



HAL
open science

A Traveling Waves Perspective on Temporal Binding

Andrea Alamia, Rufin VanRullen

► **To cite this version:**

Andrea Alamia, Rufin VanRullen. A Traveling Waves Perspective on Temporal Binding. *Journal of Cognitive Neuroscience*, 2024, 36 (4), pp.721-729. 10.1162/jocn_a_02004 . hal-04301041

HAL Id: hal-04301041

<https://hal.science/hal-04301041v1>

Submitted on 22 Nov 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

A travelling waves perspective on temporal binding

Andrea Alamia & Rufin VanRullen

CerCo, CNRS, 31052 Toulouse, France,
ANITI, Université de Toulouse, 31062, Toulouse, France

Abstract

Brain oscillations are involved in many cognitive processes, and several studies have investigated their role in cognition. In particular, the phase of certain oscillations has been related to temporal binding and integration processes, with some authors arguing that perception could be an inherently rhythmic process. However, previous research on oscillations mostly overlooked their spatial component: how oscillations propagate through the brain as travelling waves, with systematic phase delays between brain regions. Here, we argue that interpreting oscillations as travelling waves is a useful paradigm shift to understand their role in temporal binding and address controversial results. After a brief definition of traveling waves, we propose an original view on temporal integration that considers this new perspective. We first focus on cortical dynamics, then speculate about the role of thalamic nuclei in modulating the waves, and on the possible consequences for rhythmic temporal binding. In conclusion, we highlight the importance of considering oscillations as travelling waves when investigating their role in cognitive functions.

Introduction

Neuronal oscillations have been reliably associated with many cognitive processes, such as perception (Dugué et al., 2011; Giraud & Arnal, 2012; Vanrullen & MacDonald, 2012), memory (Benchenane et al., 2011; Lundqvist et al., 2018), attention (Bollimunta et al., 2011; Dugué et al., 2016; Klimesch, 2012; Sauseng et al., 2005; Thut et al., 2006; VanRullen, 2016), time perception (van Wassenhove, 2016), and even consciousness (Di Gregorio et al., 2022; Engel & Singer, 2001; Palva & Palva, 2007). Several studies have demonstrated that oscillatory dynamics play an active, causal role in modulating effective neuronal connectivity and shaping cortical plasticity (Galuske et al., 2019; Steriade, 1999). Yet, despite a myriad of studies investigating oscillatory processes, most research focused on their temporal features, such as phase, frequency and amplitude, overlooking their spatial component, that is how oscillations propagate through brain regions. Even when considering different cortical areas, most studies focused on zero-lag synchrony, i.e. oscillations sharing precisely the same phase across cortical regions (figure 1B). However, recent studies are challenging this approach, supporting a novel interpretation that characterizes oscillations as travelling waves, which propagate across cortical regions with different phase offsets (figure 1C) (Alexander et al., 2019; Muller et al., 2018; Zhang et al., 2018). This new view provides novel insights to open questions about the role of oscillations in various cognitive functions. Here, after a brief introduction on travelling waves, we discuss how oscillatory travelling waves can provide an original view on the question of temporal binding.

Oscillations as travelling waves

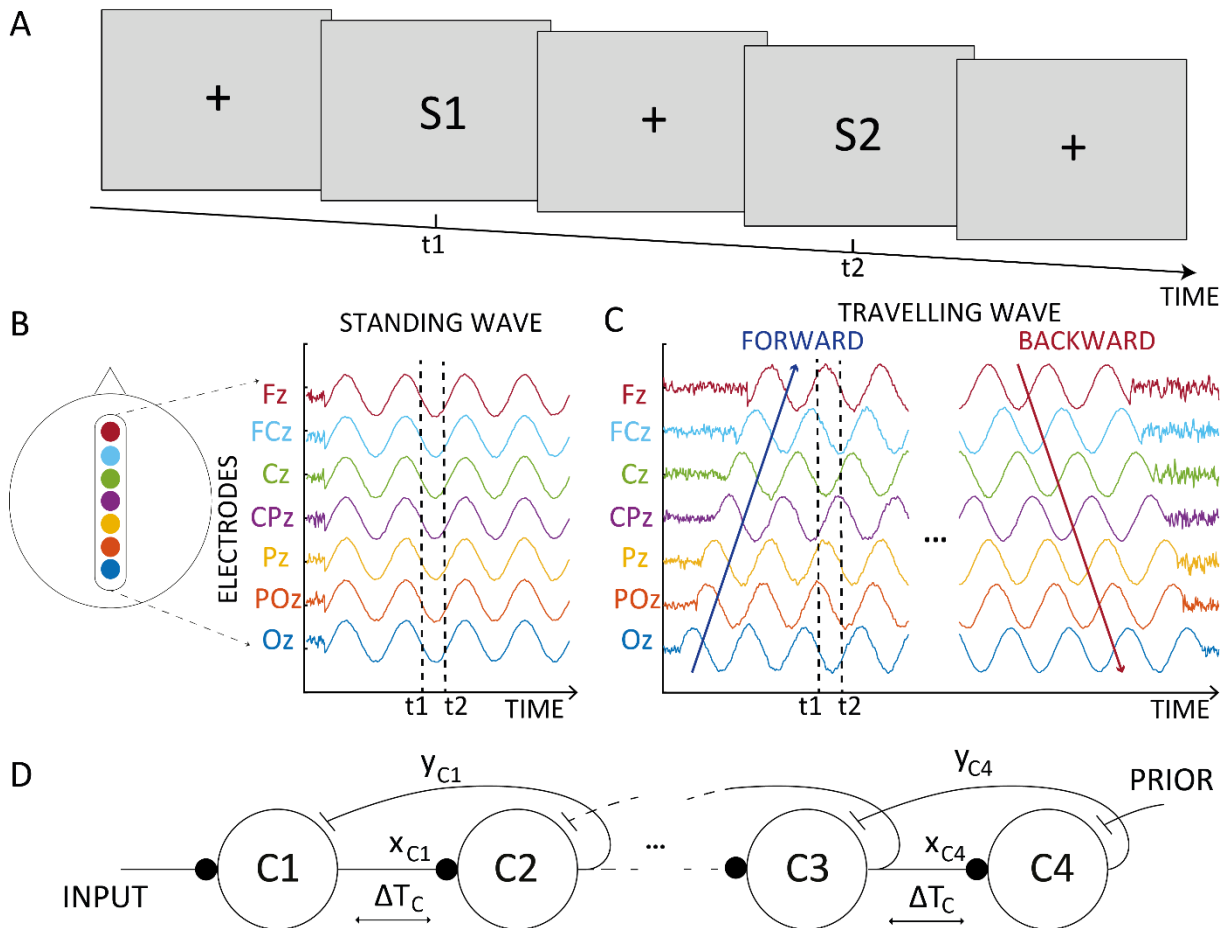
Different phenomena have been characterized as “travelling waves” in the literature. Previous work described as travelling waves the spatial propagation of non-periodic evoked responses to stimulus onset, for instance rising from occipital to frontal areas (Klimesch et

1 al., 2007; Zauner et al., 2014), or sweeping across a single retinotopic region (Bringuier et al.,
2 1999; Reynaud et al., 2012) Similarly, periodic stimulation, such as a flickering visual
3 stimulus, gives rise to oscillatory waves that share the same temporal features as the
4 entraining stimulus (Sato et al., 2012). Here, we focus on intrinsic oscillatory travelling
5 waves, i.e., truly periodic waves with an intrinsic frequency that does not necessarily match
6 that of the sensory stimulus, and generated by endogenous processes (for an overview of
7 wave generation, see Ermentrout & Kleinfeld, 2001 but also Alamia & VanRullen, 2019).

8
9 Despite a growing number of studies investigating this type of wave, little is known about
10 their functional role and relation to cognitive functions. Interestingly, oscillatory travelling
11 waves can propagate at different speeds, both at the mesoscopic scale (within brain regions,
12 Fakche & Dugué, 2022; Han et al., 2008; Sreekumar et al., 2020; Zanos et al., 2015) as well as
13 at the macroscopic one (between cortical areas, Halgren et al., 2019; Pang et al., 2020;
14 Zhang et al., 2018), and they have been reported in several frequency bands, e.g., theta
15 (Bhattacharya et al., 2022; Zhang & Jacobs, 2015), alpha (Alamia et al., 2020; Lozano-
16 Soldevilla & VanRullen, 2019; Luo et al., 2021) and beta (Das et al., 2022). In our previous
17 work investigating macroscopic alpha-band travelling waves, we proposed a key distinction
18 between two main categories determined by the waves' direction. Specifically, forward
19 waves propagate from lower to higher sensory regions and reflect sensory processes (Alamia
20 & VanRullen, 2019; Lozano-Soldevilla & VanRullen, 2019; Pang et al., 2020). On the contrary,
21 backward waves propagate in the opposite direction and primarily relate to top-down
22 functions, such as attention and visual selection (Alamia et al., 2023; Maris et al., 2013). In
23 addition, forward and backward waves may rely on different anatomical substrates. In line
24 with previous studies (Bastos et al., 2012, 2015; Buffalo et al., 2011), it's possible to separate
25 forward and backward streams in superficial and deep layers, respectively. However, it's
26 important to keep in mind the cortical laminae's spectral profile, as superficial layers relate
27 primarily to faster gamma-band oscillations, whereas lower beta-band oscillations originate
28 in deeper layers. In this paper, we mainly focused on alpha-band oscillations, assuming that
29 the interaction between brain regions generates the oscillatory dynamics, focusing on the
30 global rather than local level (i.e., not at a specific layer). In other words, the interaction
31 between cortical areas generates alpha oscillatory dynamics, which propagate forward and
32 backward, coordinating the activity of faster oscillations in each region (Fries, 2015; Lisman
33 & Jensen, 2013; McLelland & VanRullen, 2016).

34
35 Yet, what makes an oscillation a traveling wave? Considering non-invasive EEG recordings
36 (for example, along the electrode midline, as in figure 1B), we can assume that each
37 electrode mainly records activity from a limited and distinct cortical area (it is important,
38 though, to keep in mind several limitations when analyzing travelling waves in EEG
39 recordings: for example, in EEG recordings, only waves longer than twice the electrode
40 separation distance can be resolved (Nyquist criterion in space), and lower spatial resolution
41 and volume conduction may mask shorter waves providing different results than invasive
42 cortical recordings, as detailed in Alexander et al., 2019; Freeman & Barrie, 2000; Nunez,
43 1974). Given this assumption, an oscillatory traveling wave is defined by a phase shift
44 between signals from different electrodes, as shown in figure 1C: if the phase shift grows
45 from occipital to frontal electrodes, the wave propagates in the forward direction;
46 otherwise, it flows backward. In other words, the sign of the phase shift determines whether
47 the waves travel from occipital to frontal regions or vice-versa. In some of our recent work

1 combining EEG experiments and computational modeling (Alamia & VanRullen, 2019), we
 2 showed that a predictive coding system with biologically plausible neural time constants and
 3 hierarchical communication delays would naturally produce alpha-band travelling waves
 4 (figure 1D). These waves could flow in either the forward or backward direction, depending
 5 on the behavioral task and the state of the system; however, in either case, the phase
 6 gradient of the wave was driven by inter-areal communication delays, and thus directly
 7 followed the bottom-up or top-down activation latencies across the hierarchy of brain areas.
 8 What can this traveling wave approach to brain oscillations tell us about temporal binding?
 9



10
 11 **Figure 1. Difference between standing and travelling waves.** A) Consider an experiment in which
 12 two visual stimuli, S1 and S2, are displayed sequentially at times t_1 and t_2 . B) Oscillatory waves can
 13 be measured for instance along the mid-line of scalp EEG electrodes. Depending on the timings t_1
 14 and t_2 and on the phase of the ongoing oscillation, the two stimuli may be perceived as one
 15 “merged” item or two distinct ones (Baumgarten et al., 2015; Valera et al., 1981; VanRullen & Koch,
 16 2003). In the case of a standing wave, the oscillations share the same phase over all electrodes, and
 17 there is only one phase relative to the two stimuli across electrodes. C) If the oscillation is actually a
 18 forward (or backward) traveling wave, it presents a phase offset increasing (or decreasing) across
 19 electrodes. In this case, the onset of the two stimuli, t_1 and t_2 , falls at different relative phases along
 20 the line of electrodes; this could challenge the idea of a unique optimal (or poor) phase for temporal
 21 integration across the visual system. D) A cortical model of predictive coding with mutually
 22 connected hierarchical regions exchanging predictions (via feedback connections, y_c) and prediction
 23 errors (x_c). In a predictive coding implementation, higher regions predict the activity of the lower
 24 regions, and the difference between the predictions and the actual activity (i.e., the prediction error)
 25 is used to update the next prediction. When taking into account neural time constants and inter-
 26 areal communication delays (ΔT_c), this model naturally produces alpha-band travelling waves as in

1 panel C), flowing in the forward direction during sensory input processing, and in the backward
2 direction when top-down priors are present in the absence of stimuli (Alamia & VanRullen, 2019).
3 The key intuition is that communication delays introduce a temporal offset in the predictions that
4 generate oscillatory dynamics due to overshooting and compensations. Interestingly, as we showed
5 in our previous work, the temporal delay relates to the frequency of the oscillations: shorter delays
6 (more local interactions) generate faster dynamics, in line with the biological plausible interpretation
7 of such dynamics.

9 **Is a hierarchical system more rhythmic during globally synchronized oscillations, or during** 10 **traveling waves?**

11 For many years, some authors have debated whether relying on oscillatory neural
12 mechanisms makes the brain a periodic system, with “optimal” and “poor” phases for
13 temporally integrating information (Busch et al., 2009; Fakche et al., 2022; Herbst & Landau,
14 2016; Ronconi et al., 2017, 2018; Ronconi & Melcher, 2017; Samaha et al., 2015a; Venskus &
15 Hughes, 2021; Wiener & Kanai, 2016; Wutz et al., 2018). The notion of rhythmic or periodic
16 processing implies that information is preferentially processed by each brain region at the
17 “optimal” oscillation phase. In this case, two sequential objects with the proper temporal
18 delay could be “merged” in one percept when they fall within one phase or “segregated” in
19 two distinct percepts when landing on different phases (as schematically shown in figure 1).
20 This experimental prediction, which stems from considering sensory systems as rhythmic,
21 has been tested in several experimental works, providing arguably controversial results. On
22 the one hand, some authors found experimental evidence that corroborates this hypothesis,
23 demonstrating that individual participants’ alpha-band features predict temporal aspects of
24 visual perception (Ronconi et al., 2018; Samaha et al., 2015b; Samaha & Postle, 2015; Wutz
25 et al., 2018); on the other hand, other authors failed in reproducing these results using
26 similar paradigms, leaving controversial the question about the role of phase in temporal
27 binding processes (Buergers & Noppeney, 2022; Ruzzoli et al., 2019). However, re-
28 interpreting oscillations as travelling waves challenges the whole narrative and provides a
29 more subtle view that allows re-evaluating -if not reconciling- previous findings.

30
31 As described above, when interpreting oscillations as waves propagating through brain
32 regions, it is natural to obtain a gradient of phases throughout the sensory system (figure
33 1C). Hence, at a given moment, some brain regions within the visual stream may be at the
34 “optimal” phase for temporal integration while other regions would *simultaneously* reach
35 their “poor” phase. For example, suppose feedforward latencies and communication delays
36 drive the phase gradient across areas, and we can assume a 50ms difference between
37 optimal and poor phase in the alpha band, corresponding to activity in V1 and IT. In this
38 case, these two regions may be simultaneously at opposite alpha phases, one in the optimal
39 and one in the poor phase. That is, the travelling wave perspective puts into question the
40 assumption that there is one unique phase across the whole visual system at any given time;
41 instead, instantaneous oscillatory phase would be specific to each brain region. Considering
42 the example shown in figure 1A with two temporally sequential stimuli, it now becomes less
43 obvious to answer the question of whether we perceive 1 or 2 objects, if these can be
44 simultaneously “merged” in one region (because they are processed at a given phase) and
45 “segregated” in the next brain area (because they are processed at the opposite phase).
46 More generally, one could argue that oscillatory phase has more functional influence on
47 sensory perception when each area happens to be at its “optimal” (or. poor) phase at the
48 precise moment when the relevant stimulus information reaches it. The “optimal” phase

1 with respect to stimulus onset would thus differ for each region, being mainly driven by the
2 activation latency delay between successive hierarchical regions. As mentioned above, in our
3 previous work (Alamia & VanRullen, 2019) we proposed a model of cortical information
4 processing based on Predictive Coding principles, which could naturally produce oscillatory
5 feedforward traveling waves with a phase gradient that followed the activation delays across
6 the cortical hierarchy (Figure 1D). In such a system, one could argue that temporal binding
7 would be most rhythmic during forward oscillatory waves, when the successive activation
8 delays imply that each area receives the stimulus information at its own optimal (or poor)
9 phase; in turn, the system would behave less rhythmically during standing waves (i.e.,
10 synchronized oscillations, having the same phase across regions, see fig. 1B), and even less
11 so during backward waves. Note, however, that this reasoning mainly characterizes the
12 rhythmicity of temporal binding processes associated with bottom-up stimulus processing
13 (e.g. judging the temporal order of two successive flashes); in a task whose outcome
14 depends on top-down information transfer (e.g. related to attention or expectations), the
15 same reasoning could imply that backward-travelling waves (Alamia et al., 2023; Alamia &
16 VanRullen, 2019; Pang et al., 2020) are the most conducive to rhythmic perception... In
17 short, while a “naïve” view of brain oscillations would suggest that rhythmic temporal
18 binding corresponds with episodes of large-scale phase synchronization across the brain, the
19 more nuanced view detailed here implies that temporal binding could be less rhythmic in
20 such a globally synchronized state, and most affected by oscillatory activity when the task-
21 relevant sequence of cortical activations follows a feedforward or a feed-back travelling
22 wave pattern (depending on exact task specifications). Importantly, this new view supports
23 the counterintuitive conclusion that contrary to common intuition, global synchronization
24 and rhythmic perception are not necessarily identical: a globally synchronized state, in which
25 all the regions have the same phase, acts less rhythmically than a system having a gradient
26 of phases. This complexity could go some way to explaining the observed discrepancies in
27 the literature.

28

29 **The pulvinar as the conductor orchestrating the alpha-band symphony?**

30 However complicated it might be to establish the role of oscillations in a (simplified) cortical
31 system with a strict hierarchical structure (as in Figure 1D), things get even more difficult
32 when considering the potential implication of sub-cortical regions that could be reciprocally
33 connected with multiple cortical areas. We have long known that non-cortical nuclei play an
34 important role in the generation and synchronization of oscillatory rhythms in the brain.
35 Here, we consider the role of a specific thalamic nucleus, the pulvinar, in synchronizing the
36 whole cortical symphony, and the associated consequences for the temporal integration of
37 sensory information.

38

39 Thalamic nuclei, such as the pulvinar and the reticular nuclei, are known to generate
40 oscillatory dynamics, especially in the alpha rhythms (Fiebelkorn & Kastner, 2019; Halgren et
41 al., 2019; Lopes da Silva et al., 1980; Saalman et al., 2012). In addition, the pulvinar
42 reciprocally and topographically connects with several cortical regions, including visual areas
43 at different hierarchical levels. Electrophysiological recordings demonstrated that alpha
44 oscillations modulate the interaction between cortical regions and the pulvinar (Halgren et
45 al., 2019; Lopes da Silva et al., 1980). Interestingly, previous studies demonstrated the
46 critical role of the pulvinar in several cognitive and perceptual tasks, coordinating the activity
47 along both feedforward and feedback pathways (Jaramillo et al., 2019). Specifically, the

1 pulvinar is crucially involved in spatial attention (Saalmann et al., 2012; Zhou et al., 2016)
2 and visual working memory (Rotshtein et al., 2011). Given its oscillatory dynamics, its
3 widespread connectivity pattern, and its implication in cognitive and perceptual tasks, it is
4 logical to consider the pulvinar as a potential candidate for generating and coordinating
5 oscillatory traveling waves through the cortex.

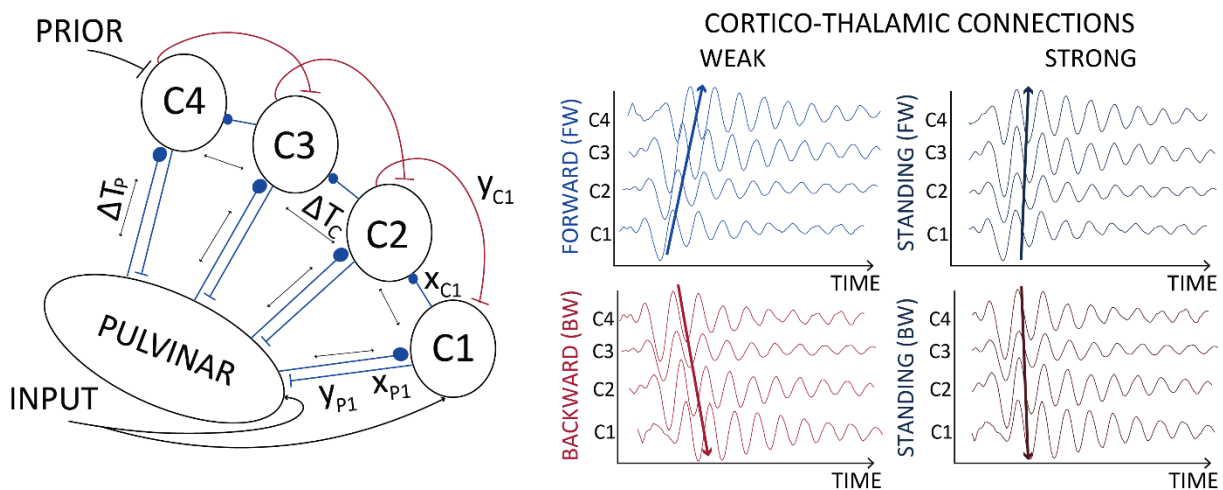
6
7 The “hubness” property of the pulvinar, reciprocally connected with distinct cortical regions
8 (figure 2), implies that its activity would have an overall synchronizing effect on the
9 oscillatory dynamics in the cortex. That is, common inputs from the pulvinar would tend to
10 increase global synchronization of oscillatory phases across multiple cortical regions. This
11 influence should be directly related to the strength of thalamo-cortical connections: the
12 stronger the connections, the more synchronous the activity across cortical regions, i.e., the
13 smaller the phase difference between regions; in the extreme case, when cortical activity
14 would be dominated by the common thalamic signals, forward or backward waves could
15 become nearly indistinguishable from standing waves, as schematically shown in figure 2.
16 Interestingly, the influence of thalamo-cortical connections may play an important role in
17 processes such as phase resets (Lakatos et al., 2009), as strong sensory activations may reset
18 the phases in each cortical regions, thus increasing system’s global synchronization (and
19 reducing the overall amount of travelling waves). Following our reasoning described in the
20 previous section, the effect of such an external synchronizing drive over the cortex could be
21 to reduce the overall periodicity of the system (e.g., because the phase gradients across
22 cortical regions would not strictly follow the activation latencies anymore). However, this
23 previous reasoning was based on the phase value in each cortical region at the moment
24 when it receives task-relevant sensory inputs from the preceding cortical region (or, when it
25 receives task-relevant top-down “priors” from the next cortical region). If we now consider
26 the functional role of the pulvinar to be more than a mere sensory relay of information, but
27 to also receive and convey specific task-relevant signals, then additional consequences for
28 rhythmic temporal binding could ensue, as detailed below.

29 30 **A framework to characterize travelling waves and cortico-thalamic dynamics**

31 In the early 90s, David Mumford proposed a compelling hypothesis about the role of the
32 pulvinar in perception, namely the ‘*active blackboard*’ theory (Mumford, 1991), which falls in
33 line with current Predictive Coding theories (and, more broadly, generative Bayesian
34 models). The ‘*active blackboard*’ theory recently gained renewed interest in several
35 computational and experimental studies (Ketz et al., 2015; O’reilly et al., 2021). The core
36 idea is that each cortical region behaves as a generative model whose activity represents the
37 sensory input. Each cortical area projects its specific representation of the sensory data into
38 the pulvinar, which serves as a ‘*blackboard*’ to integrate all cortical projections. In other
39 words, the pulvinar acts as a central integration space, which combines all cortical
40 representations and feeds back in the cortex the most likely interpretation of the data. This
41 functional interpretation of the cortico-thalamic connections suggests that the pulvinar
42 represents the sensory ‘*prior*’ interpretation of the data (as provided by the cortical input). It
43 forwards such prior information (or predictions) to the cortical regions, which update their
44 representation accordingly. It’s important to keep in mind, however, that irrespective of the
45 functional role of the pulvinar, the pulvinar may still synchronize phase across cortical
46 regions, making rhythmic perception easier to detect with EEG recordings. That is, contrary
47 to the previous scenario where cortico-cortical bottom-up or top-down hierarchical

1 communication was assumed to dominate processing, in the current scenario it is the
 2 synchronized pulvinar input that would mainly govern cortical processing. As we described
 3 above, such a common influence of the pulvinar across multiple cortical areas would be
 4 accompanied by increased overall synchronization and reduced phase shifts between
 5 cortical regions (see above and figure 2). However, this increased synchronization would
 6 now enhance the rhythmicity of the system, because each cortical region would tend to
 7 receive the relevant pulvinar information around the same oscillatory phase. In other words,
 8 when information from the pulvinar to the cortex is instrumental for the task at hand, the
 9 global synchronization of cortical activity could increase its rhythmicity, and favor a more
 10 'periodic' temporal binding.

11



12

13 **Figure 2. A cortico-thalamic model of oscillatory traveling waves.** The schematic represents a model
 14 of the interplay between the pulvinar and hierarchical cortical areas (C1 to C4). Following the active
 15 blackboard theory, the connections between all areas are based on Predictive Coding principles with
 16 temporal delays (ΔT_c for cortical inter-areal connections, and ΔT_p for pulvinar-cortex connections,
 17 see Alamia & VanRullen, 2019 for details), where y_{C_i} , y_{P_i} represent the predictions, and x_{C_i} , x_{P_i}
 18 represent the prediction errors. The strength of the cortico-thalamic connections determines the
 19 influence of the pulvinar on the synchronization state of the cortex: a stronger effect increases
 20 cortical synchronization, progressively reducing the phase-lag between regions from travelling to
 21 standing waves.

22

23 **Traveling waves unveil new possibilities for understanding oscillations.**

24 At the beginning of this paper, we challenged the naïve notion that “periodic temporal
 25 binding” would mostly happen in a system with globally phase-synchronized oscillations. By
 26 considering a hierarchical system performing perceptual or cognitive tasks that mainly rely
 27 on bottom-up or top-down cortical information transfer, we have established that periodic
 28 temporal binding could instead correspond to episodes of forward or backward travelling
 29 waves activity, respectively. Then, we considered the additional influence of a thalamic hub,
 30 the pulvinar, on cortical oscillatory dynamics: by synchronizing cortical oscillations, pulvinar
 31 activity could reduce travelling waves, and thus go against the idea of periodic temporal
 32 binding. However, in the last section, we showed that the pulvinar hub operating as a
 33 functional ‘blackboard’ could actually have the opposite influence—by synchronizing the
 34 phase of cortical oscillations at the exact moment they receive the central ‘blackboard’
 35 signals, it would favor rhythmic temporal binding. All in all, depending on whether relevant
 36 information for the task at hand is relayed by the thalamic nucleus ‘blackboard’ or mainly
 37 runs through the bottom-up or top-down cortical pathways, rhythmic temporal binding in

1 the brain could be associated with globally synchronized oscillatory activity, or with forward-
2 or backward-travelling waves, thus generating three possible scenarios that can be tested -a
3 priori- via M/EEG recordings. In the first case, assuming near-threshold visual stimuli that do
4 not elicit a robust thalamic response, we would predict that the phases of the alpha band
5 traveling waves propagating forward through the cortical hierarchy determine the temporal
6 segregation/integration: the sensory information will have the same delayed phase across
7 each cortical regions (i.e., non-simultaneously, but based on the temporal delays), and such
8 phase -relative to each stimulus- would determine the consequent segregation or
9 integration. In the second case, we consider a stimulus that elicited a more robust response
10 from the pulvinar, supposedly involving spatial attention or the binding of visual features. As
11 described above, the cortico-thalamic connections would produce a more powerful
12 synchronization across the cortex, whose phase would determine whether the stimuli are
13 integrated or segregated in the final perception. Lastly, it's possible to consider the third
14 case of contextual processing. When top-down expectations are involved in the task, we
15 may expect a more prominent role of the phase of alpha-band backward waves (rather than
16 the forward one, as in the previous case) in determining whether the stimuli are integrated
17 or perceived as distinct. We note that there is no currently accepted way to determine, in
18 advance, which of the above situations would be engaged by any particular cognitive task. In
19 addition, EEG recordings pose additional challenges in addressing these three scenarios.
20 Specifically, considering EEG recordings, we could unambiguously predict a rhythmic relation
21 between segregation/integration and the EEG alpha-band phase only in the case of global
22 synchronization driven by the pulvinar. On the contrary, when FW or BW waves dominate
23 the sensory, the relevant phase is region-dependent. Then, identifying the specific region
24 involved in the segregation/integration process becomes crucial. Moreover, the EEG phase
25 at the scalp level may be composed of different sources (Alamia et al., 2023), including an
26 ongoing alpha rhythm that is not involved in the traveling wave. This uncertainty may
27 explain, in part, discrepant results in the literature on periodic perception: negative results
28 do not necessarily imply that brain oscillatory phase has no influence on temporal binding; it
29 could just be that the relevant oscillation (or traveling wave) is not measured by the
30 experimenter.

31
32 In conclusion, the framework of travelling waves can provide new and essential insights to
33 re-interpret oscillations and their role in different cognitive functions. Here, we took the case
34 of temporal binding and showed how considering the spatio-temporal propagation of
35 oscillations challenges the well-established narrative, providing an original angle with novel
36 solutions (and novel problems). In particular, considering the spatial component of
37 oscillations allows disentangling of different sources. For instance, analysis of EEG recordings
38 is more likely to be blind to various sources of alpha-band oscillations when not considering
39 their spatial component: the "largest" alpha-drive, possibly driven by top-down dynamics,
40 may overwhelm the other "less prominent" alpha-band sources related to sensory processes
41 (Sokoliuk et al., 2019; Zhigalov & Jensen, 2022). On the other hand, an approach based on
42 travelling waves allows disentangling top-down and bottom-up sources (Alamia et al., 2023),
43 providing a more comprehensive view of oscillatory dynamics and thus potentially shedding
44 light on some of the controversial results in previous studies. Nevertheless, it's critical to
45 keep in mind task features and cognitive functions involved in each experimental design:
46 forward and backward waves may play an important role in understanding oscillatory
47 dynamics in tasks based on bottom-up processes and top-down expectations, respectively;

1 on the other hand, tasks involving sensory integration or other pulvina functions may reveal
2 yet a different oscillatory signature with different rhythmic properties for temporal binding.
3 All in all, travelling waves offer a new perspective and a critical paradigm shift in thinking and
4 interpreting results about neural oscillations, providing a richer and more nuanced scenario.
5

6 **References**

- 7 Alamia, A., Terral, L., Renaud D'ambra, M., & Vanrullen, R. (2023). Distinct roles of forward and
8 backward alpha-band waves in spatial visual attention. *ELife*, *12*:e85035.
9 <https://doi.org/10.7554/eLife.85035>
- 10 Alamia, A., Timmermann, C., VanRullen, R., Carhart-Harris, R. L., Nutt, D. J., VanRullen, R., & Carhart-
11 Harris, R. L. (2020). DMT alters cortical travelling waves. *ELife*, *9*, 1–16.
12 <https://doi.org/10.7554/eLife.59784>
- 13 Alamia, A., & VanRullen, R. (2019). Alpha oscillations and traveling waves: Signatures of predictive
14 coding? *PLOS Biology*, *17*(10), e3000487. <https://doi.org/10.1371/journal.pbio.3000487>
- 15 Alexander, D. M., Ball, T., Schulze-Bonhage, A., & Van Leeuwen, C. (2019). Large-scale cortical
16 travelling waves predict localized future cortical signals. *PLoS Computational Biology*, *15*(11).
17 <https://doi.org/10.1371/journal.pcbi.1007316>
- 18 Bastos, A. M., Litvak, V., Moran, R., Bosman, C. A., Fries, P., & Friston, K. J. (2015). A DCM study of
19 spectral asymmetries in feedforward and feedback connections between visual areas V1 and V4
20 in the monkey. *NeuroImage*, *108*, 460–475. <https://doi.org/10.1016/j.neuroimage.2014.12.081>
- 21 Bastos, A. M., Usrey, W. M., Adams, R. A., Mangun, G. R., Fries, P., & Friston, K. J. (2012). Canonical
22 microcircuits for predictive coding. *Neuron*, *76*(4), 695–711.
23 <https://doi.org/10.1016/j.neuron.2012.10.038>
- 24 Baumgarten, T. J., Schnitzler, A., Lange, J., & Romo, R. (2015). Beta oscillations define discrete
25 perceptual cycles in the somatosensory domain. *Proceedings of the National Academy of
26 Sciences of the United States of America*. <https://doi.org/10.1073/pnas.1501438112>
- 27 Benchenane, K., Tiesinga, P. H., & Battaglia, F. P. (2011). Oscillations in the prefrontal cortex: A
28 gateway to memory and attention. In *Current Opinion in Neurobiology* (Vol. 21, Issue 3, pp.
29 475–485). <https://doi.org/10.1016/j.conb.2011.01.004>
- 30 Bhattacharya, S., Brincat, S. L., Lundqvist, M., & Miller, E. K. (2022). Traveling waves in the prefrontal
31 cortex during working memory. *PLoS Computational Biology*.
32 <https://doi.org/10.1371/journal.pcbi.1009827>
- 33 Bollimunta, A., Mo, J., Schroeder, C. E., & Ding, M. (2011). Neuronal Mechanisms and Attentional
34 Modulation of Corticothalamic Alpha Oscillations. *Journal of Neuroscience*, *31*(13), 4935–4943.
35 <https://doi.org/10.1523/JNEUROSCI.5580-10.2011>
- 36 Binguier, V., Chavane, F., Glaeser, L., & Frégnac, Y. (1999). Horizontal propagation of visual activity in
37 the synaptic integration field of area 17 neurons. *Science*.
38 <https://doi.org/10.1126/science.283.5402.695>
- 39 Buegers, S., & Noppeney, U. (2022). The role of alpha oscillations in temporal binding within and
40 across the senses. *Nature Human Behaviour*. <https://doi.org/10.1038/s41562-022-01294-x>
- 41 Buffalo, E. A., Fries, P., Landman, R., Buschman, T. J., & Desimone, R. (2011). Laminar differences in
42 gamma and alpha coherence in the ventral stream. *Proceedings of the National Academy of
43 Sciences*, *108*(27), 11262–11267. <https://doi.org/10.1073/pnas.1011284108>
- 44 Busch, N. A., Dubois, J., & VanRullen, R. (2009). The phase of ongoing EEG oscillations predicts visual
45 perception. *Journal of Neuroscience*, *29*(24), 7869–7876.
46 <https://doi.org/10.1523/JNEUROSCI.0113-09.2009>
- 47 Das, A., Myers, J., Mathura, R., Shofty, B., Metzger, B., Bijanki, K., Wu, C., Jacobs, J., & Sheth, S. A.
48 (2022). Spontaneous Neuronal Oscillations in the Human Insula are Hierarchically Organized
49 Traveling Waves. *ELife*, *11*, 1–27. <https://doi.org/10.7554/eLife.76702>
- 50 Di Gregorio, F., Trajkovic, J., Roperti, C., Marcantoni, E., Di Luzio, P., Avenanti, A., Thut, G., & Romei,

1 V. (2022). Tuning alpha rhythms to shape conscious visual perception. *Current Biology*, 32(5),
2 988-998.e6. <https://doi.org/10.1016/j.cub.2022.01.003>

3 Dugué, L., Marque, P., & VanRullen, R. (2011). The phase of ongoing oscillations mediates the causal
4 relation between brain excitation and visual perception. *Journal of Neuroscience*.
5 <https://doi.org/10.1523/JNEUROSCI.1161-11.2011>

6 Dugué, L., Roberts, M., & Carrasco, M. (2016). Attention Reorients Periodically. *Current Biology*.
7 <https://doi.org/10.1016/j.cub.2016.04.046>

8 Engel, A. K., & Singer, W. (2001). Temporal binding and the neural correlates of sensory awareness.
9 In *Trends in Cognitive Sciences* (Vol. 5, Issue 1, pp. 16–25). [https://doi.org/10.1016/S1364-](https://doi.org/10.1016/S1364-6613(00)01568-0)
10 [6613\(00\)01568-0](https://doi.org/10.1016/S1364-6613(00)01568-0)

11 Ermentrout, G. B., & Kleinfeld, D. (2001). Traveling electrical waves in cortex: Insights from phase
12 dynamics and speculation on a computational role. In *Neuron* (Vol. 29, Issue 1, pp. 33–44).
13 [https://doi.org/10.1016/S0896-6273\(01\)00178-7](https://doi.org/10.1016/S0896-6273(01)00178-7)

14 Fakche, C., & Dugué, L. (2022). *Perceptual cycles travel across retinotopic space*. 852139, 1–33.
15 <https://doi.org/10.1101/2022.05.04.490030>

16 Fakche, C., Vanrullen, R., Marque, P., & Dugué, L. (2022). α Phase-Amplitude Tradeoffs Predict Visual
17 Perception. *ENeuro*, 9(1). <https://doi.org/10.1523/ENEURO.0244-21.2022>

18 Fiebelkorn, I. C., & Kastner, S. (2019). The Puzzling Pulvinar. In *Neuron*.
19 <https://doi.org/10.1016/j.neuron.2018.12.032>

20 Freeman, W. J., & Barrie, J. M. (2000). Analysis of spatial patterns of phase in neocortical gamma
21 EEGs in rabbit. *Journal of Neurophysiology*, 84(3), 1266–1278.
22 <https://doi.org/10.1152/jn.2000.84.3.1266>

23 Fries, P. (2015). Rhythms for Cognition: Communication through Coherence. In *Neuron* (Vol. 88, Issue
24 1, pp. 220–235). <https://doi.org/10.1016/j.neuron.2015.09.034>

25 Galuske, R. A. W., Munk, M. H. J., & Singer, W. (2019). Relation between gamma oscillations and
26 neuronal plasticity in the visual cortex. *Proceedings of the National Academy of Sciences of the*
27 *United States of America*. <https://doi.org/10.1073/pnas.1901277116>

28 Giraud, A.-L., & Arnal, L. H. (2012). Cortical oscillations and sensory predictions. In *Trends in Cognitive*
29 *Sciences* (Vol. 16, Issue 7, pp. 390–398). <https://doi.org/10.1016/j.tics.2012.05.003>

30 Halgren, M., Ulbert, I., Bastuji, H., Fabó, D., Eross, L., Rey, M., Devinsky, O., Doyle, W. K., Mak-
31 McCully, R., Halgren, E., Wittner, L., Chauvel, P., Heit, G., Eskandar, E., Mandell, A., & Cash, S. S.
32 (2019). The generation and propagation of the human alpha rhythm. *Proceedings of the*
33 *National Academy of Sciences of the United States of America*, 116(47), 23772–23782.
34 <https://doi.org/10.1073/pnas.1913092116>

35 Han, F., Caporale, N., & Dan, Y. (2008). Reverberation of Recent Visual Experience in Spontaneous
36 Cortical Waves. *Neuron*. <https://doi.org/10.1016/j.neuron.2008.08.026>

37 Herbst, S. K., & Landau, A. N. (2016). Rhythms for cognition: The case of temporal processing. In
38 *Current Opinion in Behavioral Sciences*. <https://doi.org/10.1016/j.cobeha.2016.01.014>

39 Jaramillo, J., Mejias, J. F., & Wang, X. J. (2019). Engagement of Pulvino-cortical Feedforward and
40 Feedback Pathways in Cognitive Computations. *Neuron*, 101(2), 321-336.e9.
41 <https://doi.org/10.1016/j.neuron.2018.11.023>

42 Ketz, N. A., Jensen, O., & O'Reilly, R. C. (2015). Thalamic pathways underlying prefrontal cortex-
43 medial temporal lobe oscillatory interactions. In *Trends in Neurosciences* (Vol. 38, Issue 1, pp. 3–
44 12). <https://doi.org/10.1016/j.tins.2014.09.007>

45 Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information.
46 In *Trends in Cognitive Sciences* (Vol. 16, Issue 12, pp. 606–617).
47 <https://doi.org/10.1016/j.tics.2012.10.007>

48 Klimesch, W., Hanslmayr, S., Sauseng, P., Gruber, W. R., & Doppelmayr, M. (2007). P1 and Traveling
49 Alpha Waves: Evidence for Evoked Oscillations. *Journal of Neurophysiology*, 97(2), 1311–1318.
50 <https://doi.org/10.1152/jn.00876.2006>

51 Lakatos, P., O'Connell, M. N., Barczak, A., Mills, A., Javitt, D. C., & Schroeder, C. E. (2009). The Leading
52 Sense: Supramodal Control of Neurophysiological Context by Attention. *Neuron*.

1 <https://doi.org/10.1016/j.neuron.2009.10.014>
2 Lisman, J. E., & Jensen, O. (2013). The Theta-Gamma Neural Code. In *Neuron* (Vol. 77, Issue 6, pp.
3 1002–1016). <https://doi.org/10.1016/j.neuron.2013.03.007>
4 Lopes da Silva, F. H., Vos, J. E., Mooibroek, J., & van Rotterdam, A. (1980). Relative contributions of
5 intracortical and thalamo-cortical processes in the generation of alpha rhythms, revealed by
6 partial coherence analysis. *Electroencephalography and Clinical Neurophysiology*, 50(5–6), 449–
7 456. [https://doi.org/10.1016/0013-4694\(80\)90011-5](https://doi.org/10.1016/0013-4694(80)90011-5)
8 Lozano-Soldevilla, D., & VanRullen, R. (2019). The Hidden Spatial Dimension of Alpha: 10-Hz
9 Perceptual Echoes Propagate as Periodic Traveling Waves in the Human Brain. *Cell Reports*,
10 26(2), 374–380.e4. <https://doi.org/10.1016/j.celrep.2018.12.058>
11 Lundqvist, M., Herman, P., Warden, M. R., Brincat, S. L., & Miller, E. K. (2018). Gamma and beta
12 bursts during working memory readout suggest roles in its volitional control. *Nature*
13 *Communications*, 9(1). <https://doi.org/10.1038/s41467-017-02791-8>
14 Luo, C., VanRullen, R., & Alamia, A. (2021). Conscious perception and perceptual echoes: a binocular
15 rivalry study. *Neuroscience of Consciousness*, 2021(1). <https://doi.org/10.1093/nc/niab007>
16 Maris, E., Womelsdorf, T., Desimone, R., & Fries, P. (2013). Rhythmic neuronal synchronization in
17 visual cortex entails spatial phase relation diversity that is modulated by stimulation and
18 attention. *NeuroImage*. <https://doi.org/10.1016/j.neuroimage.2013.02.007>
19 McLelland, D., & VanRullen, R. (2016). Theta-Gamma Coding Meets Communication-through-
20 Coherence: Neuronal Oscillatory Multiplexing Theories Reconciled. *PLoS Computational Biology*,
21 12(10). <https://doi.org/10.1371/journal.pcbi.1005162>
22 Muller, L., Chavane, F., Reynolds, J., & Sejnowski, T. J. (2018). Cortical travelling waves: Mechanisms
23 and computational principles. In *Nature Reviews Neuroscience* (Vol. 19, Issue 5, pp. 255–268).
24 <https://doi.org/10.1038/nrn.2018.20>
25 Mumford, D. (1991). On the computational architecture of the neocortex - I. The role of the thalamo-
26 cortical loop. *Biological Cybernetics*, 65(2), 135–145. <https://doi.org/10.1007/BF00202389>
27 Nunez, P. L. (1974). The brain wave equation: a model for the EEG. *Mathematical Biosciences*, 21(3–
28 4), 279–297. [https://doi.org/10.1016/0025-5564\(74\)90020-0](https://doi.org/10.1016/0025-5564(74)90020-0)
29 O’reilly, R. C., Russin, J. L., Zolfaghar, M., & Rohrlich, J. (2021). Deep predictive learning in neocortex
30 and pulvinar. *Journal of Cognitive Neuroscience*, 33(6), 1158–1196.
31 https://doi.org/10.1162/jocn_a_01708
32 Palva, S., & Palva, J. M. (2007). New vistas for α -frequency band oscillations. *Trends in Neurosciences*,
33 30(4), 150–158. <https://doi.org/10.1016/j.tins.2007.02.001>
34 Pang, Z., Alamia, A., & Vanrullen, R. (2020). Turning the stimulus on and off changes the direction of
35 α traveling waves. *ENeuro*, 7(6), 1–11. <https://doi.org/10.1523/ENEURO.0218-20.2020>
36 Reynaud, A., Masson, G. S., & Chavane, F. (2012). Dynamics of local input normalization result from
37 balanced short- and long-range intracortical interactions in area V1. *Journal of Neuroscience*.
38 <https://doi.org/10.1523/JNEUROSCI.1618-12.2012>
39 Ronconi, L., Busch, N. A., & Melcher, D. (2018). Alpha-band sensory entrainment alters the duration
40 of temporal windows in visual perception. *Scientific Reports*. <https://doi.org/10.1038/s41598-018-29671-5>
41
42 Ronconi, L., & Melcher, D. (2017). The role of oscillatory phase in determining the temporal
43 organization of perception: Evidence from sensory entrainment. *Journal of Neuroscience*.
44 <https://doi.org/10.1523/JNEUROSCI.1704-17.2017>
45 Ronconi, L., Oosterhof, N. N., Bonmassar, C., Melcher, D., & Heeger, D. J. (2017). Multiple oscillatory
46 rhythms determine the temporal organization of perception. *Proceedings of the National*
47 *Academy of Sciences of the United States of America*.
48 <https://doi.org/10.1073/pnas.1714522114>
49 Rotshtein, P., Soto, D., Grecucci, A., Geng, J. J., & Humphreys, G. W. (2011). The role of the pulvinar in
50 resolving competition between memory and visual selection: A functional connectivity study.
51 *Neuropsychologia*, 49(6), 1544–1552. <https://doi.org/10.1016/j.neuropsychologia.2010.12.002>
52 Ruzzoli, M., Torralba, M., Morís Fernández, L., & Soto-Faraco, S. (2019). The relevance of alpha phase

1 in human perception. *Cortex*, 120, 249–268. <https://doi.org/10.1016/j.cortex.2019.05.012>

2 Saalman, Y. B., Pinsk, M. A., Wang, L., Li, X., & Kastner, S. (2012). The pulvina regulates information
3 transmission between cortical areas based on attention demands. *Science*, 337(6095), 753–756.
4 <https://doi.org/10.1126/science.1223082>

5 Samaha, J., Bauer, P., Cimaroli, S., & Postle, B. R. (2015a). Top-down control of the phase of alpha-
6 band oscillations as a mechanism for temporal prediction. *Proceedings of the National Academy*
7 *of Sciences*, 112(27), 8439–8444. <https://doi.org/10.1073/pnas.1503686112>

8 Samaha, J., Bauer, P., Cimaroli, S., & Postle, B. R. (2015b). Top-down control of the phase of alpha-
9 band oscillations as a mechanism for temporal prediction. *Proceedings of the National Academy*
10 *of Sciences of the United States of America*. <https://doi.org/10.1073/pnas.1503686112>

11 Samaha, J., & Postle, B. R. (2015). The Speed of Alpha-Band Oscillations Predicts the Temporal
12 Resolution of Visual Perception. *Current Biology*. <https://doi.org/10.1016/j.cub.2015.10.007>

13 Sato, T. K., Nauhaus, I., & Carandini, M. (2012). Traveling Waves in Visual Cortex. In *Neuron* (Vol. 75,
14 Issue 2, pp. 218–229). <https://doi.org/10.1016/j.neuron.2012.06.029>

15 Sauseng, P., Klimesch, W., Stadler, W., Schabus, M., Doppelmayr, M., Hanslmayr, S., Gruber, W. R., &
16 Birbaumer, N. (2005). A shift of visual spatial attention is selectively associated with human EEG
17 alpha activity. *European Journal of Neuroscience*, 22(11), 2917–2926.
18 <https://doi.org/10.1111/j.1460-9568.2005.04482.x>

19 Sokoliuk, R., Mayhew, S. D., Aquino, K. M., Wilson, R., Brookes, M. J., Francis, S. T., Hanslmayr, S., &
20 Mullinger, K. J. (2019). Two spatially distinct posterior alpha sources fulfill different functional
21 roles in attention. *Journal of Neuroscience*, 39(36), 7183–7194.
22 <https://doi.org/10.1523/JNEUROSCI.1993-18.2019>

23 Sreekumar, V., Wittig, J., Chapeton, J., Inati, S., & Zaghoul, K. (2020). Low frequency traveling waves
24 in the human cortex coordinate neural activity across spatial scales. *BioRxiv*.

25 Steriade, M. (1999). Coherent oscillations and short-term plasticity in corticothalamic networks. In
26 *Trends in Neurosciences*. [https://doi.org/10.1016/S0166-2236\(99\)01407-1](https://doi.org/10.1016/S0166-2236(99)01407-1)

27 Thut, G., Nietzel, A., Brandt, S. A., & Pascual-Leone, A. (2006). α -Band electroencephalographic
28 activity over occipital cortex indexes visuospatial attention bias and predicts visual target
29 detection. *Journal of Neuroscience*, 26(37), 9494–9502.
30 <https://doi.org/10.1523/JNEUROSCI.0875-06.2006>

31 Valera, F. J., Toro, A., Roy John, E., & Schwartz, E. L. (1981). Perceptual framing and cortical alpha
32 rhythm. *Neuropsychologia*, 19(5), 675–686. [https://doi.org/10.1016/0028-3932\(81\)90005-1](https://doi.org/10.1016/0028-3932(81)90005-1)

33 van Wassenhove, V. (2016). Temporal cognition and neural oscillations. In *Current Opinion in*
34 *Behavioral Sciences* (Vol. 8, pp. 124–130). <https://doi.org/10.1016/j.cobeha.2016.02.012>

35 VanRullen, R. (2016). Perceptual Cycles. In *Trends in Cognitive Sciences* (Vol. 20, Issue 10, pp. 723–
36 735). <https://doi.org/10.1016/j.tics.2016.07.006>

37 VanRullen, R., & Koch, C. (2003). Is perception discrete or continuous? In *Trends in Cognitive Sciences*
38 (Vol. 7, Issue 5, pp. 207–213). [https://doi.org/10.1016/S1364-6613\(03\)00095-0](https://doi.org/10.1016/S1364-6613(03)00095-0)

39 Vanrullen, R., & MacDonald, J. S. P. (2012). Perceptual echoes at 10 Hz in the human brain. *Current*
40 *Biology*, 22(11), 995–999. <https://doi.org/10.1016/j.cub.2012.03.050>

41 Venskus, A., & Hughes, G. (2021). Individual differences in alpha frequency are associated with the
42 time window of multisensory integration, but not time perception. *Neuropsychologia*.
43 <https://doi.org/10.1016/j.neuropsychologia.2021.107919>

44 Wiener, M., & Kanai, R. (2016). Frequency tuning for temporal perception and prediction. In *Current*
45 *Opinion in Behavioral Sciences*. <https://doi.org/10.1016/j.cobeha.2016.01.001>

46 Wutz, A., Melcher, D., & Samaha, J. (2018). Frequency modulation of neural oscillations according to
47 visual task demands. *Proceedings of the National Academy of Sciences of the United States of*
48 *America*. <https://doi.org/10.1073/pnas.1713318115>

49 Zanos, T. P., Mineault, P. J., Nasiotis, K. T., Guitton, D., & Pack, C. C. (2015). A Sensorimotor Role for
50 Traveling Waves in Primate Visual Cortex. *Neuron*.
51 <https://doi.org/10.1016/j.neuron.2014.12.043>

52 Zauner, A., Gruber, W., Himmelstoß, N. A., Lechinger, J., & Klimesch, W. (2014). Lexical access and

1 evoked traveling alpha waves. *NeuroImage*, 91, 252–261.
2 <https://doi.org/10.1016/j.neuroimage.2014.01.041>
3 Zhang, H., & Jacobs, J. (2015). Traveling Theta Waves in the Human Hippocampus. *Journal of*
4 *Neuroscience*, 35(36), 12477–12487. <https://doi.org/10.1523/JNEUROSCI.5102-14.2015>
5 Zhang, H., Watrous, A. J., Patel, A., & Jacobs, J. (2018). Theta and Alpha Oscillations Are Traveling
6 Waves in the Human Neocortex. *Neuron*. <https://doi.org/10.1016/j.neuron.2018.05.019>
7 Zhigalov, A., & Jensen, O. (2022). Travelling waves observed in MEG data can be explained by two
8 discrete sources. *Bioarxiv*. <https://doi.org/https://doi.org/10.1101/2022.09.28.509870>
9 Zhou, H., Schafer, R. J., & Desimone, R. (2016). Pulvinar-Cortex Interactions in Vision and Attention.
10 *Neuron*, 89(1), 209–220. <https://doi.org/10.1016/j.neuron.2015.11.034>
11
12