The Influence of Alpha Frequency on Temporal Binding across the Senses: Response to the Special Focus

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Abstract

■ The papers collected in this Special Focus, prompted by S. Buergers and U. Noppeney [The role of alpha oscillations in temporal binding within and across the senses. *Nature Human Behaviour*, 6, 732–742, 2022], have raised several interesting ideas, arguments, and empirical results relating to the alpha temporal resolution hypothesis. Here we briefly respond to these, and in the process emphasize four challenges for future research: defining the scope and limitation of the hypothesis; developing experimental paradigms and study designs that rigorously test its tenets; decomposing the scalp-level signal and isolating underlying neural circuits; and bringing uniformity to the current diversity of analysis and statistical methods. Addressing these challenges will facilitate the progression from merely correlating alpha frequency with various perceptual phenomena to establishing whether and (if so) how alpha frequency influences sensory integration and segregation. ■

We thank Samaha and Romei for organizing a Special Focus on the role of alpha oscillations in temporal binding. The collection of articles raises interesting issues in response to the recent publication by Buergers and Noppeney (2022).

Buergers and Noppeney (2022) performed a comprehensive multiday study to investigate how dynamic state and an individual's trait alpha frequency affect binding within and across the senses (Noppeney, 2021). According to the alpha temporal resolution hypothesis, two signals occurring within one alpha cycle are integrated into a single percept, whereas signals in separate cycles are segregated into distinct percepts (Samaha & Postle, 2015). This hypothesis has led to distinct predictions for various sensory contexts. In the visual context, longer alpha cycles should reduce observers' ability to discriminate between two successive flashes, resulting in more "one flash percepts" (Samaha & Postle, 2015). In audiovisual contexts, longer alpha cycles are thought to widen the audiovisual binding window, thereby allowing for more extensive cross-modal interactions and biases. This is thought to lead to more "one flash percepts" when two flashes are presented with one sound (i.e., fusion illusion) and more "two flash percepts" when one flash is presented with two sounds (i.e., fission or double flash illusion; Cecere, Rees, & Romei, 2015). Although in all cases the reasoning is that with longer alpha cycles the flash(es) and the biasing sound(s) are more likely to fall within the same binding window, the predictions for the double flash illusion raise a critical question: If distinct percepts correspond to separate alpha cycles, how can the brain generate two distinct flash percepts when a single flash and two sounds occur within the same alpha cycle (i.e., binding window)? How do longer alpha cycles in the double flash illusion temporally extend audiovisual binding and yet promote the segregation of successive signals into two distinct flash percepts?

Buergers and Noppeney (2022) explored these conflicting hypotheses systematically in a 3 (sensory context: no sound, one sound, two sounds) × 3 (yes–no, threshold, two interval forced-choice [2IFC]) design. They examined the influence of alpha frequency on observers' ability to discriminate between two flashes that were presented at variable flash-onset asynchronies. The flashes were paired with no sound, one sound, or two sounds. Importantly, the study combined the complementary strengths of yes–no paradigms, threshold paradigms based on adaptive staircases, and 2IFC paradigms. 2IFC paradigms can provide threshold estimates that are unaffected by observers' decisional biases and can therefore be interpreted as observer's temporal resolution (Macmillan, Hautus, & Creelman, 2022). They are also helpful when psychometric functions cannot be fitted in yes–no paradigms because of significant decisional biases. For instance, up to 27% of participants were excluded in Cecere and colleagues (2015) because the psychometric function fit was considered insufficient based on visual inspection (Cecere et al., 2015; see also discussion in Buergers & Noppeney, supplementary material). Buergers and Noppeney (2022) enhanced the replicability of their study by employing experimenter-independent methods to assess the fit of the psychometric function and identify peak alpha frequency from resting-state and prestimulus baseline neurophysiological data (Corcoran, Alday, Schlesewsky, & Bornkessel-Schlesewsky, 2018). In addition, they reported sensor and source analysis

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results to dissociate parietal and occipital alpha oscillations. Furthermore, they substantially reduced the degrees of freedom that researchers usually face in their analysis choices through the consistent application of identical analysis parameters across all experiments.

Using formal Bayesian analyses, Buergers and Noppeney (2022) provided robust evidence that prestimulus alpha frequency as a dynamic neural state (i.e., within subject analysis) and an individual's trait index (i.e., between subject analysis) do not influence observers' perceptual sensitivity or bias in two-flash discrimination across the three sensory contexts.

Given these unexpected findings, several contributions in the Special Focus explore possible explanations for the inconsistencies in the alpha frequency literature. For instance, Wutz (2024) suggests that alpha frequency may not determine bottom–up temporal resolution per se, but influence what the author terms "perception sets." Perception sets are shaped by observers' expectations, perceptual goals, and attentional processes and are thought to impact both temporal and object processing. Wutz (2024) argues that observers may not have formed consistent perception sets in Buergers and Noppeney (2022) because of the trial-to-trial variations in sensory context (i.e., no sounds, one sound, two sounds).

Other contributions explore various methodological aspects as potential causes for the series of null results. Deodato and Melcher (2024), for instance, emphasizes that the precision of estimating the width of the temporal binding window (i.e., threshold) depends on the slope of the psychometric function. To attenuate the influence of threshold estimates that are estimated unreliably, they propose to weigh them by their corresponding slope estimates using weighted regression models. Although this approach has statistical advantages, it mixes two psychometric function parameters that may represent distinct aspects in perceptual inference and decision making.

Samaha and Romei (2024) point out that Buergers and Noppeney (2022) presented the flash in the periphery at $-15°$ of visual angle, that is, partly overlapping with the blind spot—thereby variably probing monocular and binocular vision. However, this experimental feature is unlikely a cause for the null results, because the behavioral results in Buergers and Noppeney (2022) align with prior findings in two-flash-discrimination tasks, both in visual and audiovisual contexts (Rohe, Ehlis, & Noppeney, 2019; Apthorp, Alais, & Boenke, 2013; Shams, Kamitani, & Shimojo, 2002). Moreover, Noguchi (2024) displays the flashes at $+12.5°$ visual angle and thus also partly overlapping with the blind spot. That study presents the flashes at a single flash-onset asynchrony, paired with no sound, one sound, or two sounds. Using similar analysis parameters as Buergers and Noppeney (2022), Noguchi (2024) demonstrates a significant alpha frequency effect in the two sound condition. However, because no results are reported for the no sound or one sound condition, it remains unknown whether alpha frequency effects are statistically significant across sensory contexts. A prior analysis of this data set (Noguchi, 2022) reported a significant influence of beta rather than alpha frequency on flash discrimination in the one sound context (i.e., fusion illusion).

In our companion review (Schoffelen, Pesci, & Noppeney, 2024), we provide a comprehensive analysis of between-subjects, within-subject, and causal perturbation studies that assessed the influence of alpha frequency on temporal binding. The review identifies several challenges for current research into the role of alpha frequency in sensory integration and segregation. In the light of the Special Focus, we will now briefly revisit four key aspects.

First, a primary challenge is to define the scope and limitations of the alpha temporal resolution hypothesis. Together with other contributions to this Special Focus, the meta-analysis of Samaha and Romei (2024) explores the impact of alpha frequency (and phase) on a range of perceptual aspects including flicker-fusion threshold (Baumgarten et al., 2018; Götz et al., 2013), two flash discrimination across variable sensory contexts (i.e., no sound: Deodato & Melcher, 2024; Noguchi, 2022, 2024; Buergers & Noppeney, 2022; Samaha & Postle, 2015, one sound: Buergers & Noppeney, 2022, or two sounds: Noguchi, 2022, 2024; Buergers & Noppeney, 2022), apparent motion perception (Shen, Han, Chen, & Chen, 2019), target detection (Tarasi & Romei, 2024; Trajkovic, Di Gregorio, Avenanti, Thut, & Romei, 2023), and switch rate in bistable perception (Zhang, Zhang, Cai, Luo, & Fang, 2019). However, given the distinct neural circuitries and dynamics involved, it appears questionable that such diverse perceptual phenomena rely on shared alpha oscillatory mechanisms. In support of this critique, Ronconi, Balestrieri, Baldauf, and Melcher (2024) show that alpha oscillations influence binding of two co-located flashes, whereas theta oscillations support the integration of flashes at different locations into apparent motion percepts. This finding diverges from earlier research showing that alpha frequency modulates apparent motion perception (Shen et al., 2019).

A second major challenge lies in the development of experimental paradigms and study designs that provide neuromechanistic insights into alpha frequency's role in perception. A key limitation in the field is the widespread reliance on between-subjects designs. For example, the meta-analysis by Samaha and Romei (2024) selectively includes studies that correlate observers' trait alpha frequency with the width of their temporal binding window over participants. However, between-subjects correlations are susceptible to numerous confounding variables such as age, vigilance, clinical conditions, making their interpretation ambiguous. To address this, Venskus (2024) proposes more sophisticated designs that use perceptual training to probe whether a narrowing of the temporal binding window (Powers, Hillock, & Wallace, 2009), as a result of such training, is associated with concurrent changes in observers' trait alpha frequency. Perturbation studies that manipulate alpha frequency with TMS or tACS are arguably the most powerful approaches to establish a causal role of alpha frequency in temporal binding. Using mediation analyses, such studies could determine whether changes in temporal binding induced by TMS or tACS are mediated by concurrent changes in alpha frequency (Schoffelen et al., 2024).

A third major challenge comes from the fact that alpha oscillations, when measured non-invasively with techniques such as magnetoencephalography or EEG, can originate from multiple neural circuits, each potentially operating at a different alpha frequency (Kawashima, Nakayama, & Amano, 2024; Mahjoory, Schoffelen, Keitel, & Gross, 2020). As a result, changes in alpha frequency observed at the sensor level may not result from changes in the frequency of alpha oscillations within one specific neural circuit, but from changes in the relative power and, hence, contributions of different neural circuits to the alpha oscillations measured in sensor space (Schoffelen et al., 2024). Source analyses are an important first step to help dissociate alpha oscillations arising from different neural circuitries.

Finally, current research varies substantially in analysis approaches and parameters applied to behavioral and neurophysiological data as illustrated in our companion review and the associated tables detailing the parameter choices for each study (Schoffelen et al., 2024). This diversity in analysis choices makes it difficult to assess the robustness of findings. The substantial degree of freedom that researchers typically face in their analysis choices in this field may explain the asymmetry in the funnel plots shown in Samaha and Romei (2024) and lead to overestimated effect sizes in meta-analyses (Moss & De Bin, 2023; Friese & Frankenbach, 2020). Large-scale preregistered studies are crucial to ascertain the role of alpha frequency in temporal binding, both within and across the senses.

Collectively, these advances, along with fresh perspectives from this Special Focus (e.g., Alamia & VanRullen, 2024; Karvat & Landau, 2024), will help to determine whether and, if so, how alpha frequency may affect temporal binding. They will enable us to progress from merely identifying correlations between alpha frequency and a range of perceptual phenomena toward unravelling the neural mechanisms that may underly the potential influence of alpha oscillations on sensory integration and segregation during perceptual inference.

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Author Contributions

Uta Noppeney: Conceptualization; Supervision; Writing—Original draft; Writing—Review & editing. Ugo Giulio Pesci: Conceptualization; Writing—Review & editing. Jan-Mathijs Schoffelen: Conceptualization; Supervision; Writing—Original draft; Writing—Review & editing.

Diversity in Citation Practices

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

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