70° (i.e., clockwise). Thus, the sample display always contained one clockwise and one counterclockwise-tilted bar, though their positions were randomized over trials. The sample display was followed by a 1.25-1.75 sec blank delay interval, with the specific interval randomly and independently chosen from a uniform distribution with a 5 ms resolution on each trial. At the end of the trial, a probe, defined

as a change in the color of the central fixation cross, instructed participants to recall the orientation of the matching bar. Importantly, the vertical tilt of the to-be-recalled bar determined which had should be used for recall, with counterclockwise bars requiring a left-hand response and clockwise bars requiring a right-hand response. Participants recalled counterclockwise bars by pressing and holding the "z" key with their left index finger. Upon their initial response, a recall stimulus consisting of a circle with two endpoints appeared and began to rotate counterclockwise. Participants held down the z key until the orientation of the recall stimulus matched their memory for the orientation of the to-be-recalled bar. Likewise, participants recalled clockwise bars by pressing and holding the "?" key and releasing it when the recall stimulus matched their memory. We recorded three variables: accuracy, defined as the proportion of trials where the participant used the appropriate hand for recall, error, defined as the absolute angular difference between the reported and actual bar orientations, and response initiation time, defined as the interval between probe onset and participants' initial button press response. During the pro-cue task, participants were instructed to recall the orientation of the bar matching the probe color. During the anti-cue task, participants were instructed to recall the orientation of the bar that did not match the probe color. Participants performed the pro- and anti-cue tasks sequentially, for example, 8 blocks of the pro-cue task followed by 8 blocks of the anti-cue task, though task order was counterbalanced across participants. Participants performed 4-10 (median 8) blocks of 48 trials in the pro-cue task and 6-10 blocks (median 8) of 48 trials in the anti-cue task.

*EEG Acquisition and Preprocessing*. Continuous EEG was recorded from 63 scalp electrodes using a BrainProducts actiCHamp system. Online recordings were referenced to 10-20 site FCz and digitized at 1 kHz. The following offline preprocessing steps were applied, in order: (1) resampling from 1 kHz to 200 Hz, (2) high-pass filtering (0.5 Hz using zero-phase forward- and reverse-finite impulse response filters as implemented by EEGLAB software extensions; Delorme & Makeig, 2004), (3) identification and reconstruction of noisy electrodes and epochs

via artifact subspace reconstruction (implemented via EEGLAB; Chang, Hsu, Pion-Tonachini, & Jung 2020), (4) re-referencing to the average of the left and right mastoids (operationalized as 10-20 sites TP9 and TP10), (5) epoching from −1.0 to +3.0 sec relative to probe onset, (6) interpolation of noisy electrodes, and (7) application of a surface Laplacian to remove low spatial frequency components from the signal (Perrin, Pernier, Bertrand, & Echallier, 1989).

*Eyetracking Acquisition and Preprocessing.* We obtained high-quality binocular eye position data for 21 of 30 participants. It was not possible to acquire eye position data from the remaining 11 participants due to participant-level variables (e.g., participants who wore corrective lenses or mascara during their testing session). Eye position data were acquired using an SR Research Eyelink 1000 Plus infrared eye tracker and digitized at 500 Hz or 1 kHz. The eye tracker was calibrated at the beginning of each task (i.e., pro-cue and anti-cue) and drift correction was applied at the beginning of each task block. Data were downsampled from 1 kHz to 250 Hz when necessary and filtered for blinks. Blinks were defined as periods where the recorded pupil size fell below the median pupil size recorded across all experimental trials and conditions. We additionally discarded data from 50 ms before and 50 ms after each blink. Missing data were linearly interpolated, and the resulting gaze timeseries were smoothed with a gaussian kernel (10 ms full-width half-maximum). No other preprocessing steps were applied.

*Spectral EEG Analyses*. Spectral analyses focused on occipitoparietal 10–20 electrode site pairs O1/2, PO3/4, PO7/8; analyses were restricted to a period spanning −0.5 to 1.5 around probe onset. We extracted broadband spectral power from each electrode on each trial using a short-time Fourier transform (STFT) with a frequency range of 1–40 Hz (in 0.25-Hz steps) using a 200-msec sliding window and 10-msec step size. Power was computed by squaring the absolute value of the complex Fourier coefficients within each STFT window. To quantify changes in lateralized activity during visual selection, we sorted power estimates at each occipitoparietal electrode site by the location of the retrospectively cued stimulus, that is,

contralateral versus ipsilateral hemifield, and expressed this difference as a normalized percentage:

$$L_i = 100 \times \frac{(c_i - s_i)}{(c_i + s_i)}$$

where $c_i$ and $s_i$ are the trial-averaged responses of electrode $i$ when the probe stimulus appeared in the contralateral or ipsilateral visual field, respectively. Lateralization estimates were pooled across occipitoparietal electrode sites, yielding a single time frequency matrix of power estimates per participant.

To generate topographical maps of lateralized power relative to the probed stimulus location (i.e., left vs. right visual hemifield), we repeated this analysis for every scalp electrode and averaged power estimates over 8–13 Hz ("alpha-band" activity) during a period spanning of 500–1000 msec following probe onset. These frequency bands were chosen a priori based on commonly reported values in the literature (e.g., Klimesch, 2012), and this specific temporal window was chosen a priori based on prior reports, suggesting that it takes human observers 300–500 msec to process and respond to a retrospective memory cue (e.g., Souza, Rerko, & Oberauer, 2014). To visualize changes in occipitoparietal alpha power over time we extracted and averaged lateralization estimates from 8 to 13 Hz over electrode sites O1/2, PO3/4, and PO7/8, Statistical analyses of lateralization were performed using nonparametric sign permutation tests with temporal cluster-based corrections (see Statistical Comparisons section).

*Gaze Bias Analyses.* Preprocessed eye position data were sorted by the location of the retrospectively cued stimulus (i.e., left vs. right visual field) and task (i.e., pro- vs. anti-cue). Because stimuli were rendered along the vertical meridian, we restricted our analyses to horizontal eye position measurements. Following earlier work (van Ede et al. 2019), we computed a normalized measure of gaze bias by converting pixelwise recordings into a

percentage along an axis extending from fixation to the center of each visual stimulus. Thus, a ±100% gaze bias would result from participants foveating the center of one stimulus (with negative and positive values corresponding to gaze shifts towards the left and right visual hemifields, respectively), whereas a 0% gaze bias would result from participants perfectly holding fixation.

*Statistical Comparisons - Behavior.* We expected that dependent variables of recall error, response times, and accuracy would not meet tests of normality required by standard inferential statistics (e.g., t-tests). Therefore, all statistical comparisons were based on bootstrap tests. For each dependent variable (e.g., recall error) and experimental condition (e.g., pro-cue task) we randomly selected, with replacement, and averaged data from 30 of 30 volunteers. This procedure was repeated 10,000 times, yielding 10,000-element distributions of sample means. Next, we compared the number of permutations where the estimated mean in one condition (e.g., the pro-cue task) exceeded the mean in the other condition (e.g., the anti-cue task), yielding an empirical p-value.

*Statistical Comparisons – EEG and Eyetracking.* Statistical comparisons were based on nonparametric signed randomization tests (Maris & Oostenveld, 2007). Unless otherwise specified, each test we performed assumes a null statistic of 0 (i.e., no difference in alpha-band lateralization or no detectable gaze bias). We generated null distributions by randomly relabeling each participant's data with 50% probability and averaging the data across participants. This step was repeated 10,000 times, yielding a 10,000-element null distribution for each time point. Finally, we implemented a cluster-based permutation test with cluster-forming and cluster size thresholds of $p < .05$ (two-tailed) to evaluate observed differences with respect to the null distribution while accounting for signal autocorrelation.

Task-dependent differences in the latency of visual selection were evaluated with jackknife tests. For EEG and gaze position data, we selected and averaged data from N – 1 participants, then computed the time at which the absolute value of lateralization was greatest.

This procedure repeated until every participant's data has been "held out", yielding a 30-element vector of latencies for each task (i.e., pro- vs. anti-cue). We compared latency estimates across tasks via a non-parametric bootstrap test. We created distributions of pro- and anti-cue latencies by randomly selecting (with replacement) and averaging latency estimates 10,000 times. We subtracted the distribution of pro-cue latencies from the anti-cue latencies and calculated the number of times where latency estimates for the anti-cue condition were less than those for the pro-cue condition. This approach yields an empirical p-value with a minimum of 1e-04.

**Results**

*Overview*. We recorded EEG and horizontal gaze position data while human volunteers performed a retrospectively cued visuomotor working memory task (Figure 1A). Each trial began with a 0.5-sec sample display containing two colored bars (one clockwise-tilted, one counterclockwise-tilted) presented to the left and right of central fixation. Following a 1.25–1.75 sec blank delay, a probe stimulus (a color change of the central fixation cross) instructed participants which bar to recall. Critically, the vertical tilt of the to-be-recalled bar determined which hand should be used for recall: counterclockwise bars required left-hand responses, whereas clockwise bars required right-hand responses. During the pro-cue task, participants recalled the orientation of the bar *matching* the probe color. During the anti-cue task, participants recalled the orientation of the bar that *did not match* the probe color. Thus, in pro-cue blocks, endogenous (goal-driven) and exogenous (stimulus-driven) selection factors were aligned, whereas in anti-cue blocks these factors competed.

We evaluated two models, which we term retro-capture and delayed-selection. The retro-capture account predicts that competition between endogenous and exogenous selection mechanisms elicit an involuntary shift of attention towards the location of the cue-matching but task-irrelevant bar during the anti-cue task, and thus, both EEG and eye-tracking measurements of internal selection should exhibit an initial bias towards the location of the cue-matching but task-irrelevant bar during the anti-cue task. The delayed selection account predicts that competition between endogenous and exogenous selection mechanisms does not elicit an involuntary shift of attention but engages attention control mechanisms to resolve this competition, delaying the selection of task-relevant WM content. Thus, EEG and eye-tracking measurements of internal selection should be delayed during the anti-cue compared to the pro-cue task but should not exhibit a bias towards the task-irrelevant stimulus.

To test these alternatives, we defined EEG and eye-tracking measures of internal selection time-locked to the onset of the recall probe as follows: For EEG, extracted and

calculated alpha power (8-13 Hz) over occipitoparietal electrode sites contralateral and ipsilateral to the visual hemifield containing the task-relevant bar. Based on prior work (Klimesch et al., 2012; van Ede et al., 2019a) we defined selection as the normalized difference in alpha power over electrode sites contralateral and ipsilateral to the location of the task-relevant stimulus (see Methods), where negative values reflect shifts of attention towards the task-relevant stimulus while positive values are assumed to reflect shifts of attention towards the task-irrelevant stimulus. For eye tracking, we extracted and converted records of participants' horizontal gaze position into a normalized metric where 0% represents fixation and ±100% represents foveating one of the remembered bars (where negative and positive values index leftward and rightward gaze shifts, respectively).

*Behavioral Performance.* We quantified task performance using three measures: recall error (mean absolute angular difference between reported and actual bar orientations), response time (interval between probe onset and initial button press), and accuracy (proportion of trials using the correct response hand). Behavioral data are shown in Figures 1B–D. Recall error was modestly but significantly lower during the pro-cue task compared to the anti-cue task (M = 11.77° vs. 12.54°; p = 0.042; Figure 1B). Likewise, accuracy was slightly higher during the pro-cue versus anti-cue task (M = 96.63% vs. 95.52%; p = 0.012; Figure 1B). Most notably, response times were substantially slower during the anti-cue task compared to the pro-cue task (M = 0.962 sec vs. 0.730 sec; Δ = 232 ms; p < 1e-04; Figure

Figure 1. **Visuomotor Task and Behavioral Performance**. *(A) Participants remembered two bars over a short delay, then recalled the orientation of a retrospectively probed bar by adjusting a report stimulus. During the pro-cue task, participants were tasked with reporting the orientation of the bar whose color matched the recall probe; during the anti-cue task, participants were tasked with reporting the orientation of the bar whose color did not match the recall probe. See Methods for additional details. (B) Recall error, response times, and accuracy plotted as a function of task. Accuracy refers to trials where the participant recalled the probed bar with the correct response hand.*

1B). This robust latency effect replicates prior findings (Ester & Nouri, 2023) and confirms that placing endogenous and exogenous selection slows participants' responses.

*Alpha-band EEG Signatures of Internal Selection.* Figure 2A summarizes lateralized changes in spectral power (i.e., contralateral to the task-relevant stimulus minus ipsilateral to the task-relevant stimulus) time-locked to probe onset and pooled over the pro- and anti-cue tasks. We identified a significant cluster of lateralized activity spanning ~8-13 Hz and ~0.5 to 1.0 sec after probe onset. This activity was clustered over occipitoparietal electrode sites, replicating prior findings (van Ede et al., 2019; Ester et al., 2023; Figure 2A, inset). Figure 2B plots lateralized

alpha power from 8-13 Hz calculated from posterior electrode sites as a function of task. We found no evidence for selection of the cue-matching but task-irrelevant stimulus during the anti-cue task (i.e., positive lateralization values). Instead, we observed clear evidence for selection of the task-relevant stimulus, with the onset of selection significantly faster during the pro-cue task (M = 322.97 ms) vs. the anti-cue task (M = 356.47 ms; p < 1e04; jackknife test). This pattern replicates findings by Ester and Nouri (2023) and indicates that competition between endogenous and exogenous selection mechanisms engages attention control mechanisms that delay the selection of task-relevant WM content.

*Oculomotor Signatures of Internal Selection*. Several recent studies have linked small (< 1°) biases in gaze position with the selection of information held in WM (e.g., van Ede et al., 2019a; Ester & Weese, 2023; Chota et al., 2025). In the context of the visuomotor WM task used here, the typical finding is that participants' gaze bias is subtly but robustly biased towards the location of a task-relevant stimulus following an informative retrocue (e.g., van Ede et al., 2019). Notably, van Ede et al (2020) exploited these biases to test how competition between endogenous and exogenous factors influences the selection of task-relevant WM content. During an anti-cue task, they reported that participants' gaze initially shifted towards the location of a cue-matching but task-irrelevant stimulus followed by a corrective gaze shift towards the task-relevant stimulus, an effect they termed "retro-capture". Although we found no evidence for a retro-capture effect using EEG signatures of internal selection (e.g., Figures 2A-B), there is growing evidence that oculomotor and electrophysiological signatures of external and internal attention intersect in complex ways (e.g., Liu et al., 2022; Yu et al., 2022; Liu et al., 2025). Thus, we sought to replicate findings of oculomotor retro-capture for comparison with EEG data. Surprisingly, however, we found no evidence for oculomotor retro-capture, nor evidence consistent with the delayed selection account supported by our EEG data (Figure 2C).

**Figure 2. EEG and Oculomotor Signatures of Visual Selection**. *(A) Spectrogram plotting lateralized changes EEG activity as a function time-locked to probe onset, pooled across the pro- and anti-cue tasks. Inset shows the scalp distribution lateralized alpha band activity (8-13 Hz) over a period spanning 500-1000 ms after probe onset. (B) Lateralized alpha-band activity plotted as a function of task. (C) Lateralized gaze position plotted as a function of probe stimulus location (left vs. right visual field) and task (pro- vs. anti-cue). Shaded regions in panels B and C depict the 95% confidence interval of the mean. Solid and dashed bars at the top and bottom of panels B and C depict epochs where EEG and gaze lateralization were significantly different from 0. The vertical blue and red lines in panel B depict the mean response times during the pro- and anti-cue tasks, respectively.*

Specifically, although we observed clear evidence for horizontal gaze shifts towards the task-relevant stimulus, the directions and latencies of these shifts were identical during the pro- and anti-cue tasks.

Finally, we considered the possibility that retro-capture and delayed selection effects were obscured by pooling data across trials. To evaluate this possibility, we re-computed EEG

**Figure 3. Lateralized EEG Activity Sorted by Task Performance.** *To test whether retro-capture effects were obscured by trial averaging, we recomputed EEG Lateralization during the pro-cue (left column) and anti-cue tasks (right column) after applying a median split to participants' response times (top row) and recall error (bottom row). We found no evidence for retro-capture (i.e., lateralization values significantly greater than 0%).*

lateralization (Figure 3) and gaze bias lateralization (Figure 4) after applying a median split to

participants' response times and recall errors during the pro- and anti-cue tasks. Neither EEG

nor eye-tracking measures of internal selection were influenced by response times nor recall

error, suggesting that trial averaging did not obscure critical effects.

**Figure 4. Lateralized EEG Activity Sorted by Task Performance.** *To test whether retro-capture effects were obscured by trial averaging, we recomputed EEG Lateralization during the pro-cue (left column) and anti-cue tasks (right column) after applying a median split to participants' response times (top row) and recall error (bottom row). We found no evidence for retro-capture (i.e., lateralization values significantly greater than 0%).*

**Discussion**

The present study investigated how endogenous and exogenous influences jointly shape internal selection in WM, and whether multiple physiological systems reveal convergent or dissociable selection dynamics. By combining EEG and eye-tracking during a visuomotor WM task, we found that endogenous–exogenous competition produced robust delays in behavioral responses and in lateralized alpha-band activity indexing spatial selection. Critically, these delays were not mirrored in oculomotor behavior: gaze biases toward the memorized location of the cued item emerged with similar timing in both pro- and anti-cue conditions. Thus, while cortical signatures of internal selection were slowed by competition, oculomotor signatures were not.

Our results suggest that internal selection is implemented through multiple, temporally dissociable mechanisms. Alpha-band lateralization, which tracks spatial prioritization in WM, exhibited clear delays during the anti-cue condition—consistent with prior EEG evidence that competition between endogenous and exogenous factors prolongs the selection of goal-relevant content (Ester & Nouri, 2023). In contrast, gaze biases showed no evidence for retro-capture and no measurable delay, indicating that oculomotor behavior may reflect downstream or post-competitive stages of internal selection. This dissociation aligns with recent work indicating that microsaccadic biases correlate with—but are not necessary for—oscillatory modulations during internal attention (Liu et al., 2022). Cortical oscillations may therefore reflect the internal computation of priority, whereas oculomotor outputs reflect a later implementation or expression of the selected representation.

The most striking finding in our study is the dissociation between oculomotor and neural measures of internal selection. While EEG signals revealed significant delays in the selection of task-relevant memory content during the anti-cue compared to the pro-cue task, records of participants' gaze position produced no evidence for retro-capture nor delayed selection The latter result contrasts with recent work by van Ede et al. (2020), who reported oculomotor "retro-

capture" toward task-irrelevant, cue-matching items in an anti-cue paradigm. We propose that task design differences are responsible for this discrepancy. van Ede et al. (2020) presented an abrupt-onset mid-delay retrocue—a salient visual event that directly matched or mismatched one of the memorized items. In their paradigm, the competitive selection problem had an external, perceptual component: participants witnessed a visual cue during the WM maintenance phase that was incongruent with their task goal. In contrast, our task relied on internal, rule-based competition: the pro/anti manipulation was established through block-level instructions without any salient external cue during the delay. The probe (which instantiated the competition) appeared only after the full delay period, forcing participants to maintain task rules internally throughout the maintenance interval. This distinction is theoretically important, because the explicit mid-delay retrocue in van Ede et al.'s design may have triggered stimulus-driven capture of oculomotor planning by providing a salient visual event that matched task-irrelevant WM content, analogous to attentional capture by abrupt onset in external attention (Theeuwes, 1992; Folk & Remington, 1998). In contrast, our rule-based competition may engage **c**ognitive control mechanisms that delay cortical selection processes without necessarily propagating to oculomotor planning systems.

An alternative, complementary explanation involves the computational role of different neural systems. Oculomotor outputs may reflect a downstream consequence of attentional selection rather than the site of competitive selection itself (Awh, Armstrong, & Moore, 2006). Under this view, by the time oculomotor planning systems receive input regarding which WM item is task-relevant, the competition between endogenous and exogenous factors has already been resolved at earlier cortical stages (indexed by the EEG delay). Oculomotor biases would then reflect only the "winner" of competitive selection, not the temporal dynamics of the competition itself. Consistent with this interpretation, Liu et al. (2022) recently demonstrated that while microsaccadic biases correlate with EEG alpha lateralization during internal attention, microsaccades are not necessary for alpha modulation to occur. Together, these findings

suggest that microsaccades and cortical alpha activity reflect related but dissociable aspects of internal attentional selection, with oculomotor outputs potentially reflecting a post-competitive selection output stage.

A major contribution of this work is clarifying how internal selection resolves competition differently from external attention. Exogenous–endogenous competition in the external domain often produces involuntary capture by salient but irrelevant stimuli (Folk & Remington, 1998; Theeuwes, 1992). In contrast, internal selection appears to resolve competition through slower, controlled processes, without errant prioritization of irrelevant memory content. One functional interpretation is that internal attention operates over already-encoded representations that are inherently more stable and less susceptible to fleeting salience signals. Whereas external attention must rapidly suppress irrelevant sensory inputs to protect behavior, internal attention may tolerate slower, graded resolution processes that emphasize stability over speed. This view resonates with theoretical proposals such as the Internal Dominance Over External Attention (IDEA) hypothesis (Verschooren & Egner, 2023), which posits an inherent bias toward internal information. Our findings suggest that such dominance may come at a computational cost: internal attention preserves goal-relevant content but resolves conflict more slowly than external attention. These findings inform broader debates about how WM supports action. Models that posit unified or parallel selection mechanisms across physiological systems must accommodate the present dissociation. Instead, our data support frameworks positing multiple, partially independent selection processes operating at distinct stages—from cortical prioritization to motor implementation.

Several limitations temper these conclusions. First, we obtained usable eye-tracking data from 21 of 30 participants, reducing power to detect subtle oculomotor effects. Second, our gaze preprocessing pipeline was deliberately minimal, which may have obscured microsaccade-level modulations. Future work incorporating high-resolution microsaccade detection or designs with explicit mid-delay cues (as in van Ede et al., 2020) may uncover oculomotor signatures of

competitive internal selection not apparent here. Additionally, manipulations that vary the type or strength of exogenous cue–memory matching may determine whether internal retro-capture emerges under some conditions but not others.

Together, our findings highlight that internal selection is neither a simple extension nor a direct analogue of external attention. Instead, it is supported by multiple physiological systems that resolve competition in distinct ways. This insight both extends and refines foundational theories of attentional competition by demonstrating how their principles generalize—and where they diverge—when attention operates over internal representations. This work is deeply informed by the intellectual legacy of Charles Folk and Roger Remington, whose pioneering studies revealed how endogenous and exogenous influences jointly shape the selection of external information. Their work demonstrated that attentional competition is not a simple tug-of-war between top-down goals and bottom-up salience, but a dynamic negotiation between the two. By extending this logic to the internal realm of working memory, our findings illustrate how their theoretical framework continues to inspire new questions and guide contemporary research. In showing that internal selection relies on distinct and temporally differentiated mechanisms, we hope to honor their enduring influence on the study of attention and to contribute to the ongoing evolution of ideas they helped bring to the field.

# References

Awh, E., Armstrong, KM., Moore, T. (2006) Visual and oculomotor selection: links, causes, and implications for spatial attention. Trends in Cognitive Sciences, 10, 124-130, 10.1016/j.tics.2006.01.001

Chang, C.-Y., Hsu, S.-H., Pion-Tonachini, L., & Jung, T.-P.(2020). Evaluation of Artifact Subspace Reconstruction for automatic artifact components removal in multi-channel EEG recordings. IEEE Transactions on Biomedical Engineering, 67, 1114–1121. https://doi.org/10.1109/TBME.2019.2930186, PubMed: 31329105

Chota, S., Arora, K., Kenemans, JL., Gayet, S., Van der Stigchel, S. (2025) Microsaccade biases can reflect task-specific spatial memorizations trategies. Frontiers in Neuroscience, 19, 10.3389/fnins.2025.1526213

Delorme, A., & Makeig, S. (2004). EEGLAB: An open-sourcevtoolbox for analysis of single-trial EEG dynamics including independent component analysis. Journal of Neuroscience Methods, 134, 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009, PubMed: 15102499

Ester, E. F., Nouri, A., & Rodriguez, L. (2018). Retrospective cues mitigate information loss in human cortex during working memory storage. Journal of Neuroscience, 38, 8538–8548. https://doi.org/10.1523/JNEUROSCI.1566-18 .2018, PubMed: 30126971

Ester, EF., Nouri, A. (2023) Internal selective attention is delayed by competition between endogenous and exogenous factors. iScience, 26, 107259, 10.1016/j.isci.2023.107259

Ester, E., & Weese, R. (2023). Temporally dissociable mechanisms of spatial, feature, and motor selection during working memory–guided behavior. *Journal of Cognitive Neuroscience*, *35*(12), 2014–2027. https://doi.org/10.1162/jocn_a_02061

Folk, CL., Remington, R. (1998) Selectivity in distraction by irrelevant featural singletons: Evidence for two forms of attention capture. Journal of Experimental Psychology: Human Perception & Performance, 24, 847-858. DOI:10.1037/0096-1523.24.3.847

Kleiner, M., Brainard, D., & Pelli, D. (2007). What's new in Psychtoolbox-3? Perception, 36,1–16. https://hdl.handle.net/ 21.11116/0000-0004-44C8-E

Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. Trends in Cognitive Sciences, 16, 606–617. https://doi.org/10.1016/j.tics.2012.10.007, PubMed: 23141428

Liu, B., Nobre, AC., van Ede, F. (2022) Functional but not obligatory link between microsaccades and neural modulation by covert spatial attention. Nature Communications, 13, 3503, https://doi.org/10.1038/s41467-022-31217-3

Maris, E., & Oostenveld, R. (2007). Nonparamteric statistical testing of EEG- and MEG-data. Journal of Neuroscience Methods, 164, 177–190. https://doi.org/10.1016/j.jneumeth.2007.03.024, PubMed: 17517438

Perrin, F., Pernier, J., Bertrand, O., & Echallier, J. F. (1989). Spherical splines for scalp potential and current density mapping. Electroencephalography and Clinical Neurophysiology, 72, 184–187. https://doi.org/10.1016/0013-4694(89)90180-6, PubMed: 2464490

Souza, A. S., Rerko, L., & Oberauer, K. (2014). Unloading and reloading working memory: Attending to one item frees capacity. Journal of Experimental Psychology: Human Perception and Performance, 40, 1237–1256. https://doi.org/10.1037/a0036331, PubMed: 24730737

Souza, AS., Oberauer, K. (2016) In search of the focus of attention in working memory: 13 years of the retro-cue effect. Attention, Perception, & Psychophysics, 78, 1839-1860, https://doi.org/10.3758/s13414-016-1108-5

Theeuwes, J. (1992) Perceptual selectivity for color and form. Perception & Psychophysics, 51, 599-606, https://doi.org/10.3758/BF03211656

van Ede, F., Checkroud, S. R., & Nobre, A. C. (2019a). Human gaze tracks attentional focusing in memorized visual space. Nature HumanBehavior, 3, 462–470. https://doi.org/10.1038/s41562-019-0549-y, PubMed: 31089296

van Ede, F., Chekroud, S. R., Stokes, M. G., & Nobre, A. C. (2019b). Concurrent visual and motor selection during visual working memory guided action. Nature Neuroscience, 22, 477–483. https://doi.org/10.1038/s41593-018-0335-6, PubMed: 30718904

van Ede, F., Board, AG., Nobre, AC. (2020) Goal-directed and stimulus-driven selection of internal representations. Proceedings of the National Academy of Sciences, 117, 24590-24598, https://doi.org/10.1073/pnas.2013432117

van Ede, F., & Nobre, A. C. (2023). Turning attention inside out: How working memory serves behavior. Annual Review of Psychology, 74, 137–165. https://doi.org/10.1146/annurev-psych-021422-041757, PubMed: 35961038

Verschooren, S., Egner, T. (2023) When the mind's eye prevails: The internal dominance over external attention (IDEA) hypothesis. Psychonomic Bulletin & Review, 30, 1668-1688, https://doi.org/10.3758/s13423-023-02272-8

Yu, G., Herman, JP., Katz, LN., Krauzlis, RJ. (2022) Microsaccades as a marker not a cause for attention-related modulation. eLife, https://doi.org/10.7554/eLife.74168