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A travelling waves perspective on temporal binding

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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

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

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

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

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

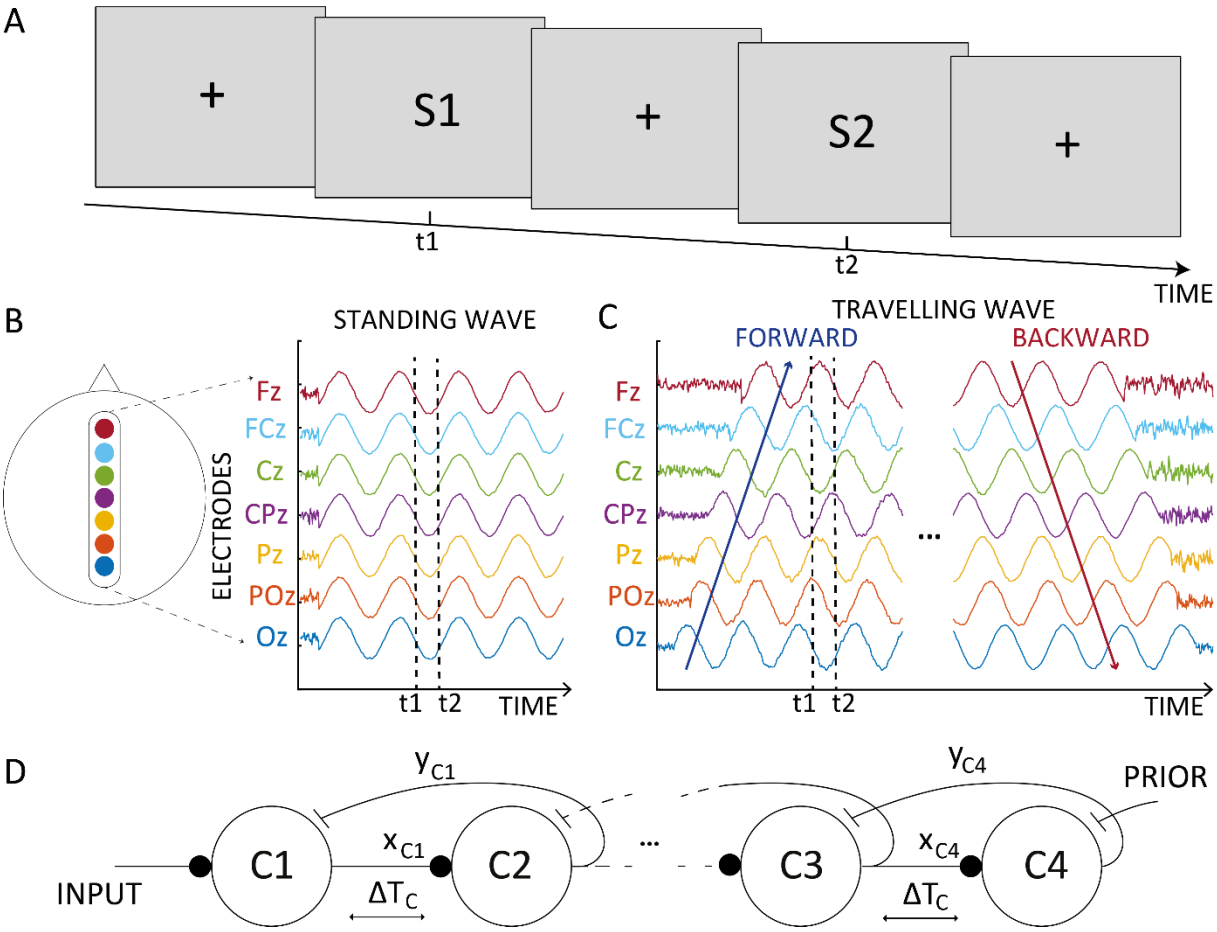

Figure 1. Difference between standing and travelling waves. A) Consider an experiment in which two visual stimuli, S1 and S2, are displayed sequentially at times t1 and t2. B) Oscillatory waves can be measured for instance along the mid-line of scalp EEG electrodes. Depending on the timings t1 and t2 and on the phase of the ongoing oscillation, the two stimuli may be perceived as one "merged" item or two distinct ones (Baumgarten et al., 2015; Valera et al., 1981; VanRullen & Koch, 2003). In the case of a standing wave, the oscillations share the same phase over all electrodes, and there is only one phase relative to the two stimuli across electrodes. C) If the oscillation is actually a forward (or backward) traveling wave, it presents a phase offset increasing (or decreasing) across electrodes. In this case, the onset of the two stimuli, t1 and t2, falls at different relative phases along the line of electrodes; this could challenge the idea of a unique optimal (or poor) phase for temporal integration across the visual system. D) A cortical model of predictive coding with mutually connected hierarchical regions exchanging predictions (via feedback connections, y_C) and prediction errors (x_C). In a predictive coding implementation, higher regions predict the activity of the lower regions, and the difference between the predictions and the actual activity (i.e., the prediction error) is used to update the next prediction. When taking into account neural time constants and inter-areal communication delays (ΔT_C), this model naturally produces alpha-band travelling waves as in

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

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

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

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

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

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

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

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

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

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

A framework to characterize travelling waves and cortico-thalamic dynamics

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

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

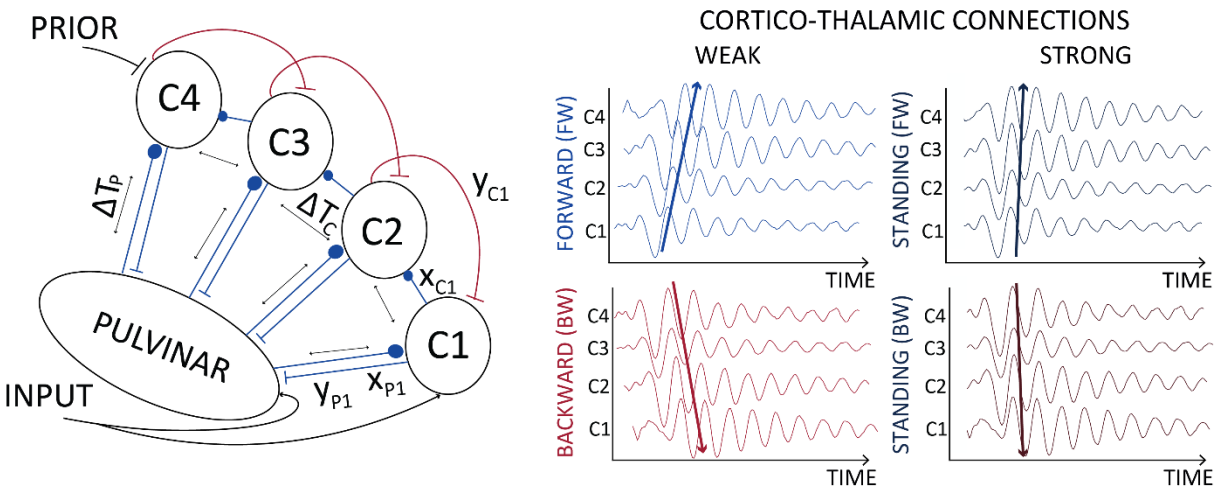

Figure 2. A cortico-thalamic model of oscillatory traveling waves. The schematic represents a model of the interplay between the pulvinar and hierarchical cortical areas (C1 to C4). Following the active blackboard theory, the connections between all areas are based on Predictive Coding principles with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

Traveling waves unveil new possibilities for understanding oscillations.

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

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

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

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

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