Alpha-band Brain Dynamics and Temporal Processing: An Introduction to the Special Focus

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Abstract

■ For decades, the intriguing connection between the human alpha rhythm (an 8- to 13-Hz oscillation maximal over posterior cortex) and temporal processes in perception has furnished a rich landscape of proposals. The past decade, however, has seen a surge in interest in the topic, bringing new theoretical, analytic, and methodological developments alongside fresh controversies. This Special Focus on alpha-band dynamics and temporal processing provides an up-to-date snapshot of the playing field, with contributions from leading researchers in the field spanning original perspectives, new evidence, comprehensive reviews and meta-analyses, as well as discussion of ongoing controversies and paths forward. We hope that the perspectives captured here will help catalyze future research and shape the pathways toward a theoretically grounded and mechanistic account of the link between alpha dynamics and temporal properties of perception. ■

BACKGROUND

For nearly a century, the primary functional role that the human alpha rhythm plays in perceptual processing has eluded consensus (Berger, 1929). Although alpha oscillations are nowadays regarded by most to reflect or instantiate some kind of inhibitory process (Dou, Morrow, Iemi, & Samaha, 2022; Iemi et al., 2019, 2022; Samaha, Iemi, Haegens, & Busch, 2020; Haegens et al., 2014; Dugué, Marque, & VanRullen, 2011; Foxe & Snyder, 2011; Klimesch, 2011; Mathewson et al., 2011; Jensen & Mazaheri, 2010; Romei et al., 2008; Klimesch, Sauseng, & Hanslmayr, 2007), the intrinsically rhythmic nature of these excitability fluctuations, with a stereotyped frequency range (Haegens, Cousijn, Wallis, Harrison, & Nobre, 2014), individual stability (Grandy et al., 2013), and developmental trajectory (Freschl, Azizi, Balboa, Kaldy, & Blaser, 2022) remains a deep mystery within the cognitive neurosciences (after all, inhibitory processes need not be rhythmic in nature). Over the decades, various theories linking the alpha rhythm to temporal properties of perceptual and cognitive processing have been proposed (for reviews, see Keitel, Ruzzoli, Dugué, Busch, & Benwell, 2022; Van Wassenhove, Herbst, & Kononowicz, 2019; VanRullen, 2016). Researchers have proposed that alpha reflects cortical excitability cycles (Lindsley, 1952; Bartley, 1940; Bishop, 1932), traveling waves that scan and integrate cortical processes (Harter, 1967), an internal clocking or pacemaker mechanism (Treisman, 1963, 1984), the fundamental temporal unit or quanta of the psychological moment (Kristofferson, 1967), temporal frames within which features are bound together (Varela, Toro, Roy John, & Schwartz, 1981), or attentional sampling periods (Busch & VanRullen, 2010). This variety of proposals has been met with a variety of sources of evidence, both in favor and against the link between alpha and temporal properties of perception and behavior. However, recent years have seen a marked uptick in research on this topic, bringing increasingly more sophisticated psychophysical techniques, behavioral modeling approaches, electrophysiological data analyses, and larger samples to bear on this 100-year-old mystery. This Special Focus in the *Journal of Cognitive Neuroscience* represents a snapshot of current research, theorizing, and controversies regarding the link between alpha-band dynamics and temporal processing.

NEW FINDINGS

Empirical contributions to the special focus highlight the ways that alpha-band dynamics do and do not contribute to temporal processing. Work by Ronconi, Balestrieri, Baldauf, and Melcher (2024) examines the role of prestimulus phase in determining trial-by-trial temporal integration across two distinct perceptual tasks. The researchers found that the phase of ongoing alpha oscillations in a right-lateralized visual network predicts whether participants perceived two brief, colocalized flashes separated by a short ISI (40 msec) as an integrated single flash or as separate events. In contrast, the percept of apparent motion between two spatially distinct flashes, which

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occurs at a longer ISI (120 msec), could be predicted by prestimulus phase in a lower theta-range frequency in parietal areas (Ronconi et al., 2024). These results closely replicate prior findings (Ronconi, Oosterhof, Bonmassar, & Melcher, 2017) and highlight the role of alpha oscillations in the two-flash fusion phenomenon.

Corroborating evidence comes from the findings of Deodato and Melcher (2024), who examine the correlation between individual alpha frequency (IAF) and the temporal threshold for fusion in the two-flash paradigm. Replicating prior work (Gray & Emmanouil, 2020; Samaha & Postle, 2015), the authors find that individuals with higher frequency (faster cycling) alpha oscillations perceive two flashes a shorter ISI compared with individuals with lower frequency alpha. Importantly, however, this effect was mediated by the slope of individual's psychometric function, such that the correlation broke down when including data from participants with shallow slopes (indicative of high levels of trial-to-trial variability in the decision process). This points to a possible explanation for prior null results using a similar paradigm (Buergers & Noppeney, 2022).

The contribution from Tarasi and Romei (2024) points toward a role of IAF in one of the most elementary of visual processes: contrast detection. The authors found, in a large sample of 122 participants, that individuals with higher IAF are more sensitive (not merely more biased) at detecting contrast differences, resulting in lower contrast detection thresholds. This invites the intriguing hypothesis that the putative sampling functions of the alpha rhythm may have implications for visual sensitivity to low-level stimulus features or possibly that alpha has a more fundamental role in visual processing beyond temporal processing.

The experiment (Karvat & Landau, 2024) and subsequent perspective piece (Karvat, Ofir, & Landau, 2024) from Karvat, Landau, and colleagues makes the novel distinction between top–down and bottom–up generated alpha activity in the context of temporal binding. They replicate prior findings (Gray & Emmanouil, 2020) showing that the correlation between IAF and two-flash fusion thresholds is attenuated when the two-flash stimuli are presented within a surrounding, high-contrast annulus. They further show that both the presence and the contrast of the surrounding stimulus greatly shortens the typical two-flash fusion threshold, leading to a clear enhancement of temporal sensitivity (Karvat et al., 2024). In their companion piece (Karvat & Landau, 2024), they introduce a model of oscillatory dynamics with lateral inhibition and a refractory period that can account for the link between spontaneous (top–down generated) alpha and temporal resolution as well as the breakdown of this relationship in the presence of a strong stimulus drive (bottom–up alpha).

SURVEYING THE EVIDENCE

Two contributions to this Special Focus seek to review, synthesize, and undertake a meta-analysis of extant work on the link between alpha frequency and temporal properties of perception spanning the past 50 years. The review and meta-analysis from Samaha and Romei (2024) surveys experiments that examine the link between IAF and temporal properties of visual and audiovisual perception, broadly defined. Across the 27 studies reviewed, random-effects meta-analysis reveal a medium-to-large association (r values between .39 and .53) between IAF and temporal perceptual processes. In the review and meta-analysis of Schoffelen, Pesci, and Noppeney (2024), the authors performed a more selective grouping of studies into those they deemed more clearly related to the concept of temporal binding windows, those using clinical population, as well as studies that examined within-subject effects of alpha frequency on temporal binding. Their fixed-effects, meta-analytic approach reveled significant associations ranging from r values of .26 to .49, depending on the exact grouping of studies. A similar range of effect sizes, although fewer significant effects, were found when using a meta-analytic approach intended to compensate for possible publication bias (Schoffelen et al., 2024). Both contributions provide extensive details about task and analysis parameters across a range of experimental approaches and discuss current controversies and future directions. These two resources combined provide a comprehensive picture and discussion of evidence to date regarding the link between alpha frequency and temporal processing. Readers are also encouraged to conduct their own meta-analysis of studies of their choosing using the free, online tool developed by Samaha and Romei (2024), which can be found at https://randfxmeta.streamlit.app/.

CONTROVERSIES AND PATHWAYS FORWARD

One impetus for this Special Focus was the recent publication of mostly null results from Buergers and Noppeney (2022), which did not replicate several findings in the field (Drewes, Muschter, Zhu, & Melcher, 2022; Noguchi, 2022; Venskus & Hughes, 2021; Gray & Emmanouil, 2020; Cooke, Poch, Gillmeister, Costantini, & Romei, 2019; Keil & Senkowski, 2017; Cecere, Rees, & Romei, 2015; Samaha & Postle, 2015). Several contributions to the Special Focus directly address the findings of Buergers and Noppeney (2022), although see also the discussions within Samaha and Romei (2024) and Schoffelen and colleagues (2024). First, Kawashima, Nakayama, and Amano (2024) consider four possible reasons underlying the varying effects in the literature. The known variety of alpha oscillation generators (Hindriks, Micheli, Mantini, & Deco, 2017) poses an analytic issue if only some alpha rhythms are related to temporal processing. Moreover, the complex relationship between alpha power and alpha frequency (e.g., Nelli, Itthipuripat, Srinivasan, & Serences, 2017) is seldom considered, despite potential implications for temporal processing, which Kawashima and colleagues (2024) unpack. Their article also highlights reasons why considering alpha frequency during stimulus processing (as opposed to during a resting or prestimulus period) may be important. Lastly, using simulations, they argue against the independent and equal-variance Gaussian assumptions underlying the signal-detection theoretic approach used by Buergers and Noppeney (2022).

In the Perspective by Noguchi (2024), a reanalysis of the author's prior data was conducted to conform to the signal-detection theoretic analysis advocated by Buergers and Noppeney (2022). In prior work, Noguchi (2022) found a medium-to-strong correlation between IAF and the probability of experiencing the sound-induced flash illusion, a paradigm case of audivisual integration whereby two sounds separated by a ~50-msec ISI onset simultaneously with a single flash and frequently cause the illusory percept of a secondary flash. In the reanalysis presented by Noguchi (2024), both sensitivity (d') and bias were computed by virtue of the author presenting both one and two-flash trials to participants (in the context 0, 1, or 2 sounds). In contrast to the findings of Buergers and Noppeney (2022), Noguchi observes a significant correlation (ranging from 0.4 and 0.5) between occipital IAF and d' in the sound-induced flash illusion, demonstrating that individuals with faster IAF are more sensitive (higher d') at discriminating one from two flashes in the context of 2 sounds because they were less likely to experience the illusory second flash at the 50-msec ISI that was tested. Noguchi (2024) further provided several analytic demonstrations of why Buergers and Noppeney (2022) may have failed to observe this same result.

Lastly, the Perspective from Venskus (2024) reviews several key findings in the literature and discusses the null effects of Buergers and Noppeney (2022) in the novel context of training effects. Venskus (2024) details the literature on how perceptual learning can shape temporal binding windows and how this may have played a role in the (multiday) experiments of Buergers and Noppeney (2022). Moreover, Venskus proposes an intriguing path forward by combining perceptual training paradigms with alpha measurements to observe whether training-related changes in temporal binding windows manifest alongside concomitant changes in alpha frequency.

FRESH PERSPECTIVES

The Special Focus contributions discussed so far collectively reflect a vibrant research topic that will likely see continued development and expanse. Where will this line of inquiry take us? Beyond the constructive pathways outlined in nearly every contribution for ironing out lingering discrepancies in the foundational findings and frameworks, several contributors highlighted all-together fresh perspectives that indicate likely heading trajectories.

In the piece by Wutz (2024), our attention is focused on recent findings that go beyond the prevailing view of alpha oscillations as reflecting a bottom–up sampling mechanisms by showcasing the variety of top–down functions that alpha modulation can serve. For instance, there is now growing evidence for the idea that alpha frequency, although relatively stable within an individual, can be guided by top–down factors such as task demands or spatial attention to adaptively narrow or widen temporal integration processes (Han, Zhang, Shen, Mo, & Chen, 2023; Trajkovic, Gregorio, Avenanti, Thut, & Romei, 2023; Sharp, Gutteling, Melcher, & Hickey, 2022; Wutz, Melcher, & Samaha, 2018). By shaping processing according to "perception sets" (think internally stored prior knowledge or routines for perceptual processes), the temporal organization imposed by brain-wide, alpha-band communication channels could ultimately shape the experience of the passing of time itself, Wutz argues. For more on the distinction between top–down and bottom–up alpha as it related to temporal integration, see also the contribution of Karvat and Landau (2024), which was also discussed in brief detail above.

The Perspective by Alamia and VanRullen (2024) highlights another critical yet less-frequently discussed dimension to alpha: its spatial dynamics. Increasing evidence, reviewed in depth by Alamia and VanRullen, indicates that the alpha rhythm may propagate across cortex as a traveling wave, mediated, perhaps, by higher-order thalamic nuclei. Not only does alpha seem to travel, but the direction and speed of its propagation has been observed to change depending on several cognitive factors. In their contribution, Alamia and VanRullen unpack how understanding the traveling wave nature of alpha presents new neurally grounded predictions that could explain under what circumstances alpha activity might relate to temporal binding, considering both bottom–up and top–down modes of processing.

Finally, a forthcoming Perspective from Noppeney, Pesci, and Schoffelen (2024) will respond to the arguments and evidence raised throughout this Special Focus.

CONCLUDING REMARKS

The connection between alpha-band brain dynamics and temporal processing has nearly undergone a centuries worth of experiment and theorizing. It may very well continue for another. However, the state of affairs today, as reflected in this Special Focus, foregrounds the tremendous progress that has been made in the last decade while also highlighting our blind spots. We hope that the contributions in this Special Focus help set our field into a firmer theoretical and methodological foothold while also clarifying what shape the path forward may take.

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Diversity in Citation Practices

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

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