

Research Paper

Anticipated relevance prepares visual processing for efficient memory-guided selection

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ABSTRACT

Finding an object typically involves using working memory to select relevant visual information *at the right time*. Using EEG, we investigated how predictable changes in stimulus relevance influence top-down visual selection. Participants memorized an oriented grating, followed by a cue indicating which of two sequentially presented probes was relevant for a memory-match/-mismatch judgment. Consistent with earlier work, relevant probes evoked stronger univariate responses than irrelevant probes. Furthermore, responses to (memory-matching and memory-mismatching) probes were more distinct when they were relevant compared to irrelevant. Crucially, using rapid invisible frequency tagging (RIFT), we found that visual responses to the (empty) probe location were enhanced even before the presentation of relevant (compared to irrelevant) probes. Predictable changes in stimulus relevance, therefore, induce both pro-active and re-active changes in visual processing. We conclude that anticipating the (ir)relevance of upcoming visual events enables the visual system to prepare for efficient memory-guided visual selection.

1. Introduction

Picture yourself driving on the highway and seeing a blue sign announcing your vacation destination, the city of Utrecht, in 5 km. Because you roughly know how much time it takes to reach this exit, the immediately upcoming exit signs are irrelevant to you. Instead, after a short wait, you start to look for the blue highway exit sign to Utrecht, find your exit, and enjoy your holiday.

In this example, selecting the relevant road sign is easy as you already know what to look for. Visual working memory (VWM) facilitates this selection process. VWM prioritizes relevant visual input by enhancing the processing of VWM-matching visual events (here: a blue sign) (Soto et al., 2008; Olivers et al., 2011). More specifically, VWM content modulates neural responses (Gayet et al., 2017), conscious access (Gayet et al., 2013), attentional capture (Downing, 2000), and gaze biases (Olivers et al., 2006; Silvis and Van Der Stigchel, 2014; Olmos-Solis et al., 2017) to VWM-matching compared to mismatching visual input. By doing so, VWM allows observers to guide visual selection toward currently relevant visual events (Desimone and Duncan, 1995; Duncan and Humphreys, 1989; Eimer, 2014; Kastner and Ungerleider, 2001; Wolfe, 1994; Wolfe and Horowitz, 2004).

But what will be relevant later may not yet be relevant now. In our highway example, the to-be-selected visual event (i.e., the exit

sign) only became relevant later. Anticipating *when* relevant visual events will appear would allow observers to distribute cognitive resources across time efficiently. Indeed, temporal expectations can aid in perceptual discrimination and/or detection; successfully anticipating visual events is associated with altered neural responses and improved behavioral performance (Coull and Nobre, 1998; Nobre and Van Ede, 2018; Vangkilde et al., 2012; Rohenkohl et al., 2012; Miniussi et al., 1999; Klemmer, 1956; Bertelson and Boons, 1960; Cravo et al., 2013, 2017; Denison et al., 2024). Similarly, memory-guided (i.e., VWM-based) visual selection may benefit from anticipating the appearance of relevant visual events. As our highway example illustrates, memory-guided visual selection (“what are we looking for?”) in daily life is strongly dependent on temporal expectations (“when are we looking for it?”). Thus, temporal expectations may profoundly influence working memory-guided visual selection as well.

Initial research studying anticipation in the context of memory-guided behavior shows that participants are more accurate (and faster) in change-detection tasks when the probe appears after the anticipated interval (Jin et al., 2020; Heuer and Rolfs, 2022). These findings show that temporal expectations improve performance in memory recognition tasks. Such improvements may be the result of either (A) pro-actively enhancing the representation of the memory content, or

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(B) improved sensory processing of the probe item (or both). Following the discovery that active VWM content can be decoded from fMRI data (Harrison and Tong, 2009; Serences et al., 2009), numerous studies have shown that observers can indeed alter the representational strength of VWM content over time, depending on when the recall task is expected to take place (Lewis-Peacock et al., 2012; Rose et al., 2016; LaRocque et al., 2017; Christophel et al., 2018; van Loon et al., 2018; Sahan et al., 2020; Yu et al., 2020). Converging evidence was found using a variety of methods, including pupil size measurements (Zokaei et al., 2019), directional microsaccade biases (Olmos-Solis et al., 2017), and alpha-band suppression in EEG recordings (Van Ede et al., 2017). In the auditory domain, temporal expectations were found to protect VWM content against temporal decay (Wilsch et al., 2018). Thus, it is well established that observers can alter the representational strength of VWM content in anticipation of task requirements. It remains unknown, however, whether visual processing is altered in anticipation of forthcoming sensory events that are relevant to memory-guided behavior. The reason for this is two-fold. Firstly, it is inherently challenging to measure visual processing in anticipation of (i.e., before the presentation of) visual events, because that period of interest (by definition) has no visual event to measure a response to. Secondly, existing neurophysiological markers that are often used to index anticipatory effects are not specific to visual processing (e.g., contingent negative variation, or CNV (Walter et al., 1964)) and/or their role in visual processing is not well understood (e.g., endogenous neural oscillations, such as alpha-band activity) and therefore may be contaminated by VWM-related processes, task difficulty, or motor preparation.

Here, we leveraged a novel EEG-based method that allows for continuous tracking of early visual processing in the absence of any perceptible stimulation. In doing so, we directly tested whether visual processing is enhanced in anticipation of visual events that are relevant (versus irrelevant) to memory-guided selection.

Participants memorized a single oriented grating on each trial, followed by a cue. The cue indicated which of two subsequent gratings had to be compared to the initial memory item (relevant probe) and which could be ignored (irrelevant probe; see Fig. 1 for the paradigm). This design allowed us to investigate (1) how the anticipation of relevant versus irrelevant visual events affects visual processing pro-actively (before stimulus presentation), and how (2) the memory content influences the response to relevant versus irrelevant visual events re-actively (upon stimulus presentation). Importantly, relevant and irrelevant probes were physically identical across trials and only differed in terms of task-relevance, since stimulus changes (cue, orientation, etc.) were counterbalanced within participants. The present design deviates from classical research on attentional selection processes, which typically involves multiple spatial locations. Such task designs prompt participants to prioritize specific spatial locations over others. In contrast, this task design only involves a single spatial location, with relevance varying over time. This approach uniquely allows us to measure changes in visual processing per se, separating them from local changes in visual processing caused by the reallocation of spatial attention.

To measure changes in early visual processing evoked by the mere anticipation of relevant and irrelevant visual events, EEG-based rapid invisible frequency tagging (RIFT) was employed (Arora et al., 2024; Hustá et al., 2025). RIFT can continuously track changes in early visual processing, even in the absence of any perceptible stimulus. This is achieved by ‘tagging’ a location of interest on the screen (here: the stimulus area). Tagging refers to periodic luminance modulation of the screen at 60 Hz (imperceptible to participants). This luminance modulation induces a corresponding oscillatory response in the EEG signal. The strength of this oscillatory response in the EEG (measured as RIFT coherence) varies with how much cognitive resources (attention) are allocated to visual processing of the tagged location (Arora et al., 2025a; Duecker et al., 2024; Ferrante et al., 2023; Zhigalov et al., 2019; Wang et al., 2025a; Çelik et al., 2025). Crucial to the present purpose,

RIFT produces an experimenter-induced marker of early visual processing, which enables us to isolate pro-active effects on visual processing that are not triggered (or modulated) by the conscious perception of a stimulus. In contrast, typical approaches using visible probes inevitably confound pro-active effects with re-active effects, which may not have emerged without said probes. Other approaches using endogenous markers of visual processing (e.g., alpha oscillations) cannot be unequivocally attributed to early visual processing, because they are not experimentally induced (‘tagged’) and may therefore reflect a variety of (early and late, perceptual and post-perceptual) processes. To summarize, RIFT is a non-invasive, location-specific, experimenter-induced oscillatory signal with high temporal resolution that tracks early visual processing at the tagged location.

We predicted that if observers indeed (pro-actively) enhance sensory processing in anticipation of relevant visual events during memory-guided selection, the RIFT response should increase before presentation of a relevant probe compared to an irrelevant probe.

2. Methods

2.1. Experimental model and study participant details

Twenty-five participants with normal or corrected-to-normal vision were recruited at Utrecht University. Each participant attended a 2-hour session and was compensated with either participation credits or €24. Informed consent was obtained, and participants provided their age and gender. The study was conducted in accordance with the protocol approved by the Ethics Committee of the Faculty of Social and Behavioral Sciences at Utrecht University with reference number 863732 – HOMEOSTASIS (approved on 18/03/2020). Out of the initial 25 participants, two exhibited significantly poorer behavioral performance on either Cue 1 or Cue 2 trials (Cue 1: 48.61% versus Cue 2: 96.53% and Cue 1: 94.44% versus Cue 2: 62.50%). As these participants did not seem to adhere to the task instructions (they likely ignored the cue information), they were excluded from further analysis. Additionally, one participant was excluded due to poor EEG data quality. Consequently, a total of 22 participants were included in the eventual analyses.

2.2. Method details

2.2.1. Setup & apparatus

Stimuli were created using Psychtoolbox for MATLAB (Brainard and Vision, 1997; Pelli, 1997) and presented on a projection screen using a ProPixx projector (VPixx Technologies Inc., QC Canada; resolution = 960x540px; refresh rate 480 Hz). The projected screen size was 48x27.5 cm or 35.05x20.51 degree visual angle (dva) in a rear-projection format. Interfacing with the projector (e.g., turning on/off 480 Hz mode) was achieved using the custom Matlab software provided by the company, which was integrated into the experimental code. The ProPixx projector was gamma-calibrated to a linear input–output function. Luminance as measured in a dark room using an external photometer (Gossen Mavo-Monitor USB) yielded 0.95cd/m² for black (RGB [0, 0, 0]), 649cd/m² for gray (RGB [127 127 127]), and 1330cd/m² for white (RGB [255 255 255]) displays. Participants were positioned 76 cm from the screen, using a chin and headrest for alignment.

2.2.2. Task & procedure

Participants performed a modified delayed match-to-sample task (see Fig. 1, “Participant View”). Each trial began by pressing the space bar, which initiated a 1500 ms baseline of untagged fixation, followed by a first oriented grating (hereafter: the memory item), which was presented for 200 ms. Participants were instructed to memorize the orientation of this memory item for a subsequent match/mismatch judgment (i.e., they reported whether the cued probe had the same or a different orientation as the memory item). After a second fixation

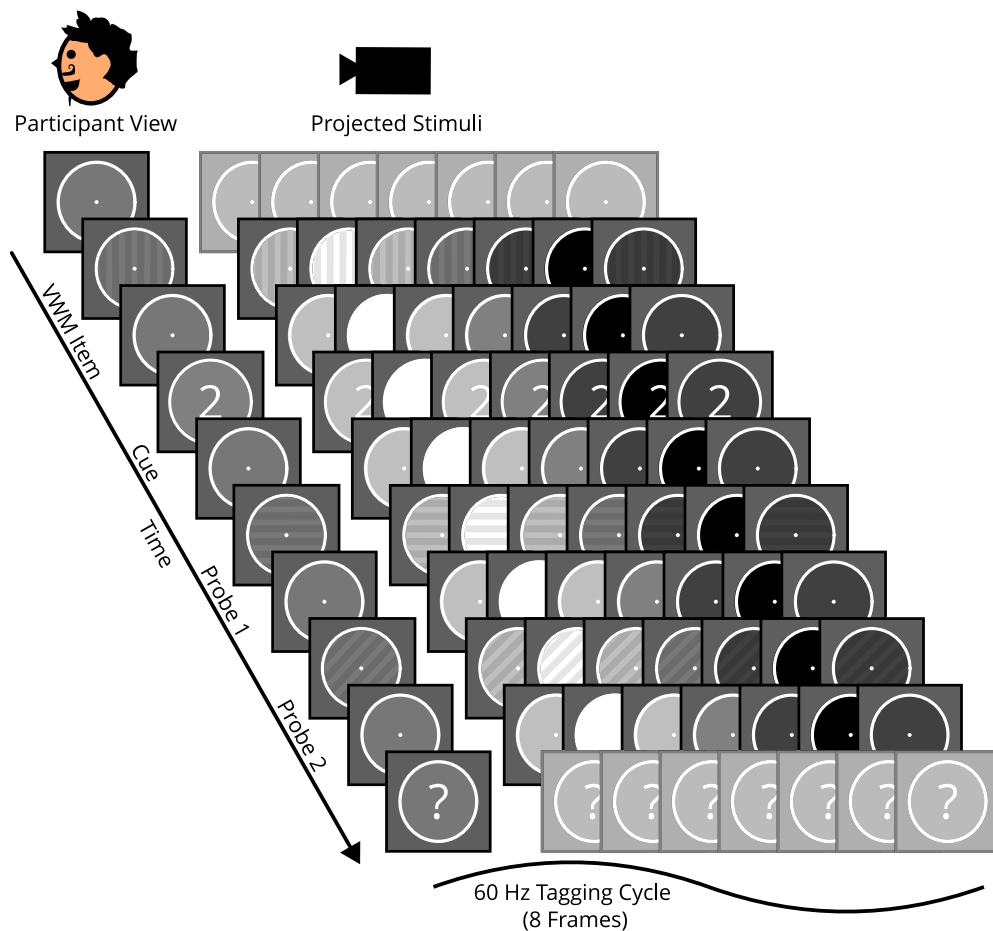


Fig. 1. The left side displays the visual events as perceived by the participants. The luminance changes of a single RIFT cycle (8 frames including the left side) for each of these events are depicted horizontally. Luminance changed periodically at 60 Hz, rendering the luminance changes imperceptible. The first fixation period and the response period are not tagged (continuous gray background). This is an example of a cue “2” trial (participants have to compare the memory item to the second probe) requiring a “different” response (the orientation of the second probe differs from that of the memory item). Untagged periods (fixation before the VWM Item and the response period) are grayed out.

period (1000 ms), a cue was presented for 200 ms (“1” or “2”) informing participants which of two subsequent oriented gratings (the probes; each presented for 200 ms, with a 1500 ms inter-stimulus interval) was relevant for the memory match/mismatch judgment. After a 500 ms fixation period following the offset of the second probe, a question mark was presented, indicating the forced-choice response window (1000 ms). Participants indicated whether the orientation of the cued probe (i.e., first or second) matched the orientation of the memory item by pressing either the left or right control key with the corresponding hand. Each trial ended with a blue circle, signaling a self-paced break. Participants were asked to refrain from using strategies to circumvent the memory component of the task. As an example, we specifically prohibited using one’s fingers as a memory aid for stimulus orientation. Participants were instructed that the irrelevant (i.e., uncued) probe could be ignored.

2.2.3. Stimuli

The stimuli were oriented square-wave gratings (diameter: 6 dva). Twelve orientations, ranging from 10 to 190° to avoid fully vertical and horizontal orientation in 15° steps, were randomly selected. The gratings consisted of alternating shades of gray (127.5 RGB & 95% of 127.5 RGB). The phase value was a random integer between –180 and 180, excluding 0, to prevent fixation on the stripes. The background color was a darker gray (100 RGB) to reduce eyestrain. Fixation dot, response indicator, and stimulus area frame were white (200 RGB). The gratings had soft borders (2D-Gaussian transparency mask) to prevent

edge-based orientation memorization or recall strategies. 60 Hz RIFT was achieved by multiplying the stimulus area RGB values with eight discrete steps of a sinusoidal curve from 0 to 1. A complete tagging cycle takes ~16.667 ms, which corresponds to a frequency of 60 Hz (Fig. 1 - Projector view). This caused the lighter parts of the grating stimuli and the framed stimulus area to vary fully from 0 to 255 RGB, while the darker parts of the grating stimuli varied from 0 to 95% of 255 RGB. RIFT started at the onset of the memory item and ended at the onset of the response screen. Consequently, each trial had a period of 5300 ms of uninterrupted 60 Hz tagging.

2.2.4. Design

Participants completed 12 blocks of 24 trials each, lasting approximately one hour in total, excluding one practice block. The additional practice block consisted of 12 trials, with feedback provided for the first six trials. Per two blocks, trials were balanced for relevant/irrelevant (Cue 1/2) probe, the 12 orientation conditions (10° to 190°), and presented in random sequence. Probes were rotated in one-third of the trials (equally 45° to the right, left, or by 90°). Orientations of all gratings were independent of each other. Each memory item orientation appeared four times per two blocks. Trials within each set of two blocks were presented in a different random order per participant. At the start of a block, participants were informed about the current block number and afterward about their accuracy in the past block for 3000 ms.

2.2.5. Eyetracking

The eyes were binocularly recorded at 500 Hz using an Eyelink 1000 eye tracker (SR Research, Ontario, Canada), with nine-point calibration and validation performed at the start and after each block.

2.2.6. Invalid trials

If participants failed to give a response within the forced-choice window, the response was considered invalid. To ensure adherence to central gaze, trials were aborted and considered invalid if the gaze was outside the stimulus area for more than 208 ms (25 frames at 120 Hz), thus allowing a few short blinks. Blinks were monitored, using the live eyetracking data to detect NaN values. Participants were reminded before the next trial on screen to avoid blinking during trials. If invalid, trials were repeated up to two times at the end of blocks in a random sequence.

Quantification and statistical analysis

2.3. EEG data collection & preprocessing

EEG data were collected using a 64-channel ActiveTwo BioSemi system at 2048 Hz. Preprocessing was done using the Fieldtrip toolbox for MATLAB (Oostenveld et al., 2011). Data was re-referenced to the average of all electrodes, line noise removed (50, 100, 150 Hz) using a discrete Fourier transform, high-pass filtered (0.01 Hz), and split into trials of 6800 ms (1500 ms before VWM onset & 5300 ms until response screen start). Independent component analysis was used to remove oculomotor artifacts. Trials containing other artifacts were identified using visual inspection and removed (average trials excluded per participant = 40.41, $SD = 26.62$).

2.3.1. RIFT - data analysis

Magnitude Squared Coherence (as described in Pan et al., 2022) was used to quantify the strength of the EEG responses at our tagging frequency (60 Hz). To this end, the EEG trials were band-pass filtered (± 1.9 Hz) at 60 Hz using a two-pass Butterworth filter (4th order, Hamming taper). The filtered data were then Hilbert transformed to obtain the analytic signal, which was used to calculate time-varying coherence:

$$\text{coh}(t) = \frac{\left| \sum_{tr=1}^n \vec{M}_x(t) \vec{M}_y(t) e^{i\Delta\phi_{xy}(t)} \right|^2}{n \sum_{tr=1}^n \vec{M}_x(t)^2 \vec{M}_y(t)^2} \quad (1)$$

With n being the number of trials. For each time sample t in trial tr , the time-varying magnitude of an EEG signal is represented by $\vec{M}_x$ and by $\vec{M}_y$ for a synthetic sinusoidal reference signal. The phase difference as a function of time is defined by $e^{i\Delta\phi_{xy}(t)}$. Coherence, therefore, reflects the degree to which the 60 Hz phase (weighted by magnitude) is consistently aligned across trials for each channel. The 60 Hz coherence traces per condition (Cue 1, Cue 2) were averaged across each participant's top five RIFT coherence channels. The top five channels were identified per participant by averaging RIFT coherence across all conditions (Cue 1 and 2) and time points throughout a trial. Previous literature indicates that the number of top channels included does not impact the results (Arora et al., 2025a). Subsequently, per participant, the difference between the Cue 1 RIFT trace and the Cue 2 RIFT trace was calculated to reveal changes in visual processing for the two probe intervals.

2.3.2. Univariate analysis

The preprocessing procedure was the same for all univariate analyses. To preprocess data for univariate analysis, data were downsampled to 128 Hz and frontal channels were removed (FT7, T7, FT8, T8, AF7, AF3, AFZ, AF4, AF8, F7, F8, FP1, FP2, FPz), as these channels are not relevant for the analysis and prone to noise. The data were baseline corrected by subtracting the average of the baseline window (−600 to

−100 ms, before probe onset) from each trial per channel. The EEG data were segmented around probe onset from −650 to 1200 ms (Probe 1) and from −650 to 700 ms (Probe 2; I.e., until response onset).

To confirm how participants engaged with the temporal structure of the task, we compared univariate EEG responses to relevant versus irrelevant and memory-matching versus memory-mismatching visual events. Previous research suggests that responses to relevant (i.e., prioritized) compared to irrelevant visual events should be stronger in posterior channels (parietal/occipital) (Mangun and Hillyard, 1990; Hillyard et al., 1998; Miniussi et al., 1999; Correa et al., 2006). To test for the effect of relevant versus irrelevant visual events on the univariate EEG signal, we averaged EEG data across three consecutive evenly spaced time windows (200 ms) starting at probe onset. We chose this data driven approach because we had no prior expectation for the topographical location of the effect of relevance. Within each window and for every channel, the response difference between relevant and irrelevant visual events was assessed using a two-sided t-test (p-values adjusted for multiple comparisons by controlling the false discovery rate FDR; Benjamini and Yekutieli, 2005; Benjamini and Hochberg, 1995; Benjamini and Yekutieli, 2001).

Furthermore, if observers made effective use of the temporal expectations during memory-guided visual selection, the neural response difference between memory-matching and memory-mismatching visual events should be stronger when events are relevant compared to irrelevant. To test whether this is the case, we leveraged the same approach as described above (relevant vs irrelevant ERP effect); Here, however, we compared the effect of memory-matching versus memory-mismatching visual events when they are relevant and when irrelevant (see Fig. 3A). Because this approach is agnostic about the spatial location of the effect (but lacks temporal resolution), it allowed us to determine the shared set of channels between Probe 1 and Probe 2 capturing the difference between memory-matching and memory-mismatching responses for further analysis investigating the temporal development of the effects with more precision. For the channel selection, we only considered the memory-match versus memory-mismatch effect when the probe was relevant, because then the effect should be the strongest (i.e., the effect should be weaker/absent when probes are irrelevant). Based on this shared set of channels (marked with black asterisks in Fig. 3A, middle row), we averaged across participants split on the conditions of interest (relevant & irrelevant, memory-match & memory-mismatch; see Fig. 3B). The increased temporal resolution of the ERPs allowed us to employ tests with increased sensitivity to time resolved effects (i.e., permutation cluster tests; see Significance testing) to test the four key comparisons:

1. Neural responses to relevant versus irrelevant visual events
2. Neural responses to relevant memory-matching versus memory-mismatching visual events
3. Neural responses to irrelevant memory-matching versus memory-mismatching visual events
4. Neural responses to relevant versus irrelevant memory-matching versus memory-mismatching visual events

2.3.3. Significance testing

Significance for all time-re analyses was determined using non-parametric cluster-based permutation tests (see Maris and Oostenveld, 2007). The testing procedure consisted of three steps: 1) For each time point of the to-be-tested trace, a t-test identified samples differing significantly from zero (one-sided, $p < 0.1$). For clusters of at least 5 consecutively significant samples, the sum of t-values was computed, resulting in a cluster-level-t-mass. 2) To produce a null-distribution of t-masses (reflecting the expected distribution under the null hypothesis), all traces were randomly sign-reversed (preserving autocorrelations between time points in the null distribution) 5000 times, resulting in 5000 new datasets containing a randomized trace per participant.

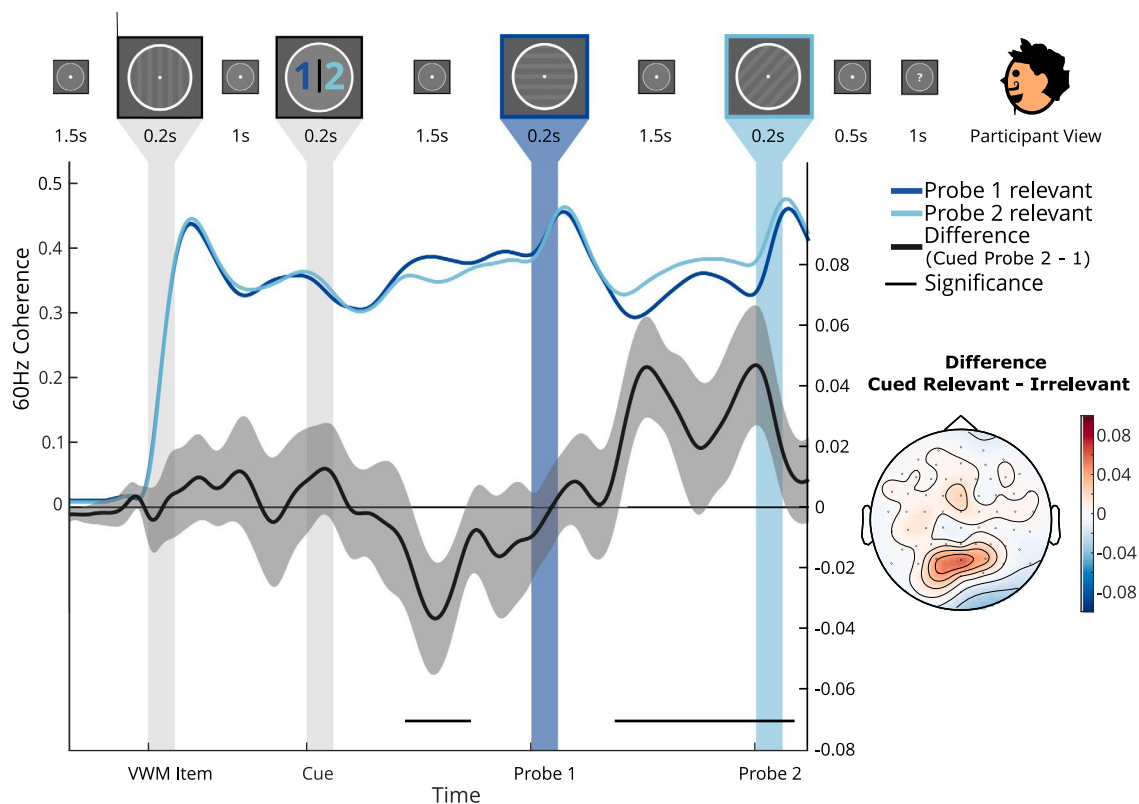


Fig. 2. Anticipating a relevant (compared to irrelevant) probe enhanced visual processing *before* probe presentation. The top row depicts the time course of events as seen by participants. Average RIFT coherence (quantifying early visual processing; left y-axis) over time, separated for trials in which Probe 1 (dark blue) or Probe 2 (light blue) was relevant. The paired difference between conditions (right y-axis) is depicted in black. Shaded area: 95%-CI. Horizontal black line: significance according to a permutation-based cluster analysis, $p < .05$. Topography: The average RIFT coherence difference between relevant and irrelevant probes (i.e., Probe 1 & 2 relevant versus irrelevant) across significant intervals.

The same analysis procedure used for the observed data (Step 1) was applied to each of these 5000 datasets; except, only the largest cluster identified in each of the datasets was included in the null distribution. 3) t-mass values of the observed clusters higher than 95% (i.e., $\alpha = 0.05$) of the t-mass values in the null distribution were marked as significant. For all significant clusters, we report the exact p -value (2 decimals) and the time range where the 95%-CIs of the observed data differ from zero (the longest deviation was reported). Note that we do not report the time range of the cluster itself, because cluster-level significance establishes only that an effect exists, not where it is situated in time (Sassenhagen and Draschkow, 2019). Since the procedure only tested for positive deviations from zero, time series with suspected negative deviations were sign-reversed.

3. Results

3.1. Behavioral performance

All participants completed the task with an average accuracy (percentage of correctly identified relevant probes as mis-/matching the VWM Item) of $M = 94.44\%$ across all trials ($SD = 4.90\%$). On average, participants performed similarly for both cues, with 94.89% ($SD = 5.53\%$) for Cue 1 and 93.96% ($SD = 4.95\%$) for Cue 2.

3.2. RIFT reveals anticipatory early visual processing enhancements prior to relevant visual events

First, we addressed the main question by testing for pro-active neural responses before probe onset. To this end we ensured 60 Hz RIFT coherence was observed strongest in the posterior electrodes (Supplementary Fig. 1). To determine whether visual processing was enhanced

in anticipation of relevant compared to irrelevant visual events, we investigated the level of RIFT coherence before probe presentation.

In the interval before Probe 1 presentation, 60 Hz RIFT coherence was higher when Probe 1 was cued to be relevant versus when it was cued to be irrelevant (permutation test, $p = .04$), supporting our hypothesis (Fig. 2); 95%-CIs [2.00, 2.40]s. Similarly, RIFT coherence was higher before Probe 2 presentation when Probe 2 was cued as relevant compared to irrelevant (permutation test, $p < .001$), again supporting our hypothesis (Fig. 2); 95%-CIs [3.57, 4.821]s. The average RIFT difference between relevant and irrelevant probes (i.e., Probe 1 & 2 relevant versus irrelevant) across significant intervals was localized in posterior electrodes. Interestingly, these differences in RIFT coherence did not persist beyond the anticipatory period. That is, the difference in RIFT responses between relevant and irrelevant conditions disappeared shortly after probe presentation.

3.3. Enhanced response to relevant probes

Next, we analyzed re-active neural responses to the probes to confirm that participants engaged with the temporal structure of the task. We expected that relevant probes would evoke a stronger univariate response than irrelevant probes. Indeed, we found an overall stronger EEG response to relevant visual events compared to irrelevant visual events, for both Probe 1 and Probe 2 (see Fig. 3A: t-test, $p_{adj} < .05$; & Fig. 3C: permutation test_{Probe1}, $p < .001$; 95%-CIs [0.17, 1.20]s; permutation test_{Probe2}, $p < .001$; 95%-CIs [0.28 0.70]s).

Finally, effective use of temporal expectations during memory-guided visual selection of memory-matching and memory-mismatching visual events (i.e., blue highway exit signs versus white traffic signs) should evoke differential responses when they are relevant (i.e., in

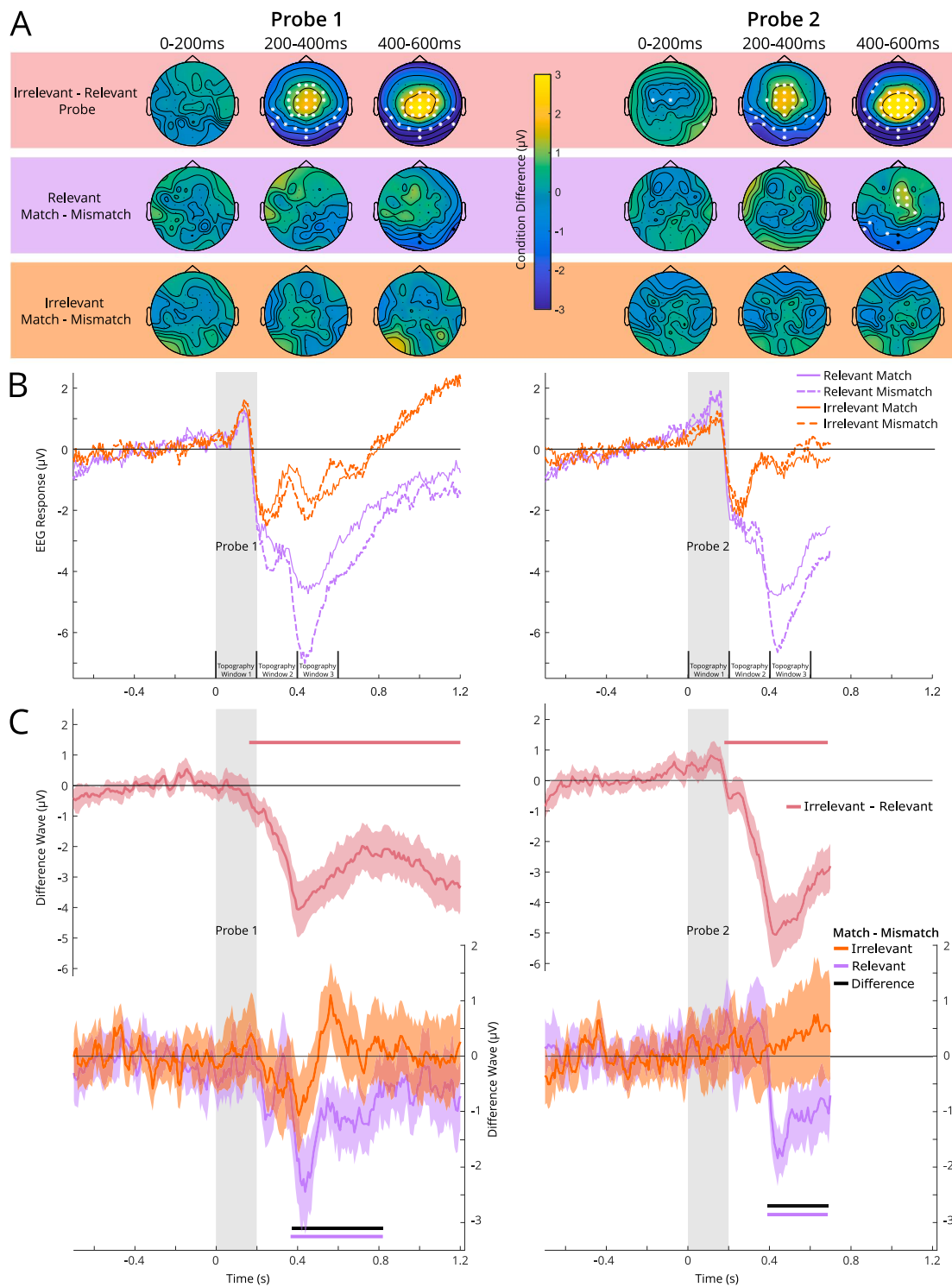


Fig. 3. Univariate responses (i.e., event-related potentials) to Probe 1 and 2, for the four different conditions of interest (relevant and irrelevant, matching and mismatching probes). **A** depicts whole-scalp topographies of the difference between relevant and irrelevant probes (top), and the difference between matching and mismatching probes when they are relevant (middle) and when they are irrelevant (bottom). Asterisks denote significant channels according to a two-sided t-test (FDR corrected for multiple comparisons, $p < .05$). **B** depicts the full time course of the event-related potential (ERP) for a selection of posterior electrodes (based on the whole-scalp topographies in Panel A; black asterisks), averaged across participants. **C** depicts the difference between relevant and irrelevant time courses (top), and the difference between matching and mismatching time courses, separately for relevant and irrelevant probes (bottom). Shaded areas depict the 95%-CIs across participants. Horizontal thick lines denote significant ERP differences according to a permutation-based cluster analysis, $p < .05$.

5 km), but not when they are irrelevant (i.e., right now). Indeed, memory-matching and memory-mismatching events evoked a differential response when they were relevant (see Fig. 3A: t-test, $p_{\text{adj}} < .05$; & Fig. 3C: permutation test_{Probe1}, $p < .001$; 95%-CIs [.38 .80]s;

permutation test_{Probe2}, $p < .001$; 95%-CIs [.41, .70]s), but not when they were irrelevant (t-test, $p_{\text{adj}} < .05$), in posterior electrodes. Crucially, this differential response to relevant memory-matching versus memory-mismatch visual events was distinct from the differential

(match/mismatch) response to irrelevant visual events (Fig. 3C, Match - Mismatch: Difference; permutation test_{Probe1}, $p = .002$; 95%-CIs [.38 .70]s; permutation test_{Probe2}, $p = .002$; 95%-CIs [.41 .64]s)). This was the case for Probe 1 as well as for Probe 2. Thus to summarize: relevant visual events reliably evoked a stronger re-active response than irrelevant visual events. This response was only modulated by memory-content when the probe was cued as relevant.

4. Discussion

We examined the dynamics of memory-guided visual selection in the face of relevant and irrelevant visual events. The results demonstrate that event relevance affects visual processing during memory-guided selection. Specifically, anticipating relevant — rather than irrelevant — visual events (1) increases RIFT coherence prior to the event onset, and subsequently (2a) increases univariate responses to the events themselves, and (2b) increases the response difference between memory-matching and memory-mismatching events. In sum, the anticipated (ir)relevance of a visual event (1) pro-actively enhances early visual processing, and (2) re-actively modulates the neural response to the visual event itself. Anticipating the (ir)relevance of upcoming events, then, enables the visual system to prepare for efficient memory-guided visual selection.

4.1. Enhanced visual processing prior to relevant visual events

We hypothesized that the temporal structure of the task would allow observers to change the intensity of early visual processing over time, depending on when the relevant visual event was expected to occur. RIFT tracked anticipatory changes in visual processing (before event onset) with high temporal resolution. We found increased RIFT coherence preceding relevant compared to irrelevant probes, despite visual stimulation being constant (i.e., same temporal structure and balanced probe orientations). This was observed in the period preceding both probes, reflected in a mirrored difference wave (cued Probe 1 - cued Probe 2) across the duration of a trial. Specifically, when the first probe was relevant for the memory task, there was a relative increase in the RIFT response before the first probe, and a subsequent decrease before the second probe; conversely, when the second probe was relevant, there was a relative decrease in the RIFT response before the first probe, followed by an increase before the second probe. Our findings show that early visual processing can be flexibly up- and down-regulated over time, in anticipation of relevant visual events, relative to irrelevant visual events. These pro-active changes in early visual processing emerged well (approximately up to one second) before the actual stimulus was presented.

It is noteworthy that memory load differed in the period before Probe 1 and the period before Probe 2 due to the task design. Before Probe 1, participants had to maintain the memory item in both relevancy conditions, but in the delay period preceding Probe 2, participants could drop the memory item if Probe 1 was relevant (immediately after completing the comparison). The larger RIFT response preceding a relevant probe compared to an irrelevant probe in the second delay period (i.e., Cue 2 versus Cue 1) could therefore reflect a difference in memory load rather than a difference in relevance. This caveat similarly applies to the re-active responses to Probe 2. Critically, however, all key results were not only observed for Probe 2, but also for Probe 1, where memory load was identical between conditions (Fig. 2; Fig. 3). Therefore, both the pro-active RIFT response and the re-active univariate responses were uniquely modulated by relevance, and not confounded by differences in task demands.

Based on the present results alone, we cannot determine the absolute direction of the visual processing changes. Observers may up-regulate early visual processing in anticipation of relevant visual events (the cued item) or down-regulate early visual processing in anticipation of irrelevant visual events (the uncued item), or both. Future studies,

including a condition without visual events (i.e., a baseline), may be needed to arbitrate between these possibilities definitively. It is worth noting that it is difficult to establish a true baseline of visual processing over time (even without stimulus presentations, participants will form expectations about upcoming visual input, e.g., Hazard rates). An alternative approach would be to reduce the formation (or usefulness) of expectations by making the onset time of the target unpredictable.

The present results do align with previous behavioral and neurophysiological research, which has identified a diverse range of processing benefits for inputs that can be anticipated (Coull and Nobre, 1998; Heuer and Rolfs, 2022; Nobre and Van Ede, 2018; Vangkilde et al., 2012; Rohenkohl et al., 2012; Miniussi et al., 1999; Klemmer, 1956; Bertelson and Boons, 1960). In most of these studies, there was no “distracting” (or irrelevant) visual event that required suppression. Typically, participants are cued to expect either an imminent relevant or a distant relevant target. It is plausible that participants up-regulate processing in anticipation of imminent relevant visual events rather than (only) down-regulate processing in anticipation of distant relevant visual events. This suggests that anticipatory effects observed in the present study — at least partly — reflect up-regulation of visual processing in the face of relevant visual events (and cannot be fully explained by the suppression of irrelevant visual events). Furthermore, the results extend previous findings investigating the anticipated (ir)relevance of visual events using visible frequency tagging (SSVEPs), which already hinted at an increase in visual processing in anticipation of relevant compared to irrelevant probes (Denison et al., 2024), but could not definitively distinguish between pro-active and re-active effects due to the visibility of the tagging (while the frequency tag is irrelevant to the task, the visible changes on screen still act as an exogenous cue on visual attention and possibly interfering with top-down control).

At face value, the observed pro-active visual processing changes are similar to earlier work on temporal expectations showing anticipatory modulations in visual processing in the absence of a memory task (Samaha et al., 2015; Van Ede et al., 2020). However, it remains an open question whether and how anticipatory changes in visual processing depend on task context; particularly whether or not visual information is concurrently maintained in working memory. Future studies should thus directly compare visual processing preparation during memory-guided visual selection to visual processing during pure perceptual tasks.

Crucially, the present study expands on this previous literature on temporal expectations by measuring how anticipating the (ir)relevance of a visual event affects early visual processing in particular. RIFT is interpreted to reflect neural excitability of the early visual cortex (Duecker et al., 2025, 2021), after Studies using RIFT with MEG have localized the source of the RIFT signal to primary and secondary visual cortex (Duecker et al., 2025, 2021; Zhigalov and Jensen, 2020; Schneider et al., 2023). In addition, because RIFT is experimenter-induced (and because the measurement of the RIFT response relies on the known phase of the oscillatory response), the RIFT response can be isolated from other, non-phase-aligned oscillations in the neural signal, even when occurring in similar frequency ranges (e.g., eye-movement-induced gamma-band responses (Yuval-Greenberg et al., 2008)). Previous research using multiple RIFT frequencies (i.e., 60 Hz and 64 Hz) has shown that when phase aligning (phase-shuffled) trials for one frequency (e.g., 60 Hz), there is no coherence response for the other (e.g., 64 Hz; Wang et al., 2025a; Arora et al., 2025b). In contrast, the exact relationship of endogenous responses (e.g., alpha oscillations) to visual processing is debated (Zhigalov and Jensen, 2020; Brickwedde et al., 2025). Therefore, previous evidence relying on endogenous responses to conclude about anticipatory visual processing changes is equally ambiguous. Here we show, for the first time, that temporal expectations modulate specifically early visual processing in the period preceding (ir)relevant stimuli. These anticipatory changes in early visual processing may lie at the basis of behavioral and neural biases observed in extant studies manipulating temporal expectations.

4.2. Enhanced neural response to relevant visual events

Moving beyond the anticipatory period, we also asked how relevance influences the neural (re-active) responses to the visual events themselves. We found that relevant visual events evoke a stronger neural response than irrelevant visual events. Importantly, relevant and irrelevant visual events did not differ systematically in their visual features and, therefore, do not underlie the observed response differences. Overall then, these results align with existing work observing stronger (re-active) neural responses to targets presented at (cued) relevant compared to irrelevant spatial locations (Mangun and Hillyard, 1990; Hillyard et al., 1998), and time points (Miniussi et al., 1999; Correa et al., 2006).

Within the context of VWM-guided selection, the preparatory enhancement of visual processing may facilitate perceptual comparisons between the relevant visual events (what is seen) and VWM content (what is searched for). Thus, we hypothesized that the response difference between memory-matching and memory-mismatching visual events (i.e., the object one is looking for versus other objects) is larger when the item is currently relevant, compared to when it is not. In line with this hypothesis, we found dissociable univariate responses to (i.e., ERP differences between) memory-matching and memory-mismatching visual events when probes were relevant for the memory task, but not when they were irrelevant. Thus, temporal expectations are used to regulate the memory-based differentiation between target and distractor objects.

This finding makes intuitive sense because —both in our experiment and in daily life— target and distractor objects require different behavioral actions (exit the highway or not) when they are relevant, but not when they are irrelevant. The present findings add to a growing literature investigating how memory-based modulations of visual processing depend on the attentional state of the visual working memory content. Previous literature has shown that currently relevant memory items bias concurrent visual processing more strongly than currently irrelevant memory items (Olivers et al., 2011; Wang et al., 2025b). This line of research, however, mainly compared how multiple parallel memory items in different attentional (or: relevancy) states influence perception. In this case, however, we explicitly studied how changes in the relevance of a single memory item influenced concurrent visual processing. This may be more similar to real-world situations, in which relevancy changes over time, and observers typically do not load more than one item in memory (Draschkow et al., 2021; Sahakian et al., 2023; Van der Stigchel et al., 2019; Qing et al., 2025). Here we show that as the relevance of a single memory item for behavior waxes and wanes, its influence on visual selection follows.

An exploratory univariate analysis of the whole trial (see Supplementary Fig. 2) revealed baseline differences between relevance conditions already before probe onset; anticipating probes as relevant (compared to irrelevant) increased EEG voltage (significant only for Probe 2), thus mirroring the effects observed with RIFT. Tentatively, the (non-significant) pro-active change in EEG voltage before relevant (compared to irrelevant) probes could be regarded as a preparatory mechanism to enable a subsequent stronger re-active response to relevant probes.

4.3. Anticipatory changes in memory representations

An outstanding question pertains to whether and how memory representations change in anticipation of an upcoming visual event. Indeed, in parallel to the observed enhancement of visual processing prior to relevant visual events, one may also expect an anticipatory sharpening of the visual working memory content. In support of this latter possibility, recent studies investigating the impact of temporal expectations on memory recall revealed that VWM content is more resistant to predictable than to unpredictable visual interference (Van Ede et al., 2018; Gresch et al., 2021). However, these studies did not

directly measure the representational format or strength of the memory content in anticipation of the (relevant and irrelevant) visual events. More direct evidence comes from fMRI decoding studies, in which a cue indicated which of two items held in VWM would be relevant for the next of two consecutive recall tasks. These studies have shown that observers can indeed flexibly enhance relevant VWM representations in anticipation of a memory task (Lewis-Peacock et al., 2012; Rose et al., 2016; LaRocque et al., 2017; Christophel et al., 2018; van Loon et al., 2018; Sahan et al., 2020; Yu et al., 2020). In the context of visual search, recent fMRI decoding studies have shown that working memory representations of a search target —generated during search preparation— depend on contextual expectations (e.g., about the location of a target object, or the appearance of distractor objects; Gayet and Peelen, 2022; Lerebourg et al., 2024). These findings demonstrate that VWM contents can be strategically altered to match situational demands in a search task context. Relatedly, VWM representations can be dynamically adjusted (from a sensory to an action-oriented format) to meet current task demands (Henderson et al., 2022).

Together, these findings highlight the adaptability of working memory contents to the changing demands of dynamic environments. By extension, VWM representations likely also vary in response to the type of temporal expectations investigated. Unfortunately, EEG decoding methods thus far have been relatively unsuccessful in decoding the content of visual working memory over a prolonged period. Therefore, future work is needed (e.g., using combined fMRI-EEG) to directly test whether the changes in early visual processing established here are accompanied by a corresponding sharpening of the VWM content.

5. Conclusion

In sum, when driving on a highway, you do not continuously and indiscriminately compare the visual input of the right side of the road with the highway exit sign that you are looking for. Instead, you prioritize visual input during the period in time when you expect the sign to appear. Specifically, when the anticipated highway exit is imminent, you preemptively enhance early visual processing, which may benefit the comparison between the visual information collected by your sensory organs and the visual representation of the exit sign held in memory. Taken together, anticipating the relevance of visual events enables the distribution of scarce attentional resources over time, in support of efficient memory-guided visual selection.

CRedit authorship contribution statement

Lasse Dietz: Writing – review & editing, Writing – original draft, Visualization, Software, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Christoph Strauch:** Writing – review & editing, Supervision, Project administration, Methodology, Formal analysis, Conceptualization. **Kabir Arora:** Writing – review & editing, Software, Methodology, Formal analysis. **Stefan Van der Stigchel:** Writing – review & editing, Supervision, Project administration, Conceptualization. **Samson Chota:** Writing – review & editing, Supervision, Software, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Surya Gayet:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

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Ethics approval

The study was conducted in accordance with the protocol approved by the Ethics Committee of the Faculty of Social and Behavioral Sciences at Utrecht University with reference number 863732 – HOMEOSTASIS (approved on 18/03/2020).

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the author(s) used ChatGPT in order to generate possible alternative sentence structures. After using this tool or service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary material related to this article can be found online at <https://doi.org/10.1016/j.brainres.2026.150558>.

Data availability

Preprocessed EEG, raw behavioral data, and the corresponding analysis are available as of the date of publication at the Open Science Framework: <https://osf.io/7ve8m/>.

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