

Reviewed Preprint

v1 • September 10, 2026

Not revised

✉ For correspondence:

slu@pku.edu.cn

Competing interests:

No competing interests declared

Funding:

See [page 16](#)
Reviewing editor: Simon van Gaal,
University of Amsterdam,
Netherlands

© 2026, Wen et al. This article is distributed under the terms of the [Creative Commons Attribution License](#), which permits unrestricted use and redistribution provided that the original author and source are credited.

Sequential alpha and theta dynamics resolve competition between rival visual stimuli

Wen Wen^{1,5}, Yichen Wu¹, Robert MG Reinhart⁵, Sheng Li^{1,2,3,4} ✉

¹School of Psychological and Cognitive Sciences, Peking University, Beijing, China • ²PKU-IDG/McGovern Institute for Brain Research, Peking University, Beijing, China • ³Key Laboratory of Machine Perception (Ministry of Education), Peking University, Beijing, China • ⁴Beijing Key Laboratory of Behavior and Mental Health, Peking University, Beijing, China • ⁵Department of Psychological & Brain Sciences, Boston University, Boston, United States

eLife Assessment

In this study, electroencephalography was recorded during a binocular-rivalry paradigm in which participants viewed a target and a distractor stimulus. The stimuli were independently frequency-tagged, allowing the researchers to track target and distractor processing over time. The findings suggest that parietal alpha oscillations initially segregate competing inputs, followed by frontal theta activity associated with suppression of distractor representations. The significance of these findings is **valuable**, although the strength of the evidence remains **incomplete**, because of specific experiment design choices and methodological limitations.

<https://doi.org/10.7554/eLife.112007.1.sa3>

Abstract

Attention plays a central role in selecting information for conscious perception. Because natural environments are structured, prior knowledge about relevant and irrelevant features can guide this selection. However, prior knowledge about distractors can enhance their neural representation, raising the question of how the brain prevents such enhancement from interfering with behavior. We addressed this question by combining a binocular rivalry paradigm with frequency-tagged stimuli to independently track target and distractor signals during sustained perceptual competition. We identified a sequential pattern of oscillatory dynamics underlying stable perception. Early parietal alpha activity (8-12 Hz) was associated with the segregation of competing inputs without altering sensory gain. This was followed by frontal theta activity (3-7 Hz), which was linked to the reactive suppression of distractors representations. Importantly, alpha-mediated gating effects are most pronounced under high perceptual uncertainty, where they facilitated the stabilization of weak target signals and promoted their access to conscious awareness. Together, these findings demonstrate that perceptual competition is resolved through a coordinated sequence of proactive gating and reactive suppression.

Introduction

Our brain is constantly bombarded with more sensory input than it can fully process, yet we perceive a seamless, unified world rather than a chaotic flux of signals. This stability depends on the brain's ability to orchestrate access to consciousness, prioritizing goal-relevant inputs while suppressing irrelevant information. Selective attention serves as the primary gatekeeper in this process, resolving the competition for limited processing resources. Importantly, prior experience and learned expectations allow the brain to anticipate upcoming demands and allocate processing resources accordingly (Anderson 2021 [↗](#)). Understanding how such knowledge shapes attentional control is therefore fundamental to explaining how the brain constructs a coherent visual reality.

Extensive research has shown that prior knowledge about target features, such as knowing where or what to look for, can significantly enhance attentional performance by facilitating the selection of task-relevant input (Corbetta and Shulman 2002 [↗](#); Gazzaley and Nobre 2012 [↗](#)).

However, the converse remains less well understood: can attentional selection be improved by knowing what to ignore? This question is particularly important for two key reasons. First, natural environments are structured and governed by regularities. We typically engage with visual scenes informed by prior knowledge derived from working memory (Soto et al. 2008 [↗](#)), long-term memory (Hutchinson and Turk-Browne 2012 [↗](#)), or learning (Theeuwes et al. 2022 [↗](#)).

Second, targets rarely appear in isolation. Given the limited computational resources, the brain must arguably do more than just amplify targets; it must actively shield conscious processing from predictable interference. This raises a central question: can the brain utilize distractor knowledge to bar specific features from higher-level processing?

When distractor features are known in advance, the exclusion of irrelevant inputs can occur either proactively before stimulus onset or reactively after interference occurred (Liesefeld, Heinrich R. et al. 2024 [↗](#); Theeuwes 2025 [↗](#)). These two forms of inhibition are thought to rely on distinctive neural mechanisms (Chelazzi et al. 2019 [↗](#); Geng 2014 [↗](#); Noonan et al. 2018 [↗](#); van Moorselaar and Slagter 2020 [↗](#)). Proactive inhibition acts as a preemptive strategy to suppress distractors and reduce their ability to capture awareness. Studies have shown decreased excitability of corresponding sensory cortex in anticipation of distractors (Ferrante et al. 2023 [↗](#); Snyder and Foxe 2010 [↗](#)), as well as stronger suppression of spatial locations where distractors frequently appear (Wang et al. 2019 [↗](#)). Reactive inhibition, by contrast, is engaged after distractors are encountered and operates through mechanisms such as disengagement (Liesefeld, Heinrich René et al. 2017 [↗](#); Lin et al. 2024 [↗](#); Moher and Egeth 2012 [↗](#)) or signaled suppression (Gaspelin and Luck 2018 [↗](#); Sawaki and Luck 2010 [↗](#)). Both forms of inhibition rely on top-down control, mediated by frontal theta activity (3-7Hz), which supports the dynamic regulation of sensory input in accordance with task demands (Cavanagh and Frank 2014 [↗](#); de Vries et al. 2019 [↗](#); Wen et al. 2022 [↗](#)).

An unresolved issue is how these inhibitory signals prevent distractors from disrupting visual coherence (Noonan et al. 2018 [↗](#); van Moorselaar and Slagter 2020 [↗](#)). One class of accounts proposes that inhibition operates directly by reducing sensory gain for distractor representations. Another class emphasizes indirect control mechanisms, in which attentional priorities are enforced by regulating the flow of information without altering sensory gain. This distinction is closely linked to ongoing debates about the functional role of alpha-band oscillations (8-12 Hz) (Bonfond and Jensen 2024 [↗](#); Klimesch 2012 [↗](#); Peylo et al. 2021 [↗](#); Yang et al. 2024 [↗](#)). Alpha oscillations have long been associated with modulating neuronal excitability of sensory regions and neural responses to sensory input (Foxe and Snyder 2011 [↗](#); Iemi et al. 2022 [↗](#); Richter et al. 2025 [↗](#); Van Diepen et al. 2019 [↗](#)). Yet accumulating evidence suggests that alpha oscillations may instead gate information flow in a goal-dependent manner, routing relevant and irrelevant signals differently to determine their access to higher-order processing, without directly suppressing sensory responses (Antonov et al. 2020 [↗](#); Bonfond and Jensen 2024 [↗](#); Duecker et al. 2025 [↗](#);

Gundlach et al. 2020 [↗](#); Morrow et al. 2023 [↗](#); Zhigalov and Jensen 2020 [↗](#)). Distinguishing between direct gain modulation and indirect gating therefore remains a central challenge for understanding the neural mechanisms of distractor inhibition.

Here, we addressed this challenge using a binocular rivalry paradigm, which generates strong, sustained visual competition for access to consciousness by presenting incompatible stimuli separately to each eye. This provides a critical advantage over traditional visual search paradigms. In visual search, a target is embedded among multiple distractors within the same visual field; consequently, the perceptual competition is transient, and the corresponding neural signals are entangled. These limit mechanistic inferences about how prior knowledge shapes conscious processing. By combining sustained binocular rivalry with frequency-tagged steady-state visual evoked responses (SSVERs), we bypassed these limitations, gaining the ability to independently track the sensory gain of both the target and the distractor as they fought for perceptual dominance. Participants view two colored gratings flickering at different frequencies, one designated as the target and the other as the distractor (24 Hz for the target and 20 Hz for the distractor; Figure 1A [↗](#)). Their task was to report the color of the target grating at the end of each trial. On each trial, participants were cued in advance about the orientation of either the upcoming target or distractor grating, creating two conditions: target cueing (TgtCue) and distractor cueing (DistCue). These conditions were mixed within each block (see Methods for discussion of a no-cue condition).

Results

Absence of distractor-related cost in distractor-cueing trials

To assess how prior knowledge modulates perceptual competition, we first examined behavioral performance under target and distractor cueing. As expected, participants showed smaller color deviation in their responses when the target grating was presented to the dominant eye (hereafter ‘target-dominant trials’), compared to when distractor gratings were presented to the dominant eye (Figure 1B [↗](#), $F(1, 140) = 10.918$, $p = 0.001$, $\eta^2 = 0.199$) (Because participants were not required to report the dominant percept, we cannot directly determine which stimulus held perceptual dominance at a given moment. Instead, trials were categorized based on whether the target or distractor grating was presented to the participant’s dominant eye. While stimuli presented to the dominant eye typically gain initial perceptual dominance, this is not guaranteed on every trial and may not persist throughout the entire trial. Unless otherwise noted, the terms “target-dominant” and “distractor-dominant” refer specifically to stimulus presentation to the dominant eye, rather than the perceptual experience). Responses were more precise in target cueing condition than distractor cueing condition ($F(1, 140) = 10.484$, $p = 0.002$, $\eta^2 = 0.157$). Moreover, cueing effects differed as a function of stimuli dominance ($F(1, 140) = 4.014$, $p = 0.047$, $\eta^2 = 0.084$). In target-dominant trials, performance of the target cueing condition was better than distractor cueing condition (TgtCue vs. DistCue: $p_{\text{bonferroni}} = 0.011$). However, performance was comparable between the two cueing conditions in distractor-dominant trials (TgtCue vs. DistCue: $p_{\text{bonferroni}} = 1.000$).

To clarify which components of behavior contributed to this pattern, we applied a probabilistic mixture model on response deviations (Bays et al. 2009 [↗](#)). The results showed that cueing modulated the likelihood of reporting the target and distractor in target-dominant trials, without affecting response precision or guessing rates (see Figure. S1). Specifically, participants were more likely to report the target color and less likely to report the distractor color in target cueing condition than distractor cueing condition when target was dominant (cueing effect on probability of reporting target: $p_{\text{bonferroni}} = 0.004$; cueing effect on probability of reporting distractor: $p_{\text{bonferroni}} = 0.007$). No such cueing effect was observed in distractor-dominant trials ($p_{\text{bonferroni}} > 0.736$).

The behavioral cueing effect in target-dominant trials could arise from two mechanisms. One possibility is that target cueing enhances the sensory representation or perceptual dominance of the target, either by stabilizing its dominance (Dieter and Tadin 2011 [↗](#)) or reducing the

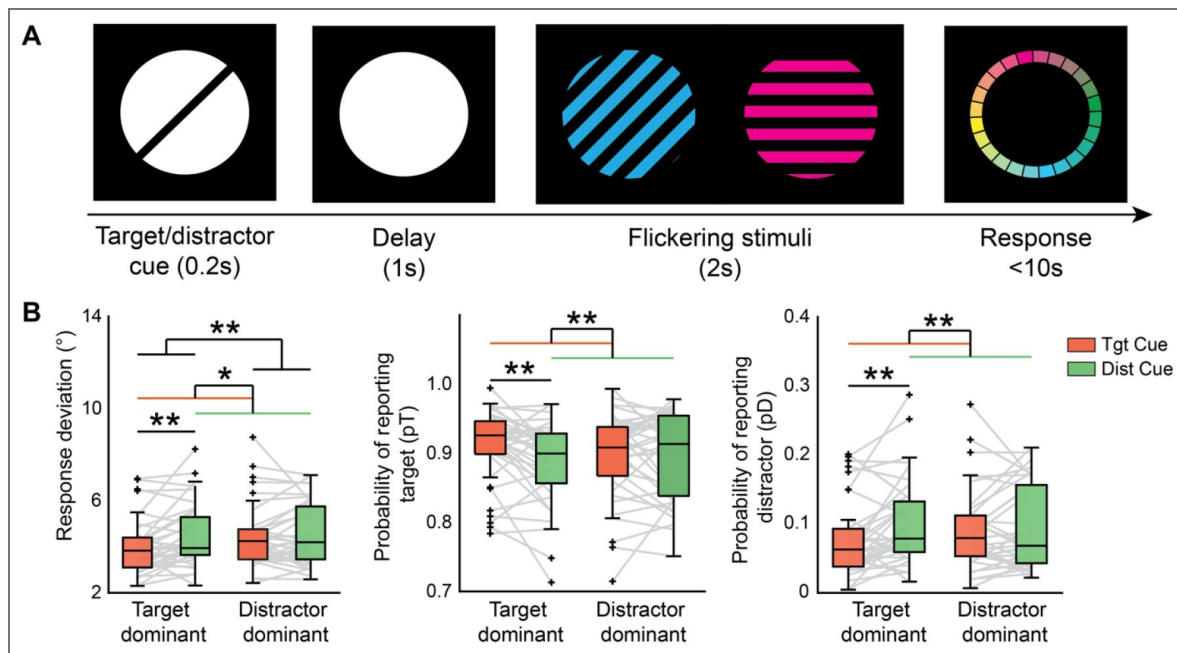


Figure 1.

(A) Trial illustration. The target/distractor cue indicates the orientation of the corresponding grating. For half of the participants, target cues were in solid lines and the distractor cues were in dashed lines, while the rules were reversed for the other half participants. Gratings were presented to each eye using a stereoscope, with the target and distractor gratings flickering at 24 Hz and 20 Hz, respectively. During binocular rivalry, participants were instructed to prioritize the target grating while suppressing the distractor grating, aiming to reproduce the color of the target grating as precisely as possible. (B) Behavioral results. Response deviation represents how many degrees a response was off from the target color. From a probabilistic mixture model, we extracted the probability of reporting target color (pT), distractor color (pD) and random guess (pU) (Figure S1). Two-way ANOVA was performed on behavioral measurements. Results are shown for target cueing (TgtCue) and distractor cueing (DistCue) conditions, separately for when target was at the dominant eye versus when distractor was at the dominant eye. *, $p < 0.05$, **, $p < 0.01$, ***, $p < 0.001$. Probability of reporting target color, main effect of cueing: $F(1, 140) = 9.939$, $p = 0.002$, $\eta^2 = 0.133$; main effect of stimuli dominance: $F(1, 140) = 3.452$, $p = 0.065$; cueing $\times$ stimuli dominance, $F(1, 140) = 4.612$, $p = 0.033$, $\eta^2 = 0.098$. Probability of reporting distractor color: main effect of cueing: $F(1, 140) = 10.859$, $p = 0.001$, $\eta^2 = 0.154$; main effect of stimuli dominance: $F(1, 140) = 3.297$, $p = 0.072$; cueing $\times$ stimuli dominance, $F(1, 140) = 4.370$, $p = 0.038$, $\eta^2 = 0.090$.

competition from the distractor grating (Hancock and Timothy 2007 [↗](#)), thereby improving performance. Under this account, distractor cueing would be expected to have little impact, as perceptual dominance already favors the target and the distractor is presented to the non-dominant eye. A key prediction of this mechanism is that distractor cueing should impair performance when the distractor occupies the dominant eye, unless such impairment is counteracted by inhibitory mechanisms.

An alternative account is that the cueing effect in target-dominant trials reflects a disruptive consequence of distractor cueing, whereby distractor cues bias initial selection toward the non-dominant distractor (Davidson et al. 2018 [↗](#); Ooi and He 1999 [↗](#)), resulting in larger response deviation. This account predicts that prior cues are effective primarily when the cued stimulus is presented to the non-dominant eye. Accordingly, in distractor-dominant trials, where the target is non-dominant, target cueing should enhance perceptual dominance of the target and improve performance. However, this prediction was not supported by our behavioral results.

A third possibility is that the observed cueing effect reflects the combined influence of target facilitation and distractor capture. To distinguish between these alternatives and determine whether cueing selectively modulates target or distractor representations, we directly examined stimulus-specific sensory representations.

Feature cues boost sensory processing selectively at the dominant eye

To determine how feature cues modulate sensory representations under visual competition, we examined orientation-selective neural responses to the two rivalrous gratings using multivariate decoding of posterior electrodes that were highly responsive to the flickering stimuli (Figure 2A [↗](#)).

Across trials, feature cues enhanced the orientation decoding accuracy of the cued stimulus, regardless of whether the cue referred to the target or the distractor (Figure 2B [↗](#), TgtCue: $t(35) = 4.181$, $p < 0.001$, Cohen's $d = 0.697$; DistCue: $t(35) = 3.053$, $p = 0.004$, Cohen's $d = 0.509$), indicating that cue-related biases in neural processing persist beyond the delay period. However, the cueing effect was further modulated by which eye the cued grating was presented to, with significant cueing effect primarily when it was shown to the dominant eye (Figure 2C [↗](#)). When the target grating was presented to the dominant eye (Figure 2C [↗](#), left), orientation decoding of the target grating was significantly higher in target cueing compared to distractor cueing ($t(35) = 2.815$, $p = 0.008$, Cohen's $d = 0.469$), whereas distractor grating did not differ between cueing conditions ($t(35) = 1.605$, $p = 0.118$). In contrast, when the distractor grating occupied the dominant eye, decoding of the distractor was enhanced by distractor cueing relative to target cueing (Figure 2C [↗](#), right; $t(35) = 2.714$, $p = 0.010$, Cohen's $d = 0.452$), with no corresponding modulation of target decoding ($t(35) = 1.180$, $p = 0.246$).

Together, these findings demonstrate that feature cues selectively boost sensory representations of the cued stimulus only when it is presented to the dominant eye. Importantly, this dominance-contingent pattern is inconsistent with the third account in which cueing effects arise from the combined but individually insignificant influences of target facilitation and distractor capture. Thus, the behavioral cueing effect observed in target-dominant trials reflects feature-based facilitation of the target representation.

Dissociable cueing effects on alpha and theta activity during preparatory and rivalry phases

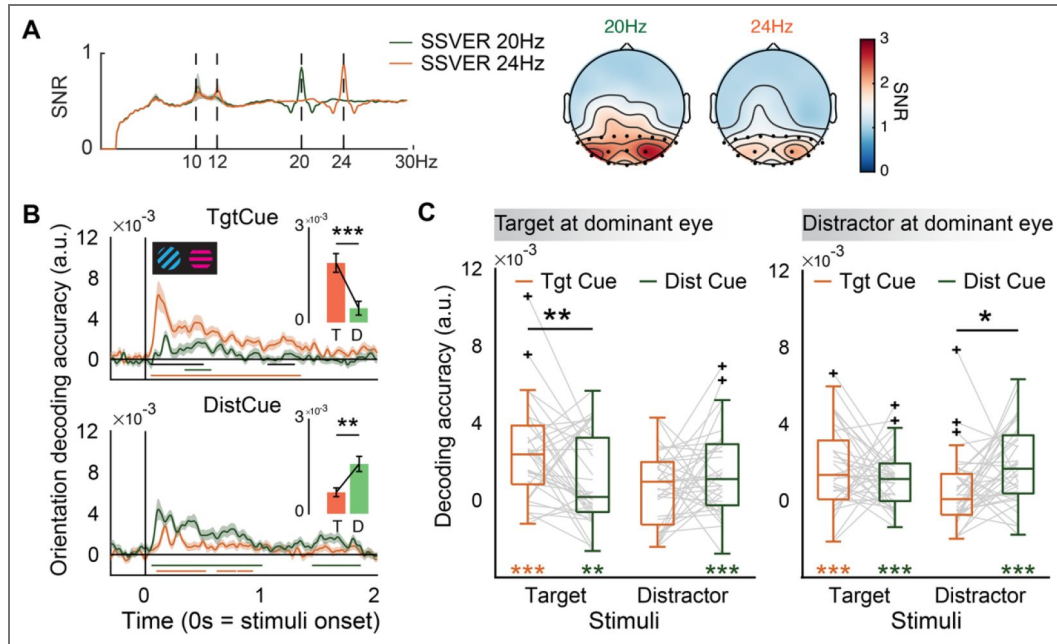


Figure 2.

(A) Signal-to-noise ratio (SNR) of SSVER. The top panel shows normalized SNR using all channels. The topography highlights the most responsive channels to SSVER. (B) Mahalanobis-based distance decoding of target and distractor grating orientations in different cueing conditions. Colored lines above the x-axis represent time intervals with above-chance decoding accuracy, identified using cluster-based permutation testing. Black lines indicate the decoding accuracy difference between target and distractor gratings. Inserted panels show averaged decoding slopes calculated between 0 and 2 s during the rivalry phase. (C) Orientation decoding of target and distractor gratings based on stimulus dominance. Black asterisks mark significant differences between cueing conditions, while colored asterisks indicate significant decoding above chance level 0. For target dominant trials, target grating in TgtCue, $t(35) = 5.916$, $p < 0.001$, Cohen's $d = 0.986$; distractor grating in TgtCue, $t(35) = 1.852$, $p = 0.072$, Cohen's $d = 0.309$; target grating in DistCue, $t(35) = 2.721$, $p = 0.010$, Cohen's $d = 0.454$; distractor grating in DistCue, $t(35) = 3.887$, $p < 0.001$, Cohen's $d = 0.648$; For distractor-dominant trials, target grating in TgtCue, $t(35) = 4.778$, $p < 0.001$, Cohen's $d = 0.796$; distractor grating in TgtCue, $t(35) = 1.677$, $p = 0.103$, Cohen's $d = 0.279$; target grating in DistCue, $t(35) = 4.611$, $p < 0.001$, Cohen's $d = 0.769$; distractor grating in DistCue, $t(35) = 5.559$, $p < 0.001$, Cohen's $d = 0.926$.

Although distractor cueing increased neural processing of the distractor in distractor-dominant trials, this enhancement did not translate into behavioral costs. This dissociation suggests that additional top-down control mechanisms counteracted distractor-related interference during perceptual competition. To identify the controlling mechanism, we examined neural rhythmic activities during the preparatory (pre-stimulus onset) and rivalry phases, focusing on theta (3-7 Hz) and alpha (8-12 Hz) frequency bands.

During the preparatory phase, distractor cueing elicited stronger alpha power over right parietal regions compared to target cueing (Figure 3A, $t(35) = 2.152$, $p = 0.038$, Cohen's $d = 0.359$), whereas frontal theta power did not differ between cueing conditions during this period (Figure 3B). If increased alpha power reflects direct suppression of the cued distractor feature, reduced neural representation of distractor orientation would be expected. However, orientation decoding revealed robust distractor representations during preparatory phase (Figure 3C). Moreover, the orientation-based representations for target and distractor features were highly similar and could be generalized across cueing conditions (Figure 3C right), indicating that preparatory alpha modulation did not attenuate feature-specific sensory representations. The generalizability of target and distractor representations is unlikely to reflect task indifference, as brain responses to target and distractor cues were reliably classifiable (Figure 3D), indicating that the brain maintained distinct task states for the two cueing conditions. In addition, the persistence of strong distractor representations into the rivalry phase under distractor cueing further argues against early elimination of distractor features during preparation following a search-and-destroy process. Taken together, these findings argue against direct inhibition of distractor features during preparation, and instead suggest a feature-based gating mechanism that may shape upcoming sensory processing.

During the rivalry phase, distractor cueing was associated with significantly stronger frontal theta activity relative to target cueing (Figure 3B, cluster-based permutation, 1.65 to 4.55 s, 3 to 16 Hz, $p < 0.001$; repeated ANOVA: main effect of dominance, $F(1, 35) = 0.013$, $p = 0.911$; main effect of cueing, $F(1, 35) = 19.515$, $p < 0.001$, $\eta^2 = 0.358$, cueing $\times$ dominance, $F(1, 35) = 0.344$, $p = 0.561$), while parietal alpha power no longer differed between conditions. This temporal dissociation suggests a two-stage control process: preparatory alpha activity reflects proactive gating based on prior knowledge, whereas frontal theta activity during rivalry implements reactive control to suppress distractor interference as competition unfolds.

Sequential alpha-theta control of distractor interference

To determine how the brain resolves distractor interference when sensory representations of the distractor are enhanced but behavior remains unaffected, we examined trial-by-trial relationships between neural oscillations, sensory gain, and performance using a general linear mixed model (see Table S1 for full model output and control analyses regarding theta during preparatory phase and alpha during rivalry phase).

Behavioral performance of each trial depended jointly on sensory evidence from both the target and the distractor (Figure 4A left: target SSVER $\times$ distractor SSVER, $F(1, 23147) = 8.463$, $p = 0.004$). When target-related SSVERs were weak, stronger distractor SSVERs were associated with greater response deviations ($F(1, 11595) = 4.962$, $p = 0.026$), indicating increased interference (Figure 4A right). This interference effect attenuated when target power was high ($F(1, 11575) = 1.266$, $p = 0.261$). Importantly, this target $\times$ distractor interaction effect was further modulated by cueing and stimulus dominance, particularly in the target cueing condition compared to the distractor cueing condition (target SSVER $\times$ distractor SSVER $\times$ cueing, $F(1, 23147) = 9.251$, $p = 0.002$), and especially when the target appeared in the dominant eye (target SSVER $\times$ distractor SSVER $\times$ cueing $\times$ stimuli dominance, $F(1, 23147) = 7.751$, $p = 0.005$). Thus, we separated target-dominant and distractor-dominant trials to examine the controlling mechanism.

Frontal theta activity during the rivalry phase selectively modulated the impact of sensory evidence on behavior in target-dominant trials (Figure 4B: theta $\times$ target SSVER $\times$ distractor SSVER $\times$ stimuli dominance, $F(1, 23147) = 4.128$, $p = 0.042$). Higher theta power was associated with better performance, regardless of the SSVER of the target or distractor (main effect of theta power,

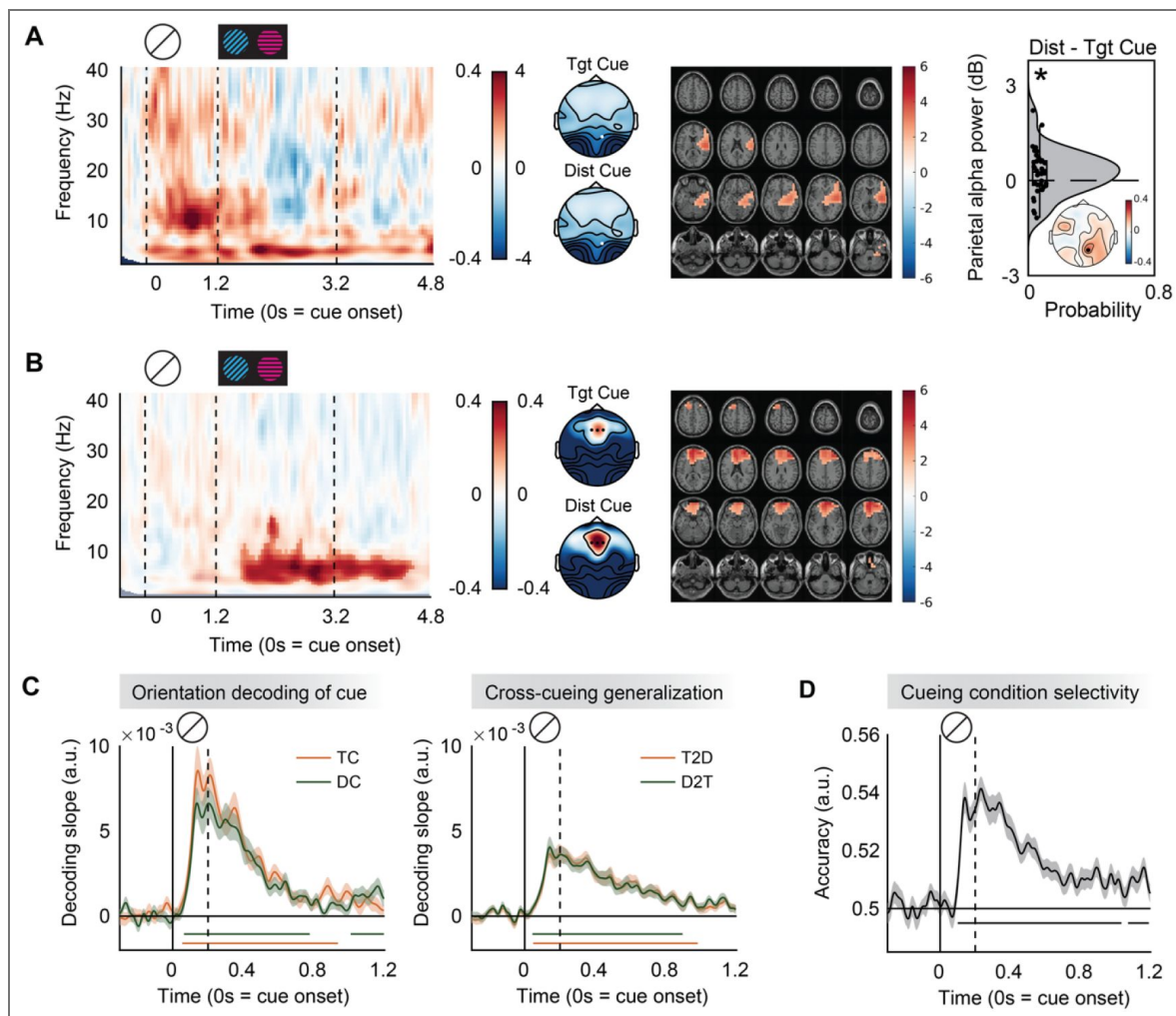


Figure 3.

(A) Parietal alpha activity. The time-frequency map shows the power difference between target and distractor cueing conditions at electrode P2 (marked white). The right lateralized topographical distribution is consistent with previous findings showing the right posterior intraparietal sulcus in anticipatory alpha modulation (Capotosto et al. 2011). Source reconstruction revealed brain regions showed stronger alpha power (8-12 Hz) in distractor cueing condition compared to target cueing condition. Colorbar indicates t-value from cluster-based permutation test. The raincloud plot shows individual alpha power difference between cueing conditions. The inserted topography displays the averaged alpha power difference between cueing conditions during 0 to 1.2 s after cue onset. (B) Frontal theta activity. The time-frequency map shows the power difference between distractor and target cueing conditions, with the highlighted cluster indicating time-frequency points that passed cluster-based permutation testing. These results were derived from frontal channels highlighted in the topography. Source reconstruction revealed enhanced theta power in the distractor cueing condition during the rivalry phase. (C) Orientation decoding of cued orientations using posterior channels. Left, orientation decoding of each cueing condition separately; Right, robust cross-condition generalization (T2D: train target cueing data, test distractor cueing data; D2T: reverse) indicates that target and distractor templates utilize shared sensory-level representations. (D) Distinct task states. Multivariate classification of cueing conditions (TgtCue vs. DistCue) reveals distinct neural profiles throughout the delay, suggesting that the functional role of the template is maintained. The classifier was trained on data from all EEG.

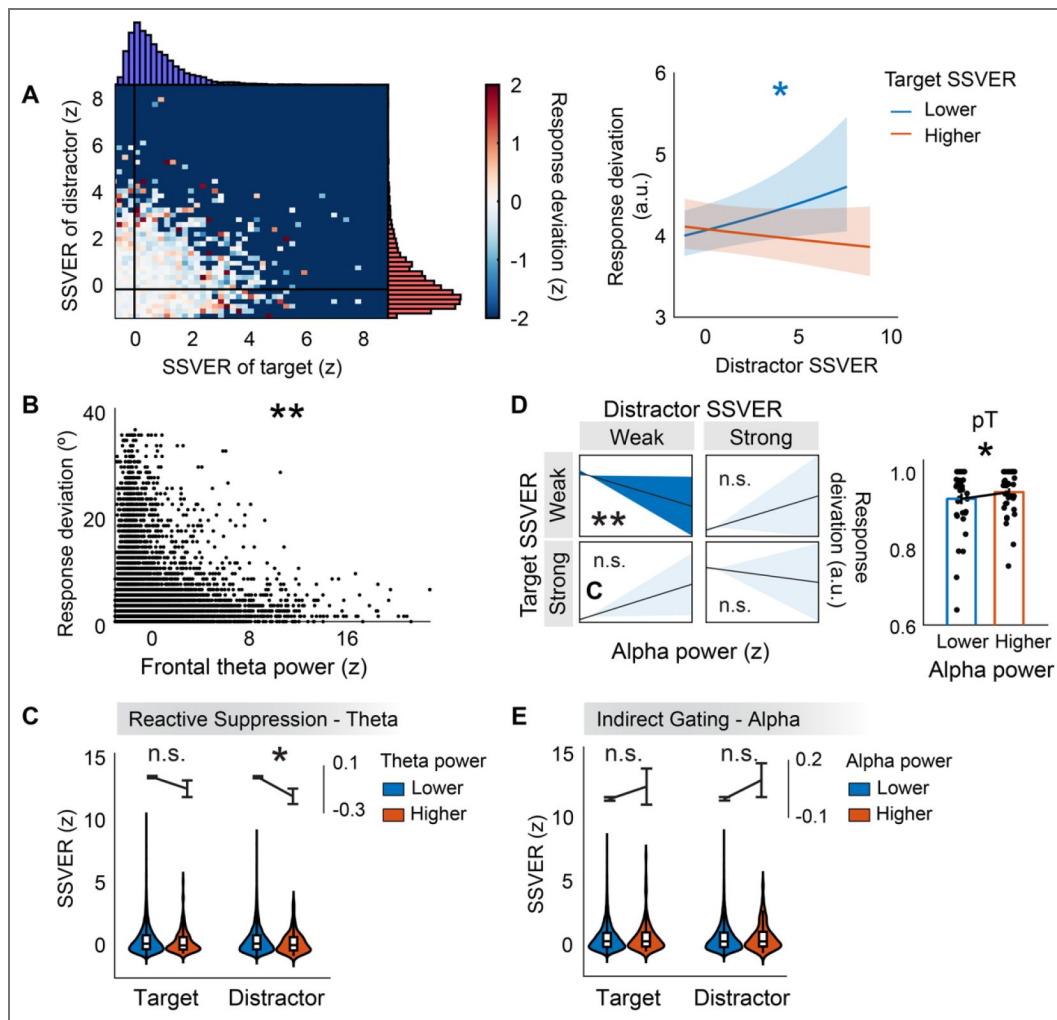


Figure 4.

(A) Target SSVER and distractor SSVER jointly affect behavioral performance. Left, heatmap of response deviation (z-scored) as a function of target and distractor SSVERs (binned into 50 units) in target-dominant trials. The color of the scatter dots represents the average z-scores of behavioral response deviation within each bin. Dark regions indicate bins with insufficient trials. The top and right histograms show the probability density of target SSVER and distractor SSVER respectively (scale: 0 to 0.1). Right, linear regression coefficients for distractor SSVER in predicting deviation, median-split by target SSVER. Interference is significantly higher when target signals are weak (blue line). The intercept is not shown; the y-axis units are arbitrary reflecting relative values. (B-C) Frontal theta oscillations facilitate reactive suppression of distractors in target-dominant trials. (B) Increased frontal theta power (z-scored) correlates with reduced behavioral response deviation. (C) Stronger theta power is specifically associated with attenuated distractor SSVER, while target SSVER remains unaffected, suggesting a distractor-specific inhibitory mechanism. For visualization purpose, trials were median split based on frontal theta power of each participant to facilitate graphical interpretation of the effects. All statistical analyses were conducted on continuous single-trial data, and the categorical grouping was used solely for graphical presentation. (D-E) Parietal alpha power indexes indirect gating without altering sensory gain in distractor-dominant trials. (D) Under conditions of weak sensory gain (low SSVER), higher preparatory parietal alpha power is associated with smaller response deviations and an increased probability of target reporting (pT). (E) Preparatory alpha power does not directly modulate the SSVER of either target or distractor stimuli, supporting a role in higher-level gating rather than direct gain control.

$F(1, 11578) = 7.112, p = 0.008$). Follow-up analysis showed that increased theta power was accompanied by reduced distractor power, without significant changes in target power (Figure. 4C, distractor, $t(11584) = 2.105, p = 0.035$; target, $t(11584) = 0.425, p = 0.671$). These results indicate that frontal theta activity reflects a reactive inhibition that selectively suppresses distractor sensory gain during perceptual competition (Figure. 5 left).

Preparatory parietal alpha activity modulated behavior in a qualitatively different manner (Figure. 4D: alpha $\times$ target SSVER $\times$ distractor SSVER $\times$ stimuli dominance, $F(1, 23147) = 8.296, p = 0.004$). Critically, in distractor-dominant trials, alpha power interacted with both target and distractor SSVERs (alpha $\times$ target SSVER $\times$ distractor SSVER, $F(1, 11617) = 5.705, p = 0.017$), such that higher alpha was associated with better performance only when sensory evidence for both stimuli was weak (Figure. 4D left, $t(35) = 2.938, p = 0.006$, Cohen's $d = 0.490$), suggesting that alpha-mediated control is particularly effective under conditions of high perceptual uncertainty. Under these high perceptual uncertainty conditions, increased alpha power selectively increased the probability of reporting the target (Figure. 4D right, $t(35) = 2.330, p = 0.026$, Cohen's $d = 0.199$), without affecting the precision or probability of reporting the distractor or random guesses (Figure. S2). This effect was unique to trials with weaker target and distractor SSVERs, with no significant alpha modulation effect observed in the other three scenarios (Figure. S2, target weak-distractor strong, target strong-distractor weak, target strong-distractor strong). Together, these findings suggest that increased preparatory alpha enhanced target identification and consequently facilitated behavioral performance, particularly under conditions of high perceptual uncertainty (Jensen 2024).

In light of the behavioral influence of preparatory alpha activity, we further asked whether this alpha effect stemmed from direct modulation of sensory gain. To test this, we compared target and distractor SSVERs of trials with higher or lower preparatory alpha power. We failed to find alpha-related modulation of target SSVER (Figure. 4E, $t(11623) = 0.458, p = 0.647$) or distractor SSVER ($t(11623) = 1.155, p = 0.248$). Even when focusing on trials with weak target and distractor SSVER, alpha-related modulation effects on sensory gains were insignificant (target SSVER, $t(3036) = 0.648, p = 0.517$; distractor SSVER, $t(3036) = 0.426, p = 0.670$).

Together, these results reveal two dissociable control mechanisms operating at distinct stages of perception. Preparatory parietal alpha activity biases target selection through a gating process that becomes effective under weak sensory evidence, without altering sensory gain. In contrast, frontal theta activity during rivalry implements reactive inhibition by suppressing distractor sensory gain in real time. This sequential alpha-theta control architecture explains how distractor representations can be enhanced at the sensory level without incurring behavioral costs.

We propose that elevated preparatory alpha reflects enhanced gating through the establishment of negative attentional templates informed by prior knowledge of the distractor (Carlisle 2023; de Vries et al. 2019; Jensen and Mazaheri 2010), allowing orientations mismatching the distractor to pass through (Figure. 5 right). During the feedforward processing of target and distractor, this template labels the two information streams and selectively pass the target inflow. Importantly, this separation and gating process does not alter the sensory gain of either the target or the distractor; instead, it routes them for further processing with different attentional weights. As a result, the target percept is prioritized and stabilized, increasing its likelihood of being reported, particularly when sensory evidence is weak, thereby improving behavioral performance.

Discussion

Here we show a sequential alpha-theta control architecture that resolves sustained visual competition based on distractor knowledge. By tracking the selective processing of targets and distractors during sustained competition, we demonstrate that behavioral stability does not rely on a single, static inhibitory filter. Instead, it emerges from a dynamic relay: preparatory parietal alpha proactively routes information by establishing sensory gates before stimulus onset, while

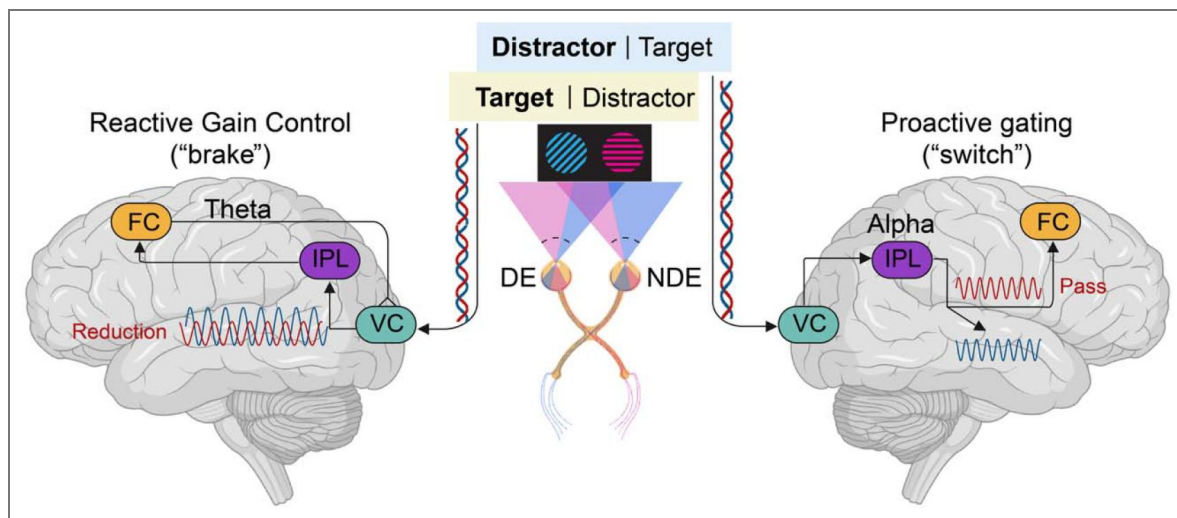


Figure 5. Reactive inhibition and proactive gating in resolving visual competition.

Reactive inhibition via frontal theta (left panel): When the target is presented to the dominant eye, it establishes initial perceptual dominance. In this state, reactive inhibition, indexed by increased frontal theta activity, is recruited to suppress the competing distractor by directly reducing its sensory gain (red sinusoidal curve). This suppression stabilizes the target's dominance and slows down perceptual switching, thereby optimizing behavioral performance. Proactive attentional gating via parietal alpha (right panel): When the distractor occupies the dominant eye, high-uncertainty competition is resolved through proactive gating. Elevated preparatory alpha activity signals the instantiation of a negative attentional template based on prior distractor knowledge. This template serves to segregate and differentially route competing inputs without altering early sensory gain. This gating mechanism is most advantageous under conditions of high perceptual uncertainty, where it stabilizes weak target signals and facilitates the high-level processing. DE, dominant eye; NDE, nondominant eye; VC, visual cortex; IPL, inferior parietal lobe; FC, frontal cortex.

frontal theta implements reactive gain control to suppress distractors during competition. This dissociation unifies conflicting theories of attentional control and suggests that alpha-mediated gating may be an important prerequisite for conscious access.

A central and initially counterintuitive finding of our study is that distractor cueing enhanced the sensory representation of distractors without incurring behavioral costs. This resolves a long-standing “behavioral paradox” in the literature, where knowledge about distractors often captures attention rather than suppressing it (Cunningham and Egeth 2016 [↗](#); Geng et al. 2019 [↗](#); Noonan et al. 2016 [↗](#); Wen et al. 2018 [↗](#)). Our data show that foreknowledge of a distractor equips the brain to dynamically counter this interference. When the enhanced distractor competes for dominance (access to consciousness), the conflict triggers a surge in frontal theta activity, which selectively reduces the sensory gain of the distractor (Figure 5 [↗](#)). This finding further demonstrates frontal theta not merely as a signal of conflict monitoring, but as an active “braking” mechanism that prevents distractors from hijacking high-level processing (Cao et al. 2020 [↗](#); Cavanagh and Frank 2014 [↗](#); Messel et al. 2021 [↗](#)).

Theta oscillations have frequently been linked to attentional sampling and rhythmic reorienting, particularly in tasks that require shifts of attention (Fiebelkorn and Kastner 2019 [↗](#); Galas et al. 2025 [↗](#); VanRullen 2016 [↗](#)). Attentional shifting likely contributes to perceptual dynamics during binocular rivalry, where perceptual dominance alternates over time. However, several aspects of our data argue against a purely sampling-based account of theta activity in the present task. At the trial level, theta power was most strongly associated with improved behavioral performance in target-dominant trials where attentional reorienting should be least necessary. Moreover, stronger theta was observed when distractor representations were weaker, as indexed by decreased distractor-related SSVER responses. A shifting account would predict less attentional shifting when distractor is weak and stronger shifting when distractor is strong. These patterns are difficult to reconcile with a purely shifting-based account in which theta reflects the effort required to disengage from the cued or dominant distractor. Instead, they are more consistent with interpretations of theta as indexing reactive inhibitory control of distractors to establish stable perception, rather than rhythmic exploration or sampling of visual information.

In contrast to the reactive “brake” of theta, preparatory parietal alpha operated as a proactive “switch.” Inconsistent with the “gain reduction” account of alpha-mediated inhibition, increased alpha power did not reduce the sensory gain of the distractor. Instead, our findings support the “gating-by-inhibition” hypothesis (Bonnefond and Jensen 2024 [↗](#); Peylo et al. 2021 [↗](#)), where alpha oscillations functionally segregate competing inputs based on prior knowledge. This is supported by three key findings: (i) alpha power did not modulate the SSVERs of targets or distractors during the rivalry phase (Figure. 4E [↗](#)), (ii) in the distractor-cueing condition where alpha power was stronger, orientation selectivity for distractor gratings was enhanced rather than reduced (Figure. 2C [↗](#)), and (iii) stronger preparatory alpha was associated with increased probability of reporting target (Figure. 4D [↗](#)). We propose that this activity reflects the instantiation of a negative attentional filter tuned to the features of the expected distractor. By actively routing these matching signals away from higher-order processing centers, alpha protects the processing channel of the target, ensuring that limited cognitive resources are not squandered on irrelevant input. Notably, while attentional gating operates on every trial, it is most beneficial under high perceptual uncertainty where target and distractor signals are weak and difficult to distinguish. In these cases, template-based gating will compensate for the weak sensory input and facilitate the identification of target, thereby improving performance. In scenarios where one stimulus or both stimuli are strong, with prior information of target or distractor orientations, identifying target is unequivocal, additional gating conferred little benefit. This finding aligns with the perspective that alpha oscillations play a complementary role in indirect distractor inhibition, modulated by the load of goal-relevant information processing (Jensen 2024 [↗](#); Redding et al. 2026 [↗](#)).

Our findings also shed light on the nature of attentional templates and how they guide behavior. Both target and distractor cues in our study provided feature information that can be used to build attentional templates. Attentional templates can shape neural activity and affect attentional allocation (Carlisle 2023 [↗](#); Chelazzi et al. 2019 [↗](#); Woodman et al. 2013 [↗](#)). An open question is

whether target and distractor templates are represented as distinct templates or as a single content-based template with functional roles determined by task demands. The generalization of feature representations across target and distractor cueing conditions observed here supports the latter view. That is, target and distractor templates may share sensory content, while their functional consequences are determined by task context and control signals. The stronger parietal alpha activity observed during distractor cueing suggests that functional distinctions between templates, such as whether a feature should be selected or gated, may be encoded in non-sensory control signals rather than in the feature representation itself. This interpretation aligns with recent work on the dual-format model of attentional templates, which posits a dominant non-sensory format and a latent sensory-like format (Chen et al. 2024 [↗](#)). Future studies comparing the dual-format representations of target and distractor templates will provide a more nuanced understanding of how attentional templates are maintained and utilized.

Beyond attentional control, our findings offer a mechanistic window into the neural signatures of conscious perception. Binocular rivalry has long served as a model system for studying the dynamics between conscious and unconscious states based on unchanging visual input (Seth and Bayne 2022 [↗](#); Tsuchiya et al. 2015 [↗](#)). Pronounced endogenous neural oscillations in the theta–alpha range have been observed when experiencing mixed percepts (Cha and Blake 2019 [↗](#)), or during perceptual switching (Davidson et al. 2018 [↗](#)). Increased frontal theta activity before perceptual alternations is associated with resolving emerging conflicts, while increased alpha activity helps stabilizing perception through interocular inhibition (Drew et al. 2022 [↗](#)). Our results extend this literature by showing that these rhythms play dissociable roles in shaping perceptual outcomes based on prior knowledge. According to Global Neuronal Workspace (GNW) theory, sensory inputs must be amplified and broadcast to a widespread network to reach awareness, which is known as ignition (Mashour et al. 2020 [↗](#); Seth and Bayne 2022 [↗](#)). We found that alpha-mediated gating was most behaviorally beneficial when sensory evidence was weak (high perceptual uncertainty). In these near-threshold conditions, alpha-mediated routing effectively improved the identification of the target, facilitating its ignition and subsequent entry into awareness. This suggests that parietal alpha plays a crucial role in the pre-conscious selection phase, acting as a spectral gatekeeper that determines which sensory streams are privileged for broadcast and which are silenced. Consistent with this view, stronger posterior alpha power has been reported in unseen correct trials than unseen incorrect trials (Trübutschek et al. 2017 [↗](#)), and entraining posterior alpha activity selectively improves short-term memory performance for unseen stimuli that are visually unaware (Cheng et al. 2022 [↗](#)). While future work is needed to directly test these ideas, our findings suggest that parietal alpha oscillations may serve as the neural signature of ignition and broadcast, facilitating the routing of information necessary for conscious perception.

In conclusion, we demonstrate that resolving competing information involves two complementary mechanisms: reactive inhibition mediated by frontal theta oscillations and proactive attentional gating indexed by parietal alpha oscillations. This sequential architecture explains how the brain maintains a stable stream of consciousness despite the constant bombardment of distracting sensory information. By actively filtering the input (alpha) and reactively suppressing the noise (theta), the brain constructs a coherent visual reality from the chaos of rivalrous signals.

Method

Participants

A total of 38 participants were recruited to ensure a statistical power of 0.8 for detecting a medium effect size ($d = 0.5$) in a within-subject design, as determined by G*Power analysis. After preprocessing the electrophysiological data, two participants were excluded due to excessive trial rejection (38.8% of trials discarded), leaving a final sample of 36 participants (16 males; all right-handed) with an average age of 21 years ($SD = 2.4$, range: 18–26 years). Eight participants exhibited left-eye dominance. All participants had normal or corrected-to-normal vision, normal color vision, and no reported history of psychiatric or neurological disorders.

Participants completed a training session on the first day to familiarize themselves with the experimental tasks and confirm the occurrence of the binocular rivalry effect. On the second day, scalp electrophysiological recording was conducted. Written informed consent was obtained from all participants before the experiment. The study was approved by the Institutional Review Board of the School of Psychological and Cognitive Sciences at Peking University (Protocol No. 2020-02-02).

Task

The experiment was conducted in a dimly lit, electromagnetically and acoustically shielded room. Visual stimuli were presented on a gray background using a Display++ monitor (refresh rate: 120 Hz, resolution: 1920 × 1080). Each trial began with a cue displayed for 0.2 seconds (length = 4°, width = 0.2°) to indicate the orientation of the target or the distractor. Target cueing and distractor cueing conditions were mixed within a block and were indicated using solid lines and dashed lines. The line type (solid or dashed) and its association with the target or distractor cueing was counterbalanced across participants. Participants were informed of the association prior to the experiment. After a 1 s delay, two gratings of different colors and orientations were presented separately to each eye for 2 s (diameter: 10°, spatial frequency: 0.04 cycles/pixel, contrast = 1). We selected the stimulus duration based on a previous study showing a mean dominance duration for about 2 seconds (Zhang et al. 2011 [\[1\]](#)). The short duration limited natural perceptual switching. Thus, performance is likely to be biased toward the distractor if it captured the initial dominance. One grating's orientation matched the cued orientation. In the target cueing condition, the orientation-matched grating served as the target, whereas in the distractor cueing condition, the non-matching grating became the target. Participants were required to recall the target grating's color and report it by selecting the corresponding hue on a color wheel within 10 seconds, with an emphasis on precision.

A no-cue condition was not included in the present experiment. In the context of binocular rivalry, the absence of a cue would require participants to attend both stimuli simultaneously in order to perform the task, imposing an attentional load of two. Such a condition would therefore introduce a qualitatively different attentional state that is not directly comparable to target-cueing or distractor-cueing conditions, in which attentional priorities are explicitly specified and therefore an attention load of one. Moreover, in a no-cue condition, prolonged mixed percepts are more likely to occur, reflecting unresolved visual competition rather than active competition resolution. This would confound the interpretation of neural signatures related to attentional gating and suppression. Although the absence of a no-cue baseline precludes direct behavioral comparison against the baseline, the within-subject contrasts between cueing and dominance are sufficient to isolate the effects of attentional guidance on perceptual competition.

The orientations of the gratings were selected from six orientation bins, with the angular difference between the target and distractor gratings always being at least 15° to enhance visual discrimination. Grating colors were randomly selected for each trial from a set of 72 colors in the Lab color space ($L = 70$; a^* , b^* plane origin at $[0, 0]$) to ensure uniform perceived brightness.

The angular difference between the colors of any two gratings was a minimum of 60°. To enhance competition between the two eyes, the phase of the gratings was reversed at different intervals: every 5 frames (24 Hz) for the target grating and every 6 frames (20 Hz) for the distractor grating. This manipulation compelled participants to selectively attend to the target grating while inhibiting the distractor. Participants were instructed to fixate on the center of the screen and minimize blinking, as eye movements and blinks can disrupt binocular rivalry.

EEG recording and preprocessing

The EEG was recorded using Ag/AgCl electrodes placed on a 64-channel EasyCap according to the international 10-10 system (Brain Products). An external electrode placed below the right eye was used to measure eye movements. Electrode impedance was kept below 10 kΩ. The data were collected at a sampling rate of 1000 Hz. Offline preprocessing was performed using the EEGLAB toolbox (Delorme and Makeig 2004 [\[2\]](#)). Raw data was down sampled to 500 Hz and re-referenced

using the average of bilateral mastoid electrodes. A bandpass filter of 1 to 40 Hz was applied. Bad channels were spherically interpolated. The continuous data were epoched into -1 s to 4 s time locked to cue onset. Typical artifacts such as blinks, eye movements, heartbeat noise, muscle noise, and line noise were identified and corrected using independent component analysis. There were on average 4.4 (SD = 1.6) components removed. After preprocessing, trials containing voltage values exceeding a threshold of 100 μ V at any time point for any electrode were excluded.

SSVER extraction

We use Rhythmic Entrainment Source Separation (RESS) to isolate SSVERs induced by flicking gratings (Cohen and Gulbinaite 2017 [↗](#)). This method combines and extends existing multivariate source separation methods to optimize the extraction of steady-state responses from EEG signals. The FWHM at peak frequency was set to be 0.5 Hz, and the distance of neighboring frequencies away from peak frequency was 1 Hz, the FWHM of the neighboring frequencies was 1 Hz. The time interval was selected to be 1.3 s to 3.1 s after cue onset to avoid transient stimulus-evoked effect. Note that while there were strong sub-harmonics in alpha band at 10Hz and 12Hz, our analysis on alpha activity was at the preparatory phase before the onset of flickering stimuli. These sub-harmonics could not have confounded our findings regarding proactive alpha-gating.

Time frequency analysis

Time-frequency analysis was conducted using a Morlet wavelet decomposition in the FieldTrip toolbox (Oostenveld et al. 2011 [↗](#)). The decomposition was implemented by specifying a range of frequencies of interest from 1 to 40 Hz on a combined linear scale (1–40 Hz) with a logarithmic scale to achieve finer frequency resolution at lower frequencies. The wavelet width was linearly scaled from 2 to 10 cycles across frequencies. Time points of interest were selected every 50 ms across the trial window. Normalization was carried out using decibel transformation, with the baseline interval set from -0.4 to -0.1 s relative to the pre-cue period. To ensure that our results reflected fluctuations in endogenous oscillatory amplitude rather than ERP differences between conditions, all time-frequency analyses were performed on non-phase-locked data. Specifically, ERP components were removed by subtracting the condition-specific ERP from the single-trial EEG data before performing the time-frequency decompositions on the residual data (Cohen, Mike X. 2014).

Source reconstruction

To investigate the cortical sources of theta activity during the rivalry and alpha activity during the preparatory phase, we performed source reconstruction using the Dynamic Imaging of Coherent Sources (DICS) beamforming method. After computing the forward model using standard MRI, the cross-spectral density matrix was computed from the averaged theta (3-7Hz) and alpha (8-12 Hz) frequency bands, derived via a multitaper fast Fourier transform. To account for the increased noise towards the center of the head, the neural activity index (NAI) was calculated for each voxel in the brain by dividing the source estimates by the corresponding local noise estimates. Power values of the theta and alpha frequency bands were extracted from 0.3 to 1.2 s after stimuli onset and 0.6 to 1.1 s after cue onset respectively. The statistical significance of clusters showing differences between target cueing and distractor cueing conditions was assessed by Monte Carlo permutation test (N = 10000) with two-tailed alpha of 0.05.

Orientation decoding

We performed orientation decoding using data from 17 posterior channels. Data was partitioned into seven training folds and one test fold for cross-validation. To ensure an unbiased classifier, we subsampled equalized number of trials for each orientation bin in the training set and then took the trial-average of each orientation bin. After obtaining the covariance matrix across orientation bins of the training set, we calculated the Mahalanobis distances between the test trials and the

training sets (Wolff et al. 2017 [DOI](#)). A smaller distance toward one specific orientation bin indicated a larger pattern similarity. Decoding accuracy was measured as the cosine weighted distances of pattern-difference between trials of increasingly dissimilar orientations.

The cross-validation procedure was iterated 100 times, with random assignment of trials to the training and test sets in each iteration. The averaged decoding accuracy was taken for the statistical analysis. We followed the same procedure for cross-condition decoding except that the model was trained from one cueing condition (e.g., target cueing) and tested on the other condition (e.g., distractor cueing).

Finally, to assess the statistical significance of the decoding accuracy, we conducted cluster-based permutation testing against the chance level (Maris and Oostenveld 2007 [DOI](#)), using an alpha threshold of 0.05. Cluster statistics were calculated using the sum of the values within each cluster, and the permutation test was run for 10,000 iterations to generate the null distribution for comparison. The cluster-based nonparametric alpha was set to 0.05.

General linear mixed model on trialwise behavioral and neural responses

We conducted a general linear mixed model to analyze trialwise behavioral and neural responses. The dependent variable (trial-wise response error) is predicted by the fixed effects (cueing condition, stimuli dominance, reactive frontal theta power, preparatory parietal alpha power, target and distractor SSVER strength, and their interactions), and the random effects between. The model formula was: $\text{beha} \sim \text{alpha} * \text{theta} * \text{target power} * \text{distractor power} * \text{cueing condition} * \text{stimuli dominance} + (1 | \text{subjects})$. Behavioral color deviation for each trial was the outcome variable. Preparatory parietal alpha power was extracted from P2, reactive frontal theta power was extracted from Fz, SSVERs for target and distractor at tagging frequencies were extracted from PO3 and PO4. Neural measurements were normalized within each participant before entering the model. The response distribution was specified as “normal,” and the link function as “identity.”

After identifying condition-specific modulations of alpha and theta power, we examined whether these oscillatory signals influenced the sensory gain of target and distractor. To this end, we performed single-trial GLMM where stimulus SSVERs were predicted by trial-wise alpha or theta power: $\text{stimulus SSVER} \sim \text{alpha (or theta)} + (1 | \text{subject})$. Oscillatory power was entered as a continuous predictor and subjects were modeled with random intercepts to account for between-participant variability. For visualization purposes only (Figure 4 [DOI](#)), trials were median-split within each participant into high- and low-alpha (or theta) subgroups. This binning was used solely to facilitate graphical interpretation of the effects and was not applied in any statistical analyses.

Data availability

Data and script can be found at OSF at <https://osf.io/3dnvy/> [DOI](#)

Acknowledgements

We thank Chenyang (Leo) Lin for constructive discussions and Yangming Zhang for assistance with data collection. This study was supported by grants from the National Natural Science Foundation of China (32271104) and STI2030-Major Projects (2021ZD0200204).

Additional information

Author contributions

WW and SL designed the study. WW and YW collected data. WW analyzed the data. WW wrote the manuscript. WW, RR, and SL revised the manuscript.

Funding

Funder	Grant reference number	Author
MOST National Natural Science Foundation of China (NSFC)	32271104	Sheng Li
STI2030-Major Projects	2021ZD0200204	Sheng Li

Author ORCID iDs

Robert MG Reinhart:  <https://orcid.org/0000-0003-2156-4633>

Sheng Li:  <https://orcid.org/0000-0002-6258-3147>

Additional files

[Supplementary information.](#) 

References

- Anderson BA** (2021) An adaptive view of attentional control. *Am Psychol* **76**:1410-1422 <https://doi.org/10.1037/amp0000917> | [PubMed](#)
- Antonov PA**, Chakravarthi R, Andersen SK (2020) Too little, too late, and in the wrong place: Alpha band activity does not reflect an active mechanism of selective attention. *Neuroimage* **219**:117006 <https://doi.org/10.1016/j.neuroimage.2020.117006> | [PubMed](#)
- Bays PM**, Catalao RFG, Husain M (2009) The precision of visual working memory is set by allocation of a shared resource. *Journal of vision* **9**:7 <https://doi.org/10.1167/9.10.7> | [PubMed](#)
- Bonnefond M**, Jensen O (2024) The role of alpha oscillations in resisting distraction. *Trends Cogn Sci* **29**:368-379 <https://doi.org/10.1016/j.tics.2024.11.004> | [PubMed](#)
- Cao C**, Wen W, Liu B, Ma P, Li S, Xu G, Song J (2020) Theta oscillations in prolactinomas. *Neurocognitive deficits in executive controls* **28**:102455 <https://doi.org/10.1016/j.nicl.2020.102455>
- Capotosto P**, Babiloni C, Romani GL, Corbetta M (2011) Differential Contribution of Right and Left Parietal Cortex to the Control of Spatial Attention: A Simultaneous EEG-rTMS Study. *Cereb Cortex* **22**:446-454 <https://doi.org/10.1093/cercor/bhr127>
- Carlisle NB** (2023) Negative and positive templates: Two forms of cued attentional control. *Attention, perception & psychophysics* **85**:585-595 <https://doi.org/10.3758/s13414-022-02590-4> | [PubMed](#)
- Cavanagh JF**, Frank MJ (2014) Frontal theta as a mechanism for cognitive control. *Trends Cogn Sci* **18**:414-421 <https://doi.org/10.1016/j.tics.2014.04.012> | [PubMed](#)
- Cha O**, Blake R (2019) Evidence for neural rhythms embedded within binocular rivalry. *Proc Natl Acad Sci U S A* **116**:14811-14812 <https://doi.org/10.1073/pnas.1905174116> | [PubMed](#)
- Chelazzi L**, Marini F, Pascucci D, Turatto M (2019) Getting rid of visual distractors: the why, when, how, and where. *Current Opinion in Psychology* **29**:135-147 <https://doi.org/10.1016/j.copsyc.2019.02.004>
- Chen Y**, Liu T, Jia K, Theeuwes J, Gong M (2024) Dual-format attentional template during preparation in human visual cortex. *eLife* **13**:RP103425 <https://doi.org/10.7554/eLife.103425>
- Cheng P**, Grover S, Wen W, Sankaranarayanan S, Davies S, Fragetta J, Soto D, Reinhart RMG (2022) Dissociable rhythmic mechanisms enhance memory for conscious and nonconscious perceptual contents. *PNAS* **119**:e2211147119 <https://doi.org/10.1073/pnas.2211147119>
- Cohen MX**, Gulbinaite R (2017) Rhythmic entrainment source separation: Optimizing analyses of neural responses to rhythmic sensory stimulation. *NeuroImage* **147**:43-56 <https://doi.org/10.1016/j.neuroimage.2016.11.036>
- Cohen MX** (2014) *Analyzing Neural Time Series Data* Cambridge, Massachusetts: The MIT Press.
- Corbetta M**, Shulman GL (2002) Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience* **3**:201-15 <https://doi.org/10.1038/nrn755>

- Cunningham CA, Egeth HE (2016) Taming the White Bear: Initial Costs and Eventual Benefits of Distractor Inhibition. *Psychological Science* **27**:476-485 <https://doi.org/10.1177/0956797615626564>
- Davidson MJ, Alais D, van Boxtel J JA, Tsuchiya N (2018) Attention periodically samples competing stimuli during binocular rivalry. *eLife* **7**:e40868 <https://doi.org/10.7554/eLife.40868>
- de Vries IEJ, Savran E, van Driel J, Olivers CNL (2019) Oscillatory Mechanisms of Preparing for Visual Distraction. *J Cogn Neurosci* **31**:1873-1894 https://doi.org/10.1162/jocn_a_01460 | PubMed
- Delorme A, Makeig S (2004) EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J Neurosci Methods* **134**:9-21 <https://doi.org/10.1016/j.jneumeth.2003.10.009> | PubMed
- Dieter KC, Tadin D (2011) Understanding attentional modulation of binocular rivalry: a framework based on biased competition. *Frontiers in human neuroscience* **5**:155 <https://doi.org/10.3389/fnhum.2011.00155> | PubMed
- Drew A, Torralba M, Ruzzoli M, Moris Fernandez L, Sabaté A, Pápai MS, Soto-Faraco S (2022) Conflict monitoring and attentional adjustment during binocular rivalry. *Eur J Neurosci* **55**:138-153 <https://doi.org/10.1111/ejn.15554> | PubMed
- Duecker K, Shapiro KL, Hanslmayr S, Griffiths BJ, Quinn AJ, Wolfe J, Pan Y, Pastuszak A, Jensen O (2025) Higher baseline alpha power is associated with faster responses in visual search. *bioRxiv* <https://doi.org/10.1101/2025.08.29.673162>
- Ferrante O, Zhigalov A, Hickey C, Jensen O (2023) Statistical Learning of Distractor Suppression Downregulates Prestimulus Neural Excitability in Early Visual Cortex. *J Neurosci* **43**:2190 <https://doi.org/10.1523/JNEUROSCI.1703-22.2022> | PubMed
- Fiebelkorn IC, Kastner S (2019) A Rhythmic Theory of Attention. *Trends Cogn Sci* **23**:87-101 <https://doi.org/10.1016/j.tics.2018.11.009> | PubMed
- Foxe JJ, Snyder AC (2011) The role of alpha-band brain oscillations as a sensory suppression mechanism during selective attention. *Frontiers in Psychology* **2**:154 <https://doi.org/10.3389/FPSYG.2011.00154>
- Galas L, Donovan I, Dugué L (2025) Attention rhythmically shapes sensory tuning. *Journal of Neuroscience* **45**:e1616242024 <https://doi.org/10.1523/JNEUROSCI.1616-24.2024>
- Gaspelin N, Luck SJ (2018) The Role of Inhibition in Avoiding Distraction by Salient Stimuli. *Trends Cogn Sci* **22**:79-92 <https://doi.org/10.1016/j.tics.2017.11.001> | PubMed
- Gazzaley A, Nobre AC (2012) Top-down modulation: Bridging selective attention and working memory. *Trends Cogn Sci* **16**:129-135 <https://doi.org/10.1016/j.tics.2011.11.014> | PubMed
- Geng JJ, Won BY, Carlisle NB (2019) Distractor Ignoring: Strategies, Learning, and Passive Filtering. *Current Directions in Psychological Science* **28**:096372141986709 <https://doi.org/10.1177/0963721419867099>
- Geng JJ (2014) Attentional Mechanisms of Distractor Suppression. *Current Directions in Psychological Science* **23**:147-153 <https://doi.org/10.1177/0963721414525780>
- Gundlach C, Moratti S, Forschack N, Müller MM (2020) Spatial Attentional Selection Modulates Early Visual Stimulus Processing Independently of Visual Alpha Modulations. *Cereb Cortex* **30**:3686-3703 <https://doi.org/10.1093/cercor/bhz335> | PubMed
- Hancock S, Timothy JA (2007) The Role of Voluntary and Involuntary Attention in Selecting Perceptual Dominance during Binocular Rivalry. *Perception* **36**:288-298 <https://doi.org/10.1068/p5494> | PubMed
- Hutchinson JB, Turk-Browne N (2012) Memory-guided attention: Control from multiple memory systems. *Trends Cogn Sci* **16**:576-579 <https://doi.org/10.1016/j.tics.2012.10.003> | PubMed
- Iemi L, Gwilliams L, Samaha J, Auksztulewicz R, Cycowicz YM, King J, Nikulin VV, Thesen T, Doyle W, Devinsky O, et al. (2022) Ongoing neural oscillations influence behavior and sensory representations by suppressing neuronal excitability. *Neuroimage* **247**:118746 <https://doi.org/10.1016/j.neuroimage.2021.118746> | PubMed

- Jensen O (2024) Distractor inhibition by alpha oscillations is controlled by an indirect mechanism governed by goal-relevant information. *Communications psychology* **2**:36 <https://doi.org/10.1038/s44271-024-00081-w> | PubMed
- Jensen O, Mazaheri A (2010) Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Frontiers in human neuroscience* **4**:186 <https://doi.org/10.3389/fnhum.2010.00186> | PubMed
- Klimesch W (2012) Alpha-band oscillations, attention, and controlled access to stored information. *Trends Cogn Sci* **16**:606-617 <https://doi.org/10.1016/J.TICS.2012.10.007> | PubMed
- Liesefeld HR, Lamy D, Gaspelin N, Geng JJ, Kerzel D, Schall JD, Allen HA, Anderson BA, Boettcher S, Busch NA (2024) Terms of debate: Consensus definitions to guide the scientific discourse on visual distraction. *Attention, Perception, & Psychophysics* **86**:1445-1472 <https://doi.org/10.3758/s13414-023-02820-3>
- Liesefeld HR, Liesefeld AM, Töllner T, Müller HJ (2017) Attentional capture in visual search: Capture and post-capture dynamics revealed by EEG. *Neuroimage* **156**:166-173 <https://doi.org/10.1016/j.neuroimage.2017.05.016> | PubMed
- Lin R, Meng X, Chen F, Li X, Jensen O, Theeuwes J, Wang B (2024) Neural evidence for attentional capture by salient distractors. *Nat Hum Behav* **8**:932-944 <https://doi.org/10.1038/s41562-024-01852-5> | PubMed
- Maris E, Oostenveld R (2007) Nonparametric statistical testing of EEG-and MEG-data. *J Neurosci Methods* **164**:177-190 <https://doi.org/10.1016/j.jneumeth.2007.03.024> | PubMed
- Mashour GA, Roelfsema P, Changeux J, Dehaene S (2020) Conscious processing and the global neuronal workspace hypothesis. *Neuron* **105**:776-798 <https://doi.org/10.1016/j.neuron.2020.01.026> | PubMed
- Messel MS, Raud L, Hoff PK, Stubberud J, Huster RJ (2021) Frontal-midline theta reflects different mechanisms associated with proactive and reactive control of inhibition. *Neuroimage* **241**:118400 <https://doi.org/10.1016/j.neuroimage.2021.118400> | PubMed
- Moher J, Egeth HE (2012) The ignoring paradox. *Cueing distractor features leads first to selection, then to inhibition of to-be-ignored items* **74**:1590-1605 <https://doi.org/10.3758/s13414-012-0358-0>
- Morrow A, Elias M, Samaha J (2023) Evaluating the Evidence for the Functional Inhibition Account of Alpha-band Oscillations during Preparatory Attention. *J Cogn Neurosci* **35**:1195-1211 https://doi.org/10.1162/jocn_a_02009 | PubMed
- Noonan MP, Crittenden BM, Jensen O, Stokes MG (2018) Selective inhibition of distracting input. *Behav Brain Res* **355**:36-47 <https://doi.org/10.1016/j.bbr.2017.10.010> | PubMed
- Noonan MP, Adamian N, Pike A, Printzlaue F, Crittenden BM, Stokes MG (2016) Distinct Mechanisms for Distractor Suppression and Target Facilitation. *The Journal of neuroscience : the official journal of the Society for Neuroscience* **36**:1797-1807 <https://doi.org/10.1523/JNEUROSCI.2133-15.2016> | PubMed
- Ooi TL, He ZJ (1999) Binocular rivalry and visual awareness. *The role of attention* **28**:551-574 <https://doi.org/10.1068/p2923> | PubMed
- Oostenveld R, Fries P, Maris E, Schoffelen J (2011) FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Comput Intell Neurosci* **2011**:156869 <https://doi.org/10.1155/2011/156869> | PubMed
- Peylo C, Hilla Y, Sauseng P (2021) Cause or consequence? Alpha oscillations in visuospatial attention. *Trends Neurosci* **44**:705-713 <https://doi.org/10.1016/J.TINS.2021.05.004> | PubMed
- Redding ZV, Ding Y, Fiebelkorn IC (2026) Frequency-specific attentional mechanisms phasically modulate the influence of distractors on task performance. *PLOS Biology* **24**:e3003664 <https://doi.org/10.1371/journal.pbio.3003664>
- Richter D, van Moorselaar D, Theeuwes J (2025) Proactive distractor suppression in early visual cortex. *eLife* **13**:RP101733 <https://doi.org/10.7554/eLife.101733>

- Sawaki R, Luck SJ (2010) Capture versus suppression of attention by salient singletons: Electrophysiological evidence for an automatic attend-to-me signal. *Attention, Perception & Psychophysics* **72**:1455-1470 <https://doi.org/10.3758/APP.72.6.1455>
- Seth AK, Bayne T (2022) Theories of consciousness. *Nature reviews. Neuroscience* **23**:439-452 <https://doi.org/10.1038/s41583-022-00587-4> | PubMed
- Snyder AC, Foxe JJ (2010) Anticipatory Attentional Suppression of Visual Features Indexed by Oscillatory Alpha-Band Power Increases. *A High-Density Electrical Mapping Study* **30**:4024-4032 <https://doi.org/10.1523/jneurosci.5684-09.2010>
- Soto D, Hodsoll J, Rotshtein P, Humphreys GW (2008) Automatic guidance of attention from working memory. *Trends Cogn Sci* **12**:342-348 <https://doi.org/10.1016/j.tics.2008.05.007> | PubMed
- Theeuwes J (2025) Attentional Capture and Control. *Annual Review of Psychology* **76**:251-273 <https://doi.org/10.1146/annurev-psych-011624-025340>
- Theeuwes J, Bogaerts L, van Moorselaar D (2022) What to expect where and when: how statistical learning drives visual selection. *Trends Cogn Sci* <https://doi.org/10.1016/J.TICS.2022.06.001> | PubMed
- Trübutschek D, Marti S, Ojeda A, King J, Mi Y, Tsodyks M, Dehaene S (2017) A theory of working memory without consciousness or sustained activity. *eLife* **6**:e23871 <https://doi.org/10.7554/eLife.23871>
- Tsuchiya N, Wilke M, Frässle S, Lamme VAF (2015) No-Report Paradigms: Extracting the True Neural Correlates of Consciousness. *Trends Cogn Sci* **19**:757-770 <https://doi.org/10.1016/j.tics.2015.10.002> | PubMed
- Van Diepen RM, Foxe JJ, Mazaheri A (2019) The functional role of alpha-band activity in attentional processing: the current zeitgeist and future outlook. *Current Opinion in Psychology* **29**:229-238 <https://doi.org/10.1016/j.copsyc.2019.03.015>
- van Moorselaar D, Slagter HA (2020) Inhibition in selective attention. *Ann N Y Acad Sci* **1464**:204-221 <https://doi.org/10.1111/nyas.14304> | PubMed
- VanRullen R (2016) Perceptual Cycles. *Trends Cogn Sci* **20**:723-735 <https://doi.org/10.1016/j.tics.2016.07.006> | PubMed
- Wang B, van Driel J, Ort E, Theeuwes J (2019) Anticipatory distractor suppression elicited by statistical regularities in visual search. *J Cogn Neurosci* **31**:1535-1548 https://doi.org/10.1162/jocn_a_01433 | PubMed
- Wen W, Huang Z, Hou Y, Li S (2022) Tracking Neural Markers of Template Formation and Implementation in Attentional Inhibition under Different Distractor Consistency. *The Journal of neuroscience : the official journal of the Society for Neuroscience* **42**:4927 <https://doi.org/10.1523/JNEUROSCI.1705-21.2022> | PubMed
- Wen W, Hou Y, Li S (2018) Memory guidance in distractor suppression is governed by the availability of cognitive control. *Attention, perception & psychophysics* **80**:1157-1168 <https://doi.org/10.3758/s13414-018-1511-1> | PubMed
- Wolff MJ, Jochim J, Akyürek EG, Stokes MG (2017) Dynamic hidden states underlying working-memory-guided behavior. *Nat Neurosci* **20**:864-871 <https://doi.org/10.1038/nn.4546> | PubMed
- Woodman GF, Carlisle NB, Reinhart RMG (2013) Where do we store the memory representations that guide attention?. *Journal of Vision* **13**:1 <https://doi.org/10.1167/13.3.1>
- Yang X, Fiebelkorn IC, Jensen O, Knight RT, Kastner S (2024) Differential neural mechanisms underlie cortical gating of visual spatial attention mediated by alpha-band oscillations. *Proceedings of the National Academy of Sciences of the United States of America* **121**:e2313304121 <https://doi.org/10.1073/pnas.2313304121> | PubMed
- Zhang P, Jamison K, Engel S, He B, He S (2011) Binocular Rivalry Requires Visual Attention. *Neuron* **71**:362-369 <https://doi.org/10.1016/j.neuron.2011.05.035> | PubMed

Zhigalov A, Jensen O (2020) Alpha oscillations do not implement gain control in early visual cortex but rather gating in parieto-occipital regions. *Hum Brain Mapp* **41**:5176-5186
<https://doi.org/10.1002/hbm.25183> | PubMed

Peer reviews

Reviewer #1 (Public review):

Summary:

These authors used a binocular rivalry task with flickering stimuli in which subjects had to report the color of the target grating at the end of each trial. Target or distractor cues provided information about the orientation of the respective stimulus prior to each trial. The stated goals of this project include testing the neural mechanisms underlying strategic target and distractor processing. Behavioral enhancement was observed for target cueing, while no cost was noted for distractor cueing. These authors present evidence for reactive suppression, characterized by pronounced frontal theta activity that reduced the sensory gain (SSVEP) of the distractor. Distractor cues also increased alpha activity over parietal areas, which these authors link to attentional gating while pointing out no relationship with sensory gain.

Strengths:

This manuscript clearly reflects thoughtful analysis of the available data. Alongside a simple and effective task design, sophisticated methods provide good support for most of the claims made by these authors.

Weaknesses:

Lack of temporal precision for SSVEP effects. I would like to see how sensory gain is/isn't dynamically modulated in the moments after the initial ERP to see if there could be differences compared to the broader window used presently (1.3 to 3.1 seconds).

These authors indicate that persistence of the neural representation of cued distractor orientations into the rivalry period is evidence against a "search-and-destroy" type mechanism where distractors are enhanced to then be suppressed reactively. This claim relies on an indirect link between the maintenance of information about distractor orientation (i.e., successful orientation decoding) and the processing of sensory representations. This claim would be backed up more substantially if the SSVEP (a measure of sensory processing) could reveal temporal dynamics on a finer scale.

<https://doi.org/10.7554/eLife.112007.1.sa2>

Reviewer #2 (Public review):

Summary:

The findings are conceptually useful - a sequential alpha-then-theta architecture for proactive gating and reactive distractor suppression would be a compelling contribution to the attention control literature - but the evidence is incomplete at best. The central dissociation rests on an inadequate proxy for perceptual dominance, the key alpha-behavior effect is small ($d = 0.199$) and confined to a single unprotected data quadrant, and the GLMM uses an inadequate random effects structure that inflates false-positive risk.

Strengths:

The SSVEP frequency-tagging + binocular rivalry combination is genuinely inventive for isolating sensory gain signals from the two competing stimuli simultaneously. The finding

that distractor cueing enhances sensory processing of the distractor yet fails to impair behavior is a clean result that directly addresses a behavioral paradox in the attentional suppression literature. The non-phase-locked TF analysis and the use of RESS for SSVER extraction are methodologically sound.

Weaknesses:

The most consequential flaw in the paper is the operationalization of "perceptual dominance." The authors explicitly acknowledge in a footnote that trial categorization as "target-dominant" or "distractor-dominant" is based on which eye received the stimulus, not on participants' actual perceptual reports. Because participants were never asked to report which stimulus was dominant (only to reproduce the target's color), the assignment is an anatomical proxy, not a perceptual measure. This matters enormously for the paper's central claims. Specifically: (a) The entire two-mechanism dissociation (theta for target-dominant trials, alpha for distractor-dominant trials) is built on a trial-type categorization that may not reflect subjective perceptual experience on a given trial, and (b) Dominant-eye stimuli do typically win initial rivalry dominance, but dominance alternates, and in a 2-second window (the stimulus duration used), perceptual states likely fluctuate in many trials. The lack of button-press perceptual tracking (e.g., continuous dominance reports) means the authors cannot verify that their neural effects actually correspond to the perceptual states they claim. This is a major structural limitation of the design that can't be retroactively corrected, and it significantly weakens the consciousness/awareness framing of the findings.

Another significant issue is that the parietal alpha effect on behavior is confined to a very specific quadrant of the data: distractor-dominant trials where both target and distractor SSVERs are weak simultaneously. The authors present this as an elegant result - "alpha helps most under high perceptual uncertainty" - but it could equally reflect insufficient statistical power for effects in the other three SSVER-strength cells (target strong/distractor weak; target weak/distractor strong; both strong). The Cohen's d for the alpha effect on target reporting probability is only $d = 0.199$, which is a very small effect. With $N=36$ and no correction for the multiple SSVER-strength subgroupings tested, there is a real risk that this specific cell-finding is a false positive, while the null in adjacent cells reflects inadequate power rather than a genuine boundary condition.

A third major limitation is that with a design that includes 6 fixed effects and all their interactions, the random effects structure should include random slopes for at least the key predictors (cueing condition, dominance). Fitting maximal random effects models or justified reduced structures (Barr et al., 2013) is standard in within-subjects EEG research. Using only random intercepts risks inflating Type I error rates for the interaction terms that form the core of the paper's claims. The authors provide a supplementary table (Table S1) but do not describe whether model convergence was verified or alternative random effects structures were tested.

Fourth, the paper's title and central claim are that alpha and theta dynamics operate sequentially. However, the temporal ordering (preparatory alpha $\rightarrow$ rivalry-phase theta) is primarily shown by examining each oscillation in its respective analysis window, not by a single analysis testing whether the sequence itself predicts behavior better than either mechanism alone. A path analysis or cross-lagged model linking trial-level alpha to subsequent theta, and both to behavior, would directly substantiate the "relay" framing. Without this, the sequential architecture is more of an interpretation than a demonstrated property.

Finally, the frontal theta cluster identified by permutation testing spans 3 to 16 Hz - a range that extends well into the alpha band. Calling this a "theta" effect while simultaneously discussing alpha as a separate mechanism is difficult to reconcile. At minimum, this frequency boundary issue warrants explicit discussion.

<https://doi.org/10.7554/eLife.112007.1.sa1>

Reviewer #3 (Public review):

Summary:

Interest was especially focused on how foreknowledge of the orientation of either the target or the distractor could be used to resolve the competition between these stimuli and properly report the target color. The target or distractor was pre-cued by a solid or dashed orientation cue. They were displayed with slightly different presentation frequencies, which allowed for examining their sensory processing with steady-state visual evoked responses (SSVERs). Furthermore, orientation decoding was performed, which revealed that orientation cues selectively affected processing after stimulus onset related to the dominant but not the non-dominant eye. EEG analyses additionally focused on parietal alpha activity and frontal theta, both during the anticipatory phase and the stimulus-processing phase. Cueing the distractor vs. the target induced increased right parietal alpha power during the anticipatory phase, but this did not result in direct inhibition of distractor features. During the stimulus-processing phase, cueing the distractor resulted in increased theta activity. Finally, a generalized linear model was employed wherein trial-by-trial behavior (precision in target color report) was predicted by target and distractor SSVERs, type of pre-cued stimulus (target/distractor), preparatory parietal alpha power, stimulus processing-related frontal theta power, eye dominance, and all their interactions. Performance in the case of reduced sensory processing of the target (based on SSVER) showed more deviations when sensory processing of the distractor was high, but no such effect was observed when sensory processing of the target was high. The latter effects were modulated by eye dominance and cue. Increased theta reduced distractor sensory processing but not target sensory processing. Increased alpha was only beneficial when sensory evidence for both target and distractor was low. Results were interpreted as favoring sensory gating before stimulus onset, reflected by increased parietal alpha (i.e., pro-active control), while theta activity especially seemed relevant to suppress distractor activity (i.e., reactive control) thereby favoring target-related performance.

Strengths:

The authors convincingly show that EEG can provide crucial information about how the human brain deals with the conflict between a target and distractor in a binocular rivalry paradigm with pre-cues signaling either the target or the distractor orientation. An important aspect of the study is the focus on precision of target color report, in combination with the possibility to assess SSVERs to the target and distractor. The strength of this study may actually also be its weakness; the question is whether the presented ideas on proactive and reactive mechanisms can be generalized to paradigms that do not employ binocular rivalry. Separation of target and distractor processing by selectively presenting them to the left/right eye increases the conflict when the target is presented at the non-dominant eye, but what happens in the absence of binocular rivalry concerning the target-distractor conflict?

Weaknesses:

An important aspect of the study relates to the cue manipulation. In many studies, cues are often informative but not mandatory. Couldn't one argue that in this study task performance crucially depends on cue processing, as without the cue, it becomes difficult to tell apart the target from the distractor. It could be argued that participants are able to do this based on the slight difference in flickering frequency, but I doubt whether this is possible at all. However, if this were the case, then they might use this as an alternative cue and ignore the orientation cue. What do participants experience while performing this task? As the cue can be considered to be mandatory, the question may be raised what strategy the participants actually employed. If the target was cued, they simply may have prepared for this orienting

and could ignore the distractor. However, if the distractor was cued, they could use two strategies: search for the stimulus without the cued orientation, or first detect the distractor, and then orient towards the other stimulus. The ideas and results on parietal alpha and frontal theta in combination with the other findings are certainly very interesting, but recently, it has also been argued that frontal theta may be more related to action control (e.g., see Panek et al., <https://doi.org/10.1093/cercor/bhaf276> ) and also pro-active control (Cooper et al., 2017). So, it might be that increased theta reflects suppression of the response related to the distractor, which feeds back on its sensory processing. This raises the question whether there is possibly also some evidence on functional connectivity between frontal and posterior regions that varies depending on the precise condition. Are the results also shining a new light on the relation between attentional orienting and eye dominance (e.g., see Schintu et al., 2020)?

<https://doi.org/10.7554/eLife.112007.1.sa0>