

A Role for Bottom–Up Alpha Oscillations in Temporal Integration

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Abstract

■ Neural oscillations in the 8–12 Hz alpha band are thought to represent top–down inhibitory control and to influence temporal resolution: Individuals with faster peak frequencies segregate stimuli appearing closer in time. Recently, this theory has been challenged. Here, we investigate a special case in which alpha does not correlate with temporal resolution: when stimuli are presented amidst strong visual drive. Based on findings regarding alpha rhythmogenesis and wave spatial propagation, we suggest that stimulus-induced, bottom–up

alpha oscillations play a role in temporal integration. We propose a theoretical model, informed by visual persistence, lateral inhibition, and network refractory periods, and simulate physiologically plausible scenarios of the interaction between bottom–up alpha and the temporal segregation. Our simulations reveal that different features of oscillations, including frequency, phase, and power, can influence temporal perception and provide a theoretically informed starting point for future empirical studies. ■

INTRODUCTION

One of the hallmarks of human electrophysiological recordings are waves in the 8–12 Hz alpha frequency band (Berger, 1929). These waves are believed to represent moments of synchronized neuronal activity (Buzsáki, Anastassiou, & Koch, 2012) and as such were proposed to represent fluctuations in perceptual acuity (VanRullen, 2018). A theoretical outcome of such rhythmic sampling is a correlation between the individual alpha frequency (IAF) and the minimal time integration window (TIW) between two flashes of light necessary to perceive them as two instead of one. According to the IAF-to-TIW theory, faster IAFs are related to shorter TIWs and vice versa (Samaha & Postle, 2015). This theory has received empirical support in numerous studies (reviewed in Samaha & Romei, 2024) but was recently challenged (Buergers & Noppeney, 2022). Here, we focus on an instance in which the IAF-to-TIW theory does not hold and its possible implications to our understanding of how alpha activity relates to perception: when the TIW stimuli are presented amidst strong visual drive (Figure 1).

In most studies, the flashes to be judged appear in isolation, that is, over a dark background and without other stimuli. Under these conditions, the ISI threshold to detect two flashes is in the range of 35–70 msec, and inter-individual differences in ISI thresholds correlate with the IAF (Deodato & Melcher, 2024; Samaha & Postle, 2015; Artieda, Pastor, Lacruz, & Obeso, 1992; Gruzelier & Venables, 1974; Venables, 1963). However, increasing

the duration, luminance, and size of the flashes, as well as allowing light adaptation or increasing the brightness of the background, reduces the thresholds (Bowen, Markell, & Schoon, 1980; Purcell & Stewart, 1971; Utial & Hieronymus, 1970; Kietzman, 1967; Lewis, 1967, 1968; Mahneke, 1958). Specifically, when participants are first presented with a light annulus and then the two flashes appear within the annulus, ISI thresholds are reduced and the correlation with the IAF is lost (Karvat, Ofir, & Landau, 2024; Gray & Emmanouil, 2020). Although the TIW does not correlate with the IAF in such cases, it is affected by features of the annulus. The TIW for flashes appearing on a dark background is longer than when they appear within gray annuli, and when the annuli overlap with the flash stimuli, the TIW is further shortened (Gray & Emmanouil, 2020). Furthermore, when the annuli are composed of black-and-white gratings, the TIW is yet shorter in a contrast-dependent manner (Karvat et al., 2024). Importantly, in at least half of the participants, the presentation of the annulus stimuli induces strong and phase-locked alpha activity, which takes ~500 msec to build up. This raises an intriguing question: How can the annulus presentation reduce the ISI threshold and induce alpha on the one hand but “break” the connection to the IAF on the other hand?

To answer this question, we propose to divide alpha activity into two types: bottom–up and top–down (Sadaghiani, Hesselmann, Friston, & Kleinschmidt, 2010; Sadaghiani, Scheeringa, et al., 2010). Often the literature focuses on top–down alpha waves. This is the prominent alpha, which is increased at rest wakefulness, reduces with attention, and is associated with decreased detection

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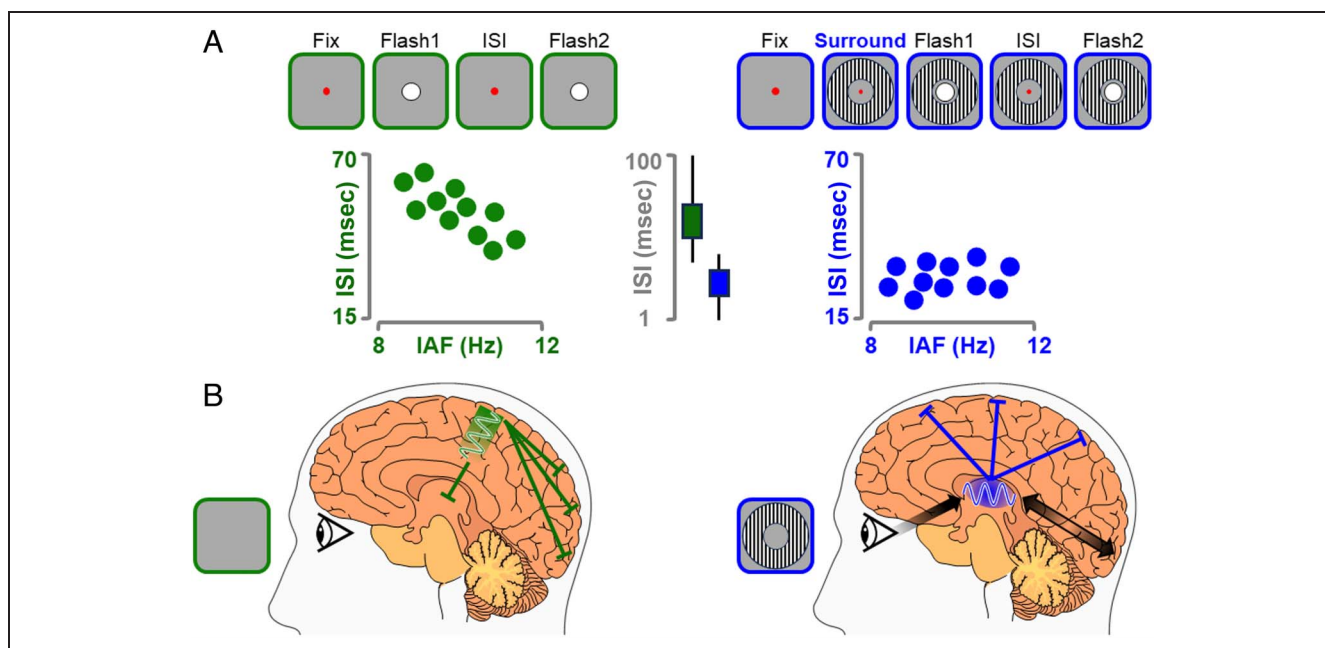


Figure 1. Possible effects of alpha oscillations in the temporal segregation task. (A) In the two-flash temporal segregation task (top left), participants fixate on the fixation point (Fix), and then two flashes of light are presented on a dark background, with a variable ISI between them. The threshold to report the presence of two stimuli instead of one is thought to correlate with the individual frequency of spontaneously occurring alpha (IAF, bottom left). However, when the test flash stimuli are presented amidst lit surrounding, the correlation between the IAF and ISI threshold is lost (bottom right). In addition, the thresholds are shorter in the “surround” condition (illustrated in middle, boxes represent schematically typical thresholds found in the studies mentioned in the main text; whiskers, extreme reported thresholds; blue, with surround light; green, without surround light). (B) Schematic representation of the effect of spontaneously occurring top-down alpha (green, left) and visually induced bottom-up alpha (blue, right). Generally, alpha oscillations represent synchronized inhibition. Left: Top-down alpha is believed to originate in deep cortical layers and to propagate from higher- to lower-order cortex and to the thalamus. Right: A relatively long (>500 msec) presentation of a visual stimulus, together with the interplay between primary visual cortex and the thalamus, can result in thalamically generated alpha, that is spread to wide areas of the cortex.

(Iemi, Chaumon, Crouzet, & Busch, 2017; Chaumon & Busch, 2014; Scheeringa, Petersson, Kleinschmidt, Jensen, & Bastiaansen, 2012; Jensen & Mazaheri, 2010; van Dijk, Schoffelen, Oostenveld, & Jensen, 2008). It is believed to originate in deep cortical layers and to propagate from higher- to lower-order cortex and to the thalamus, thus manifesting a feedback signal that is believed to be inhibitory (Halgren et al., 2019; Bastos et al., 2015; van Kerkoerle et al., 2014). Analysis of directionality of alpha traveling waves revealed that top-down waves are correlated with the overall alpha power (Alamia, Terral, D’ambra, & VanRullen, 2023). Therefore, the peak frequency of the backward-traveling alpha is likely to be the IAF, and it is influenced by both task engagement and alertness (Benwell et al., 2019; Haegens, Cousijn, Wallis, Harrison, & Nobre, 2014).

Importantly, spatial propagation analysis revealed another class of alpha waves, which travel forward from occipital to frontal areas and increase during visual stimulation (Alamia & VanRullen, 2019; Pang, Alamia, & VanRullen, 2020; but see Zhigalov & Jensen, 2023). This bottom-up, sensory-induced alpha activity (Karvat et al., 2024; Lozano-Soldevilla & VanRullen, 2019; VanRullen & Macdonald, 2012) is likely to originate in the thalamus and synchronize wide cortical areas. On the neuronal

level, attention increases firing rates and reduces correlation between neurons in brain areas related to the modality and location of the stimulus while suppressing firing rates in competing areas (Voytek et al., 2017; Foxe, Simpson, & Ahlfors, 1998; Luck, Chelazzi, Hillyard, & Desimone, 1997). Therefore, it was suggested that focally active brain areas exert inhibition to their surroundings. This inhibition is manifested by alpha oscillations aided by widespread γ -aminobutyric acid (GABA) collaterals (Cooper, Croft, Dominey, Burgess, & Gruzelier, 2003; Crick, 1984). Recent insights into the alpha rhythmogenesis suggest that thalamocortical pathways support this alpha-associated lateral inhibition, as detailed below.

Visually induced alpha oscillations are believed to originate from the activation of high-threshold (HT) thalamocortical bursting cells in the LGN. When depolarized to ~ -55 mV by glutamatergic input from the cortex or from basal cholinergic stimulation and concurrently receiving visual input, they fire short bursts of action potentials with interburst intervals of ~ 100 msec, fitting to one cycle of alpha oscillations. These bursting cells form the pacemaker of alpha oscillations that are further amplified by local interneurons, which synchronize relay-mode thalamocortical neurons with phasic inhibition. The relay-mode neurons, in turn, provide the

dominant output from the LGN to cortex (Samaha, 2018; Lőrincz, Kékesi, Juhász, Crunelli, & Hughes, 2009). Notably, thalamocortical neurons receive excitatory inputs from prethalamic and corticothalamic neurons and GABAergic input from the reticular thalamic nucleus (RTN; Jones, 1985). RTN neurons, in turn, are innervated by thalamocortical and corticothalamic axon collaterals (Sherman & Guillery, 2001) and fire robustly during thalamocortical oscillations, causing inhibition of thalamocortical neurons (Hughes & Crunelli, 2005; Pinault, 2003). The spread of this alpha-phasic inhibition is further enhanced via innervation from RTN to the pulvinar nucleus (the largest nucleus of the thalamus connected to multiple cortical areas) and from there to cortex (Eradath, Pinsk, & Kastner, 2021; Fiebelkorn & Kastner, 2019).

Therefore, an “active” area of LGN receiving visual input is in an alpha desynchronization state and relays the input to its corresponding cortical area. In concert, it induces (inhibitory) alpha and GABAergic collaterals on its surrounding via the RTN and pulvinar. Therefore, bottom-up alpha can be taken as a thalamocortical-level analogue of on- and off-center retinal cells. In this regard, the length of the stimulus is of vital importance, for both alpha genesis and center-surround effects. The HT pacemaker cells of the LGN, being classified as HT, have to be depolarized to enter a bursting mode. Accordingly, the stimulus has to appear long enough to first depolarize the HT cells and then to maintain alpha (Lőrincz et al., 2009). If the stimulus (i.e., light annulus) lasts long enough (beyond the onset evoked potentials, i.e., >500 msec), the neighboring areas can recover from the initial inhibition and exert inhibition on the area of initial activation. This can explain the presence of stimulus-dependent alpha found with long (~1 sec) visual stimuli (VanRullen & Macdonald, 2012), but not with shorter stimuli commonly used in the field.

Based on the above, we propose that the presentation of relatively long (~1 sec) light annuli leads to a switch from top-down to bottom-up alpha. The bottom-up alpha is phase-locked to the stimulus and can influence the TIW, as supported by several lines of evidence. The accuracy time course in the two-flash discrimination task, measured as proportion of correct trials as a function of the time gap between the annuli offset and the first flash, fluctuates at ~10 Hz. This provides evidence for rhythmic sampling at alpha, phase locked to the annulus presentation (Gray & Emmanouil, 2020). This alpha is not likely to be top-down, because although IAF is influenced by cognitive factors such as alertness and engagement, it is not influenced by the annulus, even when the annulus flickers at frequencies at the border of alpha (Gray & Emmanouil, 2020). In contrast, the TIW is influenced by features of the annulus (Karvat et al., 2024; Gray & Emmanouil, 2020). In addition, the power (Iemi et al., 2019) and phase (Dou, Morrow, Iemi, & Samaha, 2022) of alpha modulate the amplitude of the visually evoked potentials (VEPs),

supporting a role of alpha in gating feed-forward thalamocortical afferents. Furthermore, this effect of alpha on the VEP can explain the influence of the surround on the TIW via lateral inhibition, as described below.

Purcell and Stewart (1971) suggested that the limiting factor for separating the flashes is the persistence (i.e., neural manifestation of a stimulus beyond its physical duration) of the first flash. Perhaps counterintuitively, increasing the duration and luminance of visual stimuli reduces their persistence (Haber & Standing, 1969; Standing, Haber, Cataldo, & Sales, 1969). This conundrum can be settled in the framework of lateral inhibition; the activation of the visual area because of the first flash will decrease the effectiveness of another stimulus presented to the same area to be perceived as a segregated event. This influence persists longer than the physical presentation of the stimulus, and until this influence has dampened, the presentation of the second flash will be integrated with the first. Because lateral inhibition is a well-established phenomenon associated with visual activation—from the retinal ganglion cells, through thalamic relays, and up to early visual cortices—the stronger the surround activation (e.g., by brighter or higher contrast grating annulus), the stronger the associated inhibition. Stronger inhibition requires less time to bring the system to the prestimulus state, that is, shorter persistence, and hence, shorter TIW (Purcell & Stewart, 1971). Alpha oscillations can influence the persistence dampening by means of network refractory period; because oscillations represent the synchronized activation of many neurons, they are likely to fire together and enter the refractory period together (Buzsáki & Vöröslakos, 2023; Sanchez-Vives & McCormick, 2000). Functionally, activity that was present and held in the network, such as visual persistence, will be “deleted” by the refractory period.

Meta-analysis of the correlation of the TIW and IAF between participants revealed a medium to large effect of 0.38–0.52 (Samaha & Romei, 2024). However, this value drops to less than 0.1 when the two flashes appear surrounded by light annuli (Karvat et al., 2024; Gray & Emmanouil, 2020). This may suggest that within-participant differences in the bottom-up alpha, resulting from stimulus drive, may also play a role in temporal integration. For example, the within-participant differences in the alpha phase at the moment of stimulus presentation in each trial are likely to effect the temporal binding window (Baumgarten, Schnitzler, & Lange, 2015; Busch, Dubois, & VanRullen, 2009; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009; Varela, Toro, John, & Schwartz, 1981; but see Ruzzoli, Torralba, Morís Fernández, & Soto-Faraco, 2019). The relatively short 15–40 msec thresholds reported in previous work provide a rationale for the importance of intertrial phase differences (Karvat et al., 2024; Gray & Emmanouil, 2020; Samaha & Postle, 2015; Bowen et al., 1980; Purcell & Stewart, 1971; Utial & Hieronymus, 1970; Lewis, 1967, 1968; Kietzman, 1967;

Mahneke, 1958); if temporal integration occurs over a period encompassing one eighth to one fifth of the alpha cycle length, the two stimuli should arrive at specific parts of the wave (i.e., phase), not only on the same cycle, for alpha to have an influence. In addition, although most of the focus on the relationship between oscillations and the TIW focused on alpha, the effect of oscillatory cycle length on temporal resolution can be manifested in other frequency bands as well. For example, 15–20 msec thresholds fit well to the cycle duration of the gamma (30–80 Hz) frequencies.

Since the investigation of the effect of bottom-up alpha on temporal perception is in its infancy, in the following we present a model suggesting possible mechanisms by which different bottom-up oscillation features can affect the TIW.

METHODS

We modeled how different aspects of bottom-up alpha oscillations can influence the TIW under the assumptions of visual persistence, lateral inhibition, and network refractory period. We simulated the arrival of two light flashes to early visual cortex (e.g., V1) in the presence of alpha oscillations and manipulated the alpha frequency, phase, and power, as well as the persistence duration and ISI. In the model presented in Figure 2, impulse responses to the flashes were simulated by the decaying function suggested by van Diepen and Mazaheri (2018): $A \frac{t-t_0}{\tau} e^{1-(t-t_0)/\tau}$, where A is the amplitude of the impulse response and was set to 1, t is the time in msec, t_0 is the time in which the impulse arrived, and τ represents visual persistence and was set to 30 msec (except in Figure 2B, where it was set to 60 msec). Alpha oscillations were generated according to the formula $B \sin(2\pi ft + \theta)$, with $f = 10$ Hz (except in Figure 2F: $f = 12$ Hz), $B = A$ (in Figure 2D and H: $B = 0.25A$), and $\theta = 0$ rad (in Figure 2E–F: $\theta = -\pi/2$ rad). The effect of network refractory period on persistence dampening was modeled by setting any impulse response to 0 when the signal value (oscillation + impulse) went below 0.

The presentation of strong visual stimuli like the annuli is known to induce gamma oscillations (Scheeringa et al., 2011; Fries, Scheeringa, & Oostenveld, 2008; Hoogenboom, Schoffelen, Oostenveld, Parkes, & Fries, 2006), and gamma activity appears in bursts of short, high-power activity (Karvat, Alyahyay, & Diester, 2021; Neymotin et al., 2020; Feingold, Gibson, DePasquale, & Graybiel, 2015; Murthy & Fetz, 1992). Therefore, in Figure 2H, we modeled a gamma burst by multiplying a sinusoid with an amplitude of 1.5 A and a frequency of 40 Hz with a 101-msec-long Gaussian, centered around the arrival of the second impulse response.

Simulations were performed in MATLAB 2019b (MathWorks). The code for implementation of the model and plotting Figure 2 is provided in Appendix 1.

RESULTS AND DISCUSSION

We suggest a model to describe how different parameters of bottom-up oscillations (band, power, and phase) influence the TIW, in light of visual persistence, lateral inhibition, and network refractory period. Assume a visual Input A with Amplitude 1 and a persistence of ~ 100 msec (“first flash,” solid line in Figure 2A). As long as the impact of the stimulus on the visual network is above a threshold (shaded gray area in Figure 2A), the perception is of A. The effectiveness of an additional Stimulus B (“second flash”) arriving within 100 msec from the offset of A is decreased, and the two stimuli are integrated (dashed line in Figure 2A). However, if Stimulus B arrives more than 100 msec after A’s offset, they are segregated into two percepts (dotted line in Figure 2A). The duration it takes A to reduce below the threshold is governed by the persistence time constant, which can be reduced, for example, with a higher contrast of a continuous surrounding stimulus (Figure 2A and B).

Continuous inputs induce bottom-up alpha oscillations, and this adds another source of dynamic range to the persistence process. Because of the network refractory period (Buzsáki & Vöröslakos, 2023; Sanchez-Vives & McCormick, 2000) the oscillations can shorten the persistence of the first flash (Figure 2C), leading to shorter TIW. However, when alpha power is low relative to the flash impulse response, the persistence can be lengthened (Figure 2D). Similarly, shifting the phase (i.e., the relative timing between the appearance of the surrounding annulus and the first flash; Figure 2E) and alpha frequency (Figure 2F) can also change the TIW. Finally, gamma bursts can help segregate flashes at short ISIs by driving the system relatively fast to the refractory period after the presentation of the first flash (Figure 2G–H).

Importantly, the predictions made by the model can be tested in future empirical studies. Particularly, both persistence and bottom-up alpha can be affected by an external stimulus that is controlled by the experimenter. This provides an attractive opportunity to examine the interaction between brain oscillations and temporal segregation. For example, because the phase of bottom-up alpha is locked to the presentation of the surround stimulus (Karvat et al., 2024), the phase of alpha at the time of presentation of the first flash (Figure 2E) can be controlled by changing the interval between presenting the surround and the flash. The power of bottom-up alpha is likely to be influenced by features of the surround such as luminance and size. Therefore, adjusting them can pave the way for examining the effect of alpha power on the threshold in the two-flash task (Figure 2D). On the other hand, changing the duration or luminance of the flashes can change their evoked persistence (Figure 2B). Finally, recent advances in real-time detection of oscillatory bursts (Aksiotis, Tummyalis, & Ossadtchi, 2023; Karvat et al., 2020, 2021) allow triggering the experimental stimulus according to internally generated oscillatory bursts. Delivering the flashes according

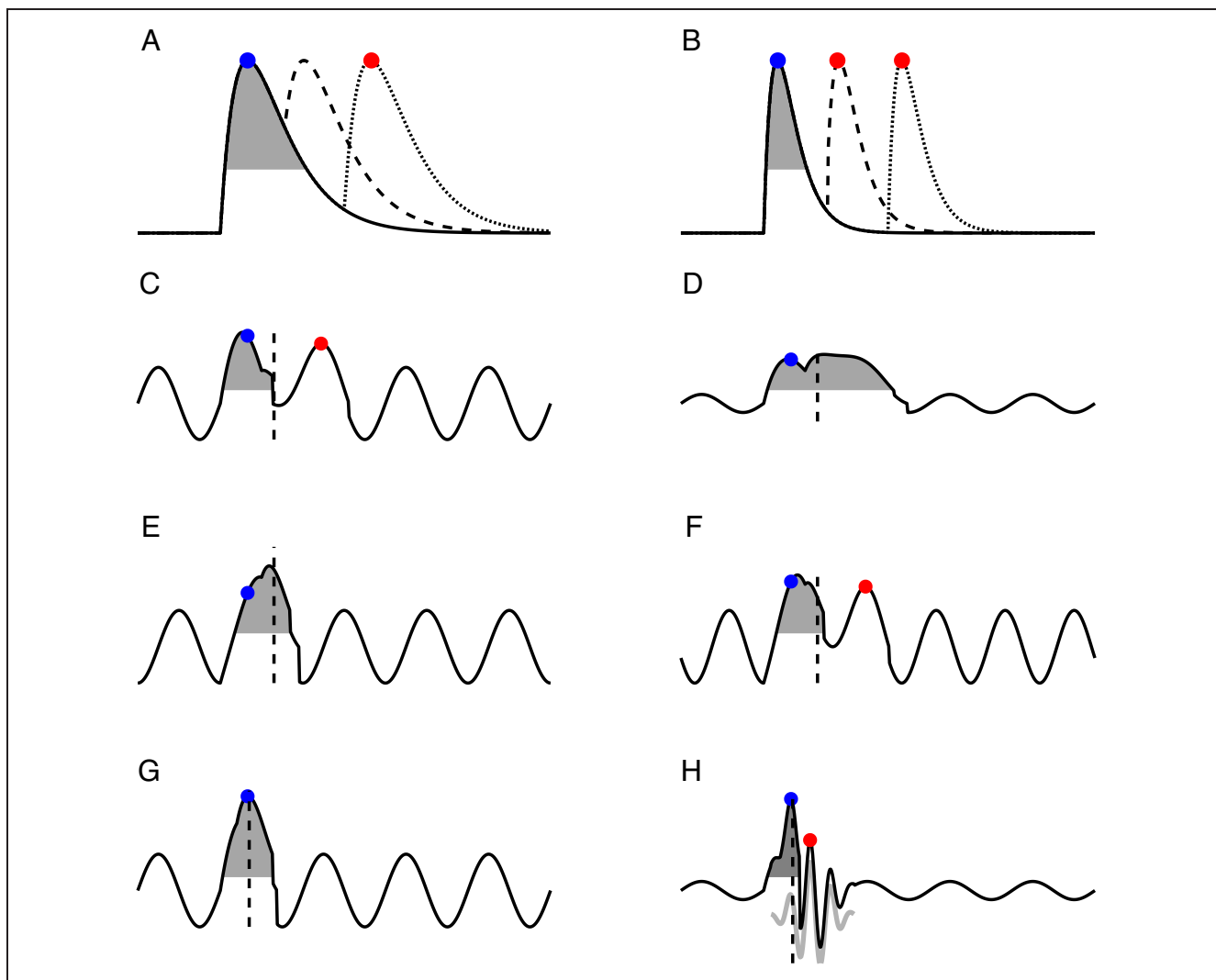


Figure 2. Suggested effects of oscillations and lateral inhibition on temporal resolution. (A) When the first flash arrives at the visual system (solid line), it reaches a maximum and has an effect that persists until it decays below a threshold (shaded area, ~ 100 msec). If a second flash arrives during the persistence duration of the first flash (dashed line, $\text{ISI} = 75$ msec), both flashes will be integrated and perceived as one. However, a flash that arrives after the decay (dotted line, $\text{ISI} = 150$ msec) is perceived as segregated. In all panels, blue dots denote the timing of maximum of the first flash, and the red dot (if exists) denotes the successful detection of a segregated second flash. (B) Same as (A), with lateral inhibition (e.g., from a high-contrast surround grating) that reduces the persistence duration. Note that under these conditions, also the $\text{ISI} = 75$ msec stimulus is perceived as a segregated event. (C–H) Oscillations further modify temporal resolution. In addition to lateral inhibition, the model follows a network refractory period rule according to which the effect of the percept is dampened entirely when the signal (i.e., percept plus oscillations) goes below 0.1, the value of the maximum of percept. (C) With the same persistence time constant as in (A), oscillation at 10 Hz allows segregation with $\text{ISI} = 50$ msec. Oscillation amplitude is equal to the maximum of the impulse response; dashed line represents the arrival time of the second flash. (D) The effect of power: When the amplitude is reduced to 0.25 of the amplitude in (C), the flashes are integrated because of lack of effect of the relatively small network refractory period on visual persistence. (E) Phase-shifting the alpha oscillation in $\pi/2$ radians relative to the timing of the first flash abolishes segregation. (F) Same as (E) with $\text{IAF} = 12$ Hz. Segregation is restored, consistent with the IAF-to-TIW theory. (G) Oscillations at 10 Hz do not support segregation of two flashes appearing with $\text{ISI} = 25$ msec. (H) A gamma (40 Hz) burst occurring around the flash presentation allows segregation of shorter ISIs, even when alpha is reduced, leading to a recovery of second flash detection (compared with D).

to the presence of bursts will allow examining the effect of the frequency, power, and timing bursts relative to the flash on temporal resolution.

To summarize, we propose a role for bottom-up alpha oscillations and visual persistence in temporal segregation. We simulated different interactions between contextual factors and endogenous brain rhythmic dynamics and listed possible ways to test them empirically. Importantly,

the list of theoretically plausible scenarios was not intended to be exhaustive, as other interactions could likely be found in future research. Our goal was to provide a theoretically informed mechanism that can inspire future examination of the predictions made by the model (and outlined in Figure 2). We believe, that together with the experimental and analytical advances presented in our companion paper published in this Special Focus issue

(Karvat et al., 2024), this theoretical framework will pave the way for a better understanding of bottom-up alpha and its interaction with top-down alpha oscillations.

Acknowledgments

The authors would like to thank Dr. Flor Kusnir and Nir Ofir for providing insightful remarks on previous drafts of this article.

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Data Availability Statement

The MATLAB script of the model and simulations is posted to GitHub: https://github.com/laanchic/Bottom_up_alpha.

Author Contributions

Golan Karvat: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Software; Validation; Visualization; Writing—Original draft; Writing—Review & editing. Ayelet N. Landau: Conceptualization; Funding acquisition; Methodology; Supervision; Visualization; Writing—Original draft; Writing—Review & editing.

Funding Information

The Brain Attention and Time Lab (PI: A. N. L.) was supported by the James McDonnell Scholar Award in Understanding Human Cognition, ISF, grant number: 958/16. This project has received funding from the European Research Council under the European Union's Horizon 2020 research and innovation programme, grant number: 852387.

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 $M(\text{an})/M = .407$, $W(\text{oman})/M = .32$, $M/W = .115$, 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. The authors of this paper report its proportions of citations by gender category to be: $M/M = .684$; $W/M = .158$; $M/W = .14$; $W/W = .018$.

REFERENCES

- Aksiotis, V., Tumyalis, A., & Ossadtchi, A. (2023). Brain state-triggered stimulus delivery helps to optimize reaction time. In D. D. Schmorrow & C. M. Fidopiastis (Eds.), *Augmented cognition* (pp. 3–15). Cham, Switzerland: Springer. https://doi.org/10.1007/978-3-031-35017-7_1
- Alamia, A., Terral, L., D'ambra, M. R., & VanRullen, R. (2023). Distinct roles of forward and backward alpha-band waves in spatial visual attention. *eLife*, *12*, e85035. <https://doi.org/10.7554/eLife.85035>, PubMed: 36876909
- Alamia, A., & VanRullen, R. (2019). Alpha oscillations and traveling waves: Signatures of predictive coding? *PLoS Biology*, *17*, e3000487. <https://doi.org/10.1371/journal.pbio.3000487>, PubMed: 31581198
- Artieda, J., Pastor, M. A., Lacruz, F., & Obeso, J. A. (1992). Temporal discrimination is abnormal in Parkinson's disease. *Brain*, *115*, 199–210. <https://doi.org/10.1093/brain/115.1.199>, PubMed: 1559154
- Bastos, A. M., Vezoli, J., Bosman, C. A., Schoffelen, J.-M., Oostenveld, R., Dowdall, J. R., et al. (2015). Visual areas exert feedforward and feedback influences through distinct frequency channels. *Neuron*, *85*, 390–401. <https://doi.org/10.1016/j.neuron.2014.12.018>, PubMed: 25556836
- Baumgarten, T. J., Schnitzler, A., & Lange, J. (2015). Beta oscillations define discrete perceptual cycles in the somatosensory domain. *Proceedings of the National Academy of Sciences, U.S.A.*, *112*, 12187–12192. <https://doi.org/10.1073/pnas.1501438112>, PubMed: 26324922
- Benwell, C. S. Y., London, R. E., Tagliabue, C. F., Veniero, D., Gross, J., Keitel, C., et al. (2019). Frequency and power of human alpha oscillations drift systematically with time-on-task. *Neuroimage*, *192*, 101–114. <https://doi.org/10.1016/j.neuroimage.2019.02.067>, PubMed: 30844505
- Berger, H. (1929). Über das elektroencephalogramm des menschen [On the electroencephalogram of man]. *Archiv für Psychiatrie und Nervenkrankheiten*, *87*, 527–570. <https://doi.org/10.1007/BF01797193>
- Bowen, R. W., Markell, K. A., & Schoon, C. M. (1980). Two-pulse discrimination and rapid light adaptation: Complex effects on temporal resolution and a new visual temporal illusion. *Journal of the Optical Society of America*, *70*, 1453–1458. <https://doi.org/10.1364/JOSA.70.001453>, PubMed: 7463184
- Buergers, S., & Noppeney, U. (2022). The role of alpha oscillations in temporal binding within and across the senses. *Nature Human Behaviour*, *6*, 732–742. <https://doi.org/10.1038/s41562-022-01294-x>, PubMed: 35210592
- Busch, N. A., Dubois, J., & VanRullen, R. (2009). The phase of ongoing EEG oscillations predicts visual perception. *Journal of Neuroscience*, *29*, 7869–7876. <https://doi.org/10.1523/JNEUROSCI.0113-09.2009>, PubMed: 19535598
- Buzsáki, G., Anastassiou, C. A., & Koch, C. (2012). The origin of extracellular fields and currents—EEG, ECoG, LFP and spikes. *Nature Reviews Neuroscience*, *13*, 407–420. <https://doi.org/10.1038/nrn3241>, PubMed: 22595786
- Buzsáki, G., & Vöröslakos, M. (2023). Brain rhythms have come of age. *Neuron*, *111*, 922–926. <https://doi.org/10.1016/j.neuron.2023.03.018>, PubMed: 37023714
- Chaumon, M., & Busch, N. A. (2014). Prestimulus neural oscillations inhibit visual perception via modulation of response gain. *Journal of Cognitive Neuroscience*, *26*, 2514–2529. https://doi.org/10.1162/jocn_a_00653, PubMed: 24742156
- Cooper, N. R., Croft, R. J., Dominey, S. J. J., Burgess, A. P., & Gruzelić, J. H. (2003). Paradox lost? Exploring the role of alpha oscillations during externally vs. internally directed attention and the implications for idling and inhibition hypotheses. *International Journal of Psychophysiology*,

- 47, 65–74. [https://doi.org/10.1016/S0167-8760\(02\)00107-1](https://doi.org/10.1016/S0167-8760(02)00107-1), PubMed: 12543447
- Crick, F. (1984). Function of the thalamic reticular complex: The searchlight hypothesis. *Proceedings of the National Academy of Sciences, U.S.A.*, *81*, 4586–4590. <https://doi.org/10.1073/pnas.81.14.4586>, PubMed: 6589612
- Deodato, M., & Melcher, D. (2024). Correlations between visual temporal resolution and individual alpha peak frequency: Evidence that internal and measurement noise drive null findings. *Journal of Cognitive Neuroscience*, *36*, 590–601. https://doi.org/10.1162/jocn_a_01993, PubMed: 37043238
- Dou, W., Morrow, A., Iemi, L., & Samaha, J. (2022). Pre-stimulus alpha-band phase gates early visual cortex responses. *NeuroImage*, *253*, 119060. <https://doi.org/10.1016/j.neuroimage.2022.119060>, PubMed: 35283286
- Erath, M. K., Pinsk, M. A., & Kastner, S. (2021). A causal role for the pulvinar in coordinating task-independent cortico–cortical interactions. *Journal of Comparative Neurology*, *529*, 3772–3784. <https://doi.org/10.1002/cne.25193>, PubMed: 34013540
- Feingold, J., Gibson, D. J., DePasquale, B., & Graybiel, A. M. (2015). Bursts of beta oscillation differentiate postperformance activity in the striatum and motor cortex of monkeys performing movement tasks. *Proceedings of the National Academy of Sciences, U.S.A.*, *112*, 13687–13692. <https://doi.org/10.1073/pnas.1517629112>, PubMed: 26460033
- Fiebelkorn, I. C., & Kastner, S. (2019). The puzzling pulvinar. *Neuron*, *101*, 201–203. <https://doi.org/10.1016/j.neuron.2018.12.032>, PubMed: 30653933
- Foxe, J. J., Simpson, G. V., & Ahlfors, S. P. (1998). Parieto-occipital ~10 Hz activity reflects anticipatory state of visual attention mechanisms. *NeuroReport*, *9*, 3929–3933. <https://doi.org/10.1097/00001756-199812010-00030>, PubMed: 9875731
- Fries, P., Scheeringa, R., & Oostenveld, R. (2008). Finding gamma. *Neuron*, *58*, 303–305. <https://doi.org/10.1016/j.neuron.2008.04.020>, PubMed: 18466741
- Gray, M. J., & Emmanouil, T. A. (2020). Individual alpha frequency increases during a task but is unchanged by alpha-band flicker. *Psychophysiology*, *57*, e13480. <https://doi.org/10.1111/psyp.13480>, PubMed: 31573080
- Gruzelier, J. H., & Venables, P. H. (1974). Two-flash threshold, sensitivity and β in normal subjects and schizophrenics. *Quarterly Journal of Experimental Psychology*, *26*, 594–604. <https://doi.org/10.1080/14640747408400451>, PubMed: 4438559
- Haber, R. N., & Standing, L. G. (1969). Direct measures of short-term visual storage. *Quarterly Journal of Experimental Psychology*, *21*, 43–54. <https://doi.org/10.1080/14640746908400193>, PubMed: 5777982
- Haegens, S., Cousijn, H., Wallis, G., Harrison, P. J., & Nobre, A. C. (2014). Inter- and intra-individual variability in alpha peak frequency. *NeuroImage*, *92*, 46–55. <https://doi.org/10.1016/j.neuroimage.2014.01.049>, PubMed: 24508648
- Halgren, M., Ulbert, I., Bastuji, H., Fabó, D., Eróss, L., Rey, M., et al. (2019). The generation and propagation of the human alpha rhythm. *Proceedings of the National Academy of Sciences, U.S.A.*, *116*, 23772–23782. <https://doi.org/10.1073/pnas.1913092116>, PubMed: 31685634
- Hoogenboom, N., Schoffelen, J.-M., Oostenveld, R., Parkes, L. M., & Fries, P. (2006). Localizing human visual gamma-band activity in frequency, time and space. *NeuroImage*, *29*, 764–773. <https://doi.org/10.1016/j.neuroimage.2005.08.043>, PubMed: 16216533
- Hughes, S. W., & Crunelli, V. (2005). Thalamic mechanisms of EEG alpha rhythms and their pathological implications. *Neuroscientist*, *11*, 357–372. <https://doi.org/10.1177/1073858405277450>, PubMed: 16061522
- Iemi, L., Busch, N. A., Laudini, A., Haegens, S., Samaha, J., Villringer, A., et al. (2019). Multiple mechanisms link prestimulus neural oscillations to sensory responses. *eLife*, *8*, e43620. <https://doi.org/10.7554/eLife.43620>, PubMed: 31188126
- Iemi, L., Chaumon, M., Crouzet, S. M., & Busch, N. A. (2017). Spontaneous neural oscillations bias perception by modulating baseline excitability. *Journal of Neuroscience*, *37*, 807–819. <https://doi.org/10.1523/JNEUROSCI.1432-16.2016>, PubMed: 28123017
- 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: 21119777
- Jones, E. G. (1985). Principles of thalamic organization. In E. G. Jones (Ed.), *The thalamus* (pp. 85–149). Boston: Springer. https://doi.org/10.1007/978-1-4615-1749-8_3
- Karvat, G., Alyahyay, M., & Diester, I. (2021). Spontaneous activity competes with externally evoked responses in sensory cortex. *Proceedings of the National Academy of Sciences, U.S.A.*, *118*, e2023286118. <https://doi.org/10.1073/pnas.2023286118>, PubMed: 34155142
- Karvat, G., Ofir, N., & Landau, A. N. (2024). Sensory drive modifies brain dynamics and the temporal integration window. *Journal of Cognitive Neuroscience*, *36*, 614–631. https://doi.org/10.1162/jocn_a_02088, PubMed: 38010294
- Karvat, G., Schneider, A., Alyahyay, M., Steenbergen, F., Tangermann, M., & Diester, I. (2020). Real-time detection of neural oscillation bursts allows behaviourally relevant neurofeedback. *Communications Biology*, *3*, 72. <https://doi.org/10.1038/s42003-020-0801-z>, PubMed: 32060396
- Kietzman, M. L. (1967). Two-pulse measures of temporal resolution as a function of stimulus energy. *Journal of the Optical Society of America*, *57*, 809–813. <https://doi.org/10.1364/JOSA.57.000809>, PubMed: 6038006
- Lewis, M. F. (1967). Two-flash thresholds as a function of luminance in the dark-adapted eye. *Journal of the Optical Society of America*, *57*, 814–815. <https://doi.org/10.1364/JOSA.57.000814>, PubMed: 6038007
- Lewis, M. F. (1968). Two-flash thresholds as a function of flash luminance and area. *Perception & Psychophysics*, *4*, 241–244. <https://doi.org/10.3758/BF03206310>
- Lórinçz, M. L., Kékesi, K. A., Juhász, G., Crunelli, V., & Hughes, S. W. (2009). Temporal framing of thalamic relay-mode firing by phasic inhibition during the alpha rhythm. *Neuron*, *63*, 683–696. <https://doi.org/10.1016/j.neuron.2009.08.012>, PubMed: 19755110
- Lozano-Soldevilla, D., & VanRullen, R. (2019). The hidden spatial dimension of alpha: 10-Hz perceptual echoes propagate as periodic traveling waves in the human brain. *Cell Reports*, *26*, 374–380. <https://doi.org/10.1016/j.celrep.2018.12.058>, PubMed: 30625320
- Luck, S. J., Chelazzi, L., Hillyard, S. A., & Desimone, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *Journal of Neurophysiology*, *77*, 24–42. <https://doi.org/10.1152/jn.1997.77.1.24>, PubMed: 9120566
- Mahneke, A. (1958). Foveal discrimination measured with two successive light flashes: A psychophysical study. *Acta Ophthalmologica*, *36*, 4–11. <https://doi.org/10.1111/j.1755-3768.1958.tb02251.x>, PubMed: 13532607
- Mathewson, K. E., Gratton, G., Fabiani, M., Beck, D. M., & Ro, T. (2009). To see or not to see: Prestimulus α phase predicts visual awareness. *Journal of Neuroscience*, *29*, 2725–2732. <https://doi.org/10.1523/JNEUROSCI.3963-08.2009>, PubMed: 19261866
- Murthy, V. N., & Fetz, E. E. (1992). Coherent 25- to 35-Hz oscillations in the sensorimotor cortex of awake behaving

- monkeys. *Proceedings of the National Academy of Sciences, U.S.A.*, *89*, 5670–5674. <https://doi.org/10.1073/pnas.89.12.5670>, PubMed: 1608977
- Neymotin, S. A., Barczak, A., O'Connell, M. N., McGinnis, T., Markowitz, N., Espinal, E., et al. (2020). Taxonomy of neural oscillation events in primate auditory cortex. *bioRxiv*. <https://doi.org/10.1101/2020.04.16.045021>
- Pang, Z., Alamia, A., & VanRullen, R. (2020). Turning the stimulus on and off changes the direction of α traveling waves. *eNeuro*, *7*, ENEURO.0218-20.2020. <https://doi.org/10.1523/ENEURO.0218-20.2020>, PubMed: 33168617
- Pinaut, D. (2003). Cellular interactions in the rat somatosensory thalamocortical system during normal and epileptic 5–9 Hz oscillations. *Journal of Physiology*, *552*, 881–905. <https://doi.org/10.1113/jphysiol.2003.046573>, PubMed: 12923213
- Purcell, D. G., & Stewart, A. L. (1971). The two-flash threshold: An evaluation of critical-duration and visual-persistence hypotheses. *Perception & Psychophysics*, *9*, 61–64. <https://doi.org/10.3758/BF03213029>
- Ruzzoli, M., Torralba, M., Moris Fernández, L., & Soto-Faraco, S. (2019). The relevance of alpha phase in human perception. *Cortex*, *120*, 249–268. <https://doi.org/10.1016/j.cortex.2019.05.012>, PubMed: 31352236
- Sadaghiani, S., Hesselmann, G., Friston, K. J., & Kleinschmidt, A. (2010). The relation of ongoing brain activity, evoked neural responses, and cognition. *Frontiers in Systems Neuroscience*, *4*, 20. <https://doi.org/10.3389/fnsys.2010.00020>, PubMed: 20631840
- Sadaghiani, S., Scheeringa, R., Lehongre, K., Morillon, B., Giraud, A.-L., & Kleinschmidt, A. (2010). Intrinsic connectivity networks, alpha oscillations, and tonic alertness: A simultaneous electroencephalography/functional magnetic resonance imaging study. *Journal of Neuroscience*, *30*, 10243–10250. <https://doi.org/10.1523/JNEUROSCI.1004-10.2010>, PubMed: 20668207
- Samaha, J. (2018). *Spontaneous brain activity and top-down mechanisms in visual perception* [Ph.D.]. The University of Wisconsin–Madison. <https://www.proquest.com/docview/2058140437/abstract/ADD86456E889471EPQ/1>
- Samaha, J., & Postle, B. R. (2015). The speed of alpha-band oscillations predicts the temporal resolution of visual perception. *Current Biology*, *25*, 2985–2990. <https://doi.org/10.1016/j.cub.2015.10.007>, PubMed: 26526370
- Samaha, J., & Romei, V. (2024). Alpha-band frequency and temporal windows in perception: A review and living meta-analysis of 27 experiments (and counting). *Journal of Cognitive Neuroscience*, *36*, 640–654. https://doi.org/10.1162/jocn_a_02069, PubMed: 37856149
- Sanchez-Vives, M. V., & McCormick, D. A. (2000). Cellular and network mechanisms of rhythmic recurrent activity in neocortex. *Nature Neuroscience*, *3*, 1027–1034. <https://doi.org/10.1038/79848>, PubMed: 11017176
- Scheeringa, R., Fries, P., Petersson, K.-M., Oostenveld, R., Grothe, I., Norris, D. G., et al. (2011). Neuronal dynamics underlying high- and low-frequency EEG oscillations contribute independently to the human BOLD signal. *Neuron*, *69*, 572–583. <https://doi.org/10.1016/j.neuron.2010.11.044>, PubMed: 21315266
- Scheeringa, R., Petersson, K. M., Kleinschmidt, A., Jensen, O., & Bastiaansen, M. C. M. (2012). EEG alpha power modulation of fMRI resting-state connectivity. *Brain Connectivity*, *2*, 254–264. <https://doi.org/10.1089/brain.2012.0088>, PubMed: 22938826
- Sherman, S. M., & Guillery, R. W. (2001). *Exploring the thalamus*. Elsevier.
- Standing, L., Haber, R. N., Cataldo, M., & Sales, B. D. (1969). Two types of short-term visual storage. *Perception & Psychophysics*, *5*, 193–196. <https://doi.org/10.3758/BF03210536>
- Utiel, W. R., & Hieronymus, R. (1970). Spatio-temporal effects in visual gap detection. *Perception & Psychophysics*, *8*, 321–326. <https://doi.org/10.3758/BF03212601>
- van Diepen, R. M., & Mazaheri, A. (2018). The caveats of observing inter-trial phase-coherence in cognitive neuroscience. *Scientific Reports*, *8*, 2990. <https://doi.org/10.1038/s41598-018-20423-z>, PubMed: 29445210
- van Dijk, H., Schoffelen, J.-M., Oostenveld, R., & Jensen, O. (2008). Prestimulus oscillatory activity in the alpha band predicts visual discrimination ability. *Journal of Neuroscience*, *28*, 1816–1823. <https://doi.org/10.1523/JNEUROSCI.1853-07.2008>, PubMed: 18287498
- van Kerkoerle, T., Self, M. W., Dagnino, B., Gariel-Mathis, M.-A., Poort, J., van der Togt, C., et al. (2014). Alpha and gamma oscillations characterize feedback and feedforward processing in monkey visual cortex. *Proceedings of the National Academy of Sciences, U.S.A.*, *111*, 14332–14341. <https://doi.org/10.1073/pnas.1402773111>, PubMed: 25205811
- VanRullen, R. (2018). Perceptual rhythms. In *Stevens handbook of experimental psychology and cognitive neuroscience* (Vol. 2, pp. 1–44). Wiley. <https://doi.org/10.1002/9781119170174.epcn212>
- VanRullen, R., & Macdonald, J. S. P. (2012). Perceptual echoes at 10 Hz in the human brain. *Current Biology*, *22*, 995–999. <https://doi.org/10.1016/j.cub.2012.03.050>, PubMed: 22560609
- Varela, F. J., Toro, A., John, E. R., & Schwartz, E. L. (1981). Perceptual framing and cortical alpha rhythm. *Neuropsychologia*, *19*, 675–686. [https://doi.org/10.1016/0028-3932\(81\)90005-1](https://doi.org/10.1016/0028-3932(81)90005-1), PubMed: 7312152
- Venables, P. H. (1963). Changes due to noise in the threshold of fusion of paired light flashes in schizophrenics and normals. *British Journal of Social and Clinical Psychology*, *2*, 94–99. <https://doi.org/10.1111/j.2044-8260.1963.tb00381.x>
- Voytek, B., Samaha, J., Rolle, C. E., Greenberg, Z., Gill, N., Porat, S., et al. (2017). Preparatory encoding of the fine scale of human spatial attention. *Journal of Cognitive Neuroscience*, *29*, 1302–1310. https://doi.org/10.1162/jocn_a_01124, PubMed: 28294717
- Zhigalov, A., & Jensen, O. (2023). Perceptual echoes as travelling waves may arise from two discrete neuronal sources. *Neuroimage*, *272*, 120047. <https://doi.org/10.1016/j.neuroimage.2023.120047>, PubMed: 37001836