

An oscillatory mechanism for prioritizing salient unattended stimuli

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To survive in a complex world, it is important that unattended, but salient, input can still draw one's attention. In this article, we suggest that posterior alpha oscillations (8–13 Hz) provide a mechanism for prioritizing and ordering unattended visual input according to 'relevance'. Gamma oscillations (30–100 Hz) that are phase-locked to the alpha oscillations keep competing unattended representations apart in time, thus creating a sequence of perceptual cycles. As inhibition gradually lowers within an alpha cycle, the ordered sequence of competing input is activated, producing a temporal phase code for saliency. The proposed mechanism is based on recent experiments indicating that the phase of alpha activity modulates perception and that alpha oscillations are produced by periodic pulses of inhibition.

When unattended stimuli draw our attention

Assume that you are driving down a busy road with incoming traffic (Figure 1). In this situation, you are likely to fixate on the road ahead, while covertly attending to the incoming traffic on the left. On the right, you suddenly spot a dog about to jump on the road and you manage to break in time. Which neuronal mechanisms allow you to identify and process the relevant, but unattended, input on the right? Such a neuronal mechanism must be able to prioritize the processing of visual objects according to saliency and then potentially redirect the covert focus of attention.

Phase coding based on nested oscillations

Investigations of the rat hippocampus have provided important evidence on temporal coding. A putative mechanism based on oscillatory theta activity (see Glossary), which orders the activation of spatial representations according to excitability, has been identified [1]. The oscillatory theta activity is produced by slow pulses of GABAergic inhibition repeated every 100–150 ms as a consequence of input from the medial septum [2]. As the inhibition reduces over a theta cycle, the most excited neuronal representation will discharge first, then the second most excitable representation and so forth. This mechanism produces a 'phase code' in which spatial representations are encoded at different phases of the theta cycle [3,4], hence providing a temporal code. Phase coding has also been identified in the visual system with respect to low frequency oscillations [5]. In this article, we propose that a related mechanism operates when unattended visual

information is processed. In this case, the rhythmic pulsed inhibition is implemented by oscillatory alpha activity. The proposed mechanism is strongly inspired by ideas accounting for the functional role of nested gamma and theta oscillations [6]. In particular we suggest that gamma oscillations that are phase-locked to the alpha oscillations keep competing unattended representations apart in time. This creates a sequence of perceptual cycles.

Our framework is consistent with recent findings demonstrating that the phase of ongoing alpha oscillations modulates neuronal excitability, gamma activity and perception (see Figure 2). Furthermore, it is supported by various studies showing that alpha activity inhibits neuronal processing [7,8]. In sum, these studies suggest that alpha activity provides a clocking mechanism that controls neuronal processing reflected by activity in the gamma band.

The proposed mechanism: release from inhibition within an alpha cycle results in sequential activation according to excitability

In this section, we outline the general model of how a temporal phase code is generated and controlled by alpha

Glossary

Alpha oscillations: neuronal activity in the 8–13 Hz band, measured in humans and non-human animals. In human EEG and MEG recordings, alpha activity is the strongest spontaneous signal measured in the awake brain. The view that alpha activity is associated with cortical idling has been replaced by the notion that alpha activity reflects functional inhibition [7,8,35].

Gamma oscillations: neuronal activity in the 30–100 Hz band, measured in humans and non-human animals. Gamma oscillations are often associated with neuronal processing [30,31].

Nested oscillations: a coupling between two rhythms in which a fast oscillation is nested within a slower oscillation. Nested oscillations are observed as a coupling between the amplitude of a fast oscillation and the phase of a slow oscillation. One example is gamma oscillations being modulated by the phase of ongoing theta oscillations in the rat hippocampus [67,68].

Oscillatory power: the magnitude of an oscillatory signal in a given frequency band. Power is typically estimated from electrophysiological signals using Fourier or wavelet transforms.

Phase code: a mechanism for coding whereby different information is represented at different phases of an oscillatory cycle. This has been observed, for instance, in the rat hippocampus where a given place cell discharges at different phases of the theta cycle depending on the rat's position [3,4].

Pulsed inhibition: a mechanism whereby pulses of inhibition silence neuronal activity. If the pulses occur periodically, this will produce an oscillatory signal. Oscillations created by pulsed activity are different from regular oscillations in the sense that only peaks but not troughs are modulated over time (think of a bouncing ball). It has been proposed that alpha oscillations are a consequence of pulsed inhibition [45].

Theta oscillations: neuronal activity in the 5–8 Hz band, measured in humans and non-human animals. Theta oscillations are particularly strong in the rat hippocampus. They are typically associated with spatial navigation and memory processing [69].

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Figure 1. When driving, typically, you will focus your gaze ahead of you, while covertly attending to the incoming traffic on the left. Suddenly, a dog is about to jump on the road from the right, but you manage to see it in time. In real-life situations, the ability to detect unattended stimuli is highly important. How is the processing of unattended stimuli implemented in the visual system? Obviously, the processing has to be fairly limited and constrained to only the most salient visual objects.

activity in the early visual system. The sections that follow discuss the empirical work in support of the proposed framework.

Let us consider the example in which covert spatial attention is directed to one's left (Box 1, Figure 1a). In these types of situations it is well established that oscillatory alpha activity is depressed over the right hemisphere, whereas it is relatively increased over the left hemisphere [9–11]. The alpha increase with respect to the unattended processing stream functionally results in pulsed inhibition (we will later make that case). Visual objects are present both in the attended left field (*A, B, C, D*) and the unattended right hemifield (*a, b, c, d*). Processing capacity is high for the attended stimuli, which might even be processed in parallel. However, for the unattended stimuli, a mechanism is needed to ensure that only the most salient stimuli will be processed. The differences in object saliency imply that the respective neuronal representations have different levels of excitability [12]. Beyond saliency, top-down effects based on context and prior expectations are also likely to influence this neuronal excitability. Which of the four neuronal representations (*a, b, c, d*) will activate first in the presence of rhythmic alpha activity? At the peak of the alpha cycle, inhibition is strongest and no neurons can fire (Box 1, Figure 1b). As inhibition reduces, the most excitable representation, *a*, will activate first. The activation of a representation is constituted by the discharge of a set of cells within a short time-window (<20 ms). The activation of *a* results in short-lasting GABAergic feedback inhibition. This feedback

inhibition should not be confused with the slower inhibitory pulses constituting the alpha oscillations. The feedback inhibition serves to temporarily prevent other representations from activating, which in effect implements a winner-take-all mechanism [6,13]. Because of refractory mechanisms such as afterhyperpolarization currents, representation *a* is prevented from further activating within the same alpha cycle [14]. When the GABAergic feedback dies out, the next most excitable representation (*b*) will activate (Box 1, Figure 1b). The GABAergic feedback inhibition has approximately the same duration as a gamma cycle, i.e., 10–30 ms [13]. Thus, nested gamma and alpha cycles provide a multiplexing mechanism, in which neuronal representations are activated sequentially. Eventually *a, b* and *c* will have activated sequentially. The representation for *d* will not activate in time before the alpha inhibition rises again, i.e. it is not processed. Note that this mechanism allows for the representational discharges to be graded in terms of firing rates as long as the firing is constrained to the slot defined by the respective gamma cycle. This is consistent with observations from hippocampal phase coding: even though the firing rate varies, the phase of firing with respect to the theta cycles is robustly coding for space [15]. The proposed scheme is much akin to the mechanism based on nested gamma and theta oscillations proposed for sequential activation of working memory and place cell representations [6,16].

Figure 1c in Box 1 depicts another example in which the amplitude of alpha oscillations is higher compared to Figure 1b. The higher alpha oscillations are due to further reduced attention. In this case, only one representation is allowed to activate. This means that the number of items which are processed outside the focus of attention is dependent on the level of alpha activity. In other words, alpha amplitude controls the duty cycle of the temporal phase code (Box 1, Figure 1a and 1b). This is also consistent with the notion that the magnitude of alpha activity regulates the gain of visual processing [7]. In short, the unattended visual stream is associated with strong alpha oscillations. The alpha oscillations then modulate the gamma activity responsible for processing visual input in a phasic manner. This provides a mechanism for prioritizing the processing of visual input according to excitability reflecting visual relevance. The gamma activity serves to keep the competing representations apart in time [6], thus creating a sequence of perceptual cycles [17]. The framework predicts that perception, neuronal firing and gamma band activity will depend on the alpha phase. Furthermore, a temporal code should be produced according to saliency – in particular in the unattended visual stream. We now turn to the evidence supporting this framework and the experiments further required to substantiate it.

Perception, gamma activity and neuronal excitability are modulated by the phase of alpha oscillations

The proposed model is consistent with a framework developed by VanRullen *et al.* to investigate the extent to which perception is discrete and clocked by ongoing rhythmic brain activity [18,19]. Recent electroencephalography (EEG) studies have indeed demonstrated that perception is modulated

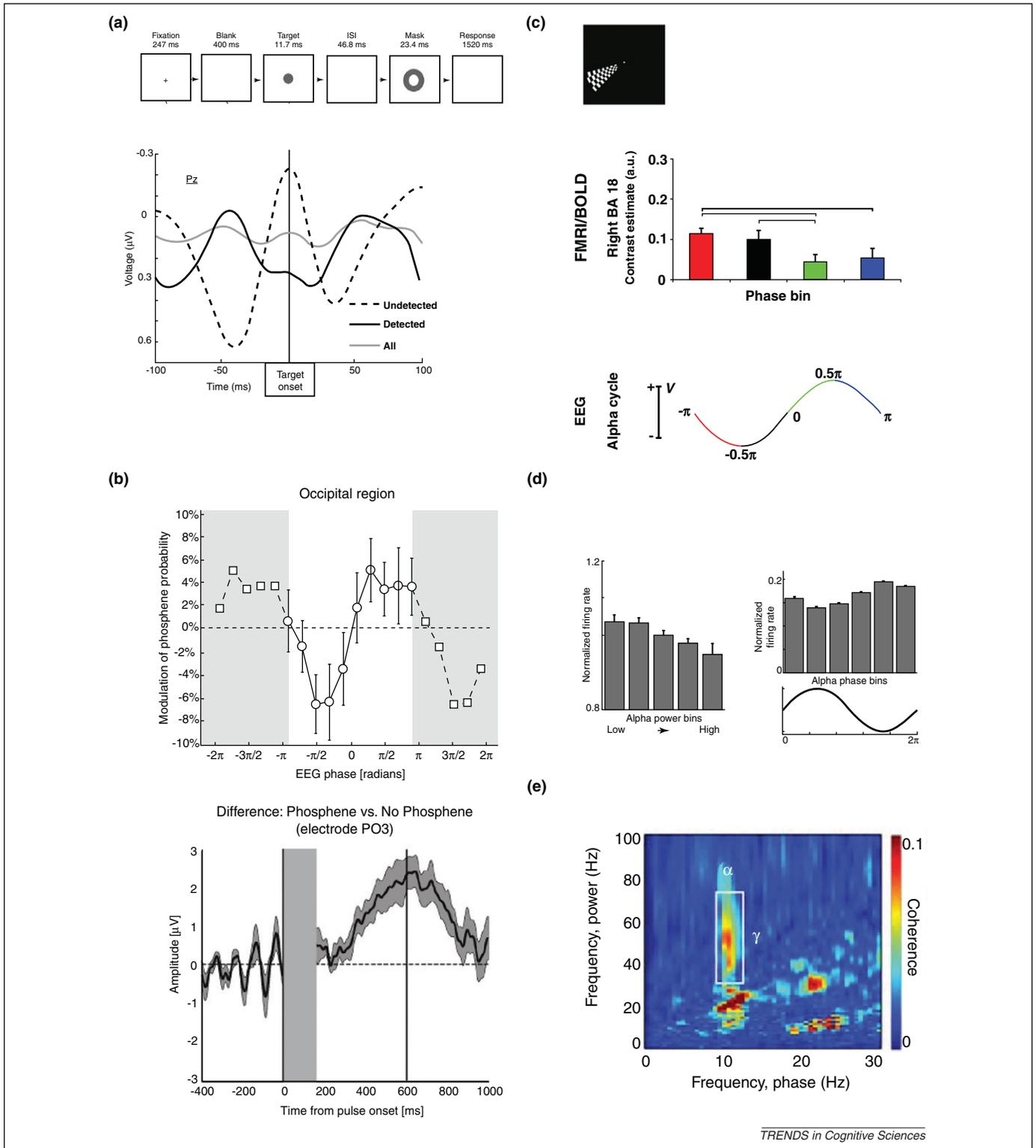


Figure 2. Converging evidence demonstrating that the phase of the posterior alpha activity modulates neuronal activation and perception. (a) In this experiment, participants were presented with target stimuli that were later masked with an annulus, while the ongoing EEG was recorded. Trials in which the target was correctly detected were associated with a different pre-stimulus alpha phase compared to trials in which the target was not detected. Reproduced, with permission, from [20]. (b) In a combined TMS-EEG study, phosphenes were induced by stimulating the occipital cortex. Subsequently, the trials were sorted according to the phase of the alpha activity just preceding the TMS pulse. The probability of phosphene detection was systematically modulated by alpha phase (top). The trials were sorted according to whether phosphenes were detected or not. The averaged trials for phosphene versus no phosphene revealed a difference in the pre-stimulus alpha phase (bottom). Reproduced, with permission, from [22]. (c) Visual stimuli were presented in the left hemifield as fMRI and EEG were simultaneously recorded. The trials were then sorted in four bins according to the phase of the pre-stimulus alpha activity. The post-stimulus BOLD response reflecting neuronal activation was modulated by the alpha phase. Reproduced, with permission, from [23]. (d) Spikes and fields were recorded simultaneously from the monkey sensorimotor cortex while the monkey was performing a tactile discrimination task. As the alpha power increased, the spike rate decreased (left panel). Moreover, the spiking was phasically modulated by the ongoing alpha rhythm (right panel). Reproduced, with permission, from [27]. (e) Ongoing MEG data were recorded in resting subjects. The plot shows an analysis in which the phase of ongoing alpha oscillations (x-axis) is related to the power of oscillations at higher frequencies (y-axis). The phase of ongoing alpha oscillations modulates gamma power (40–60 Hz). Reproduced, with permission, from [29]. In sum, these studies demonstrate that both neuronal excitability and perception are modulated by the phase of ongoing alpha oscillations [18].

Box 1. A framework for how neuronal excitability that reflects saliency can be converted to a temporal phase code by alpha oscillations

This framework (see Figure 1) is inspired by models based on nested gamma and theta oscillations that were developed to account for findings on working memory and phase precession of place cells [6,16].

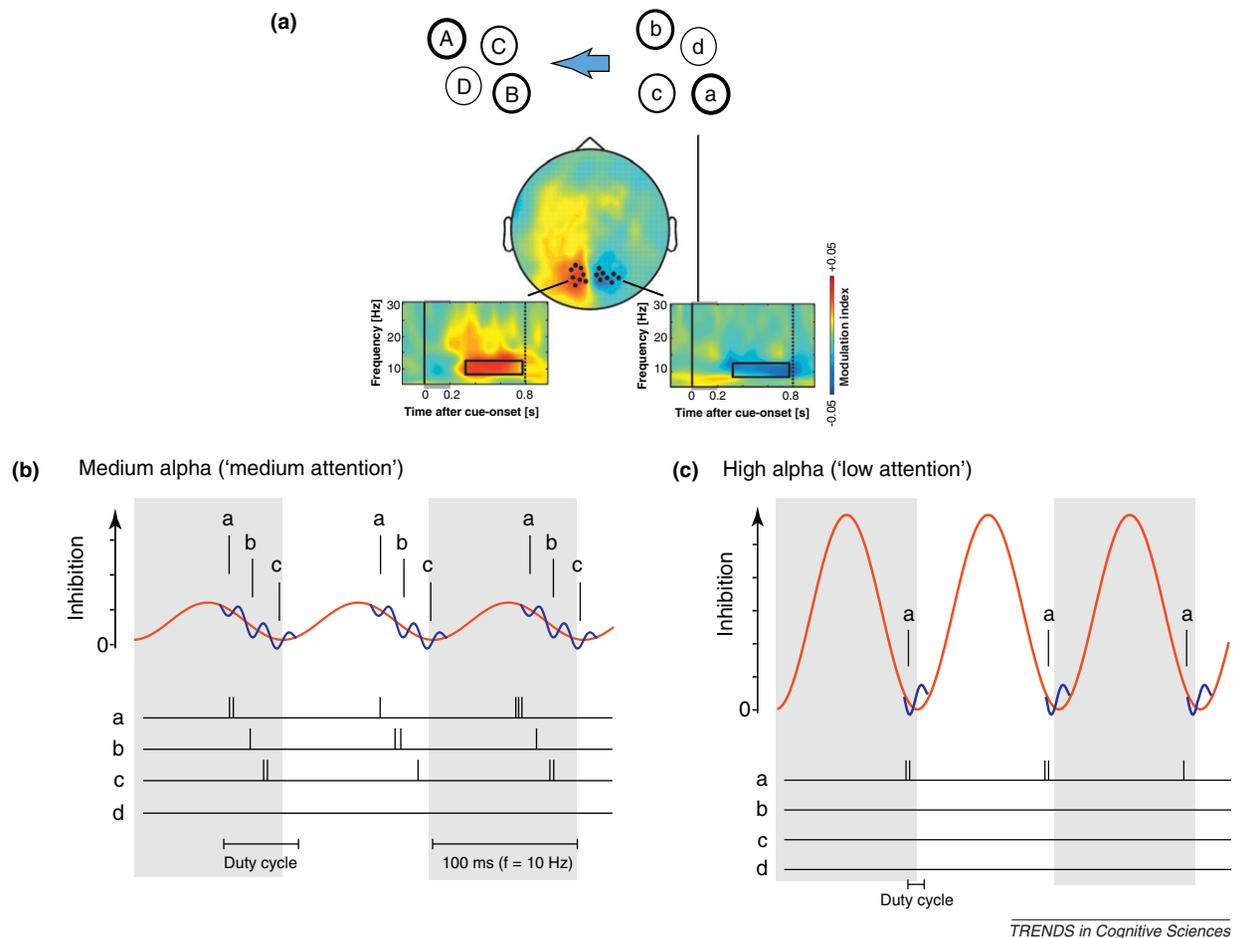


Figure 1. How neuronal excitability reflecting saliency can be converted to a temporal phase code by alpha oscillations. (a) Assume that a set of visual stimuli are presented simultaneously in the left and right hemifields. While subjects attend to the left hemifield, it is well established that posterior alpha activity decreases in the contralateral right hemisphere. At the same time, alpha activity remains strong in the left hemisphere (and *vice versa*). This hemispheric lateralization is thought to reflect the allocation of attentional resources: the alpha decrease coincides with the engagement of task-relevant areas, whereas the alpha increase coincides with functional inhibition. The data displayed at the bottom of this panel are reproduced from an MEG experiment by ter Huurne *et al.* (unpublished manuscript). (b) Four objects are presented simultaneously in each hemifield. In the unattended hemifield, they are denoted by *a*, *b*, *c*, and *d*. Alpha activity is conceived as pulses of inhibition that repeat every 100 ms (red line). Strong inhibition at the alpha peak (red line) prevents any firing. As the inhibition reduces, the most salient (and thus the most excitable) representation, *a*, will activate. The activation of *a* engages a GABAergic network that results in inhibitory feedback (blue line). This inhibition lasts for 10–30 ms and temporarily prevents any other representations from activating, i.e. it implements a winner-take-all mechanism [13]. As the inhibition dies out, representation *b* will activate, followed by representation *c*. Because of refractory mechanisms such as afterhyperpolarizing currents, a given representation will only fire once (if at all) per alpha cycle. The sequences of neuronal activation and GABAergic feedback will produce a fast rhythm in the gamma band segmenting competing stimuli in time (blue line). The neurons coding for representation *d* will, however, not have time to activate (in this specific example) since the alpha inhibitory pulse has returned. (c) For increasingly higher levels of alpha power there is increasingly less time for representations to activate. In the example shown here, only one representation (*a*) will have time to activate before alpha inhibition increases again. Thus, the level of alpha activity determines how many neuronal representations can be processed per alpha cycle. In other words, the ‘duty-cycle’ of processing decreases as alpha power increases. In short, our framework implements a mechanism in which a temporal phase code is implemented by means of oscillatory alpha inhibition. This serves to permit processing of only the most salient items in an unattended visual scene.

by the phase of ongoing rhythms in the 7–12 Hz range [20,21] (Figure 2a). Consistent with this observation, a transcranial magnetic stimulation (TMS) study combined with EEG demonstrated that the activation of phosphenes is modulated by the phase of ongoing pre-stimulus alpha activity [22] (Figure 2b). A recent study combining EEG and functional magnetic resonance imaging (fMRI) demonstrated that the time of visual presentation relative to the phase of ongoing alpha oscillations modulates the blood oxygenation level-dependent (BOLD) signal [23] (Figure 2c). Interestingly, the notion that perception is

influenced by the phase of neuronal oscillations has been linked to various visual illusions, which can be explained by rhythmic oscillatory modulation [24,25]. Studies with monkeys provide direct evidence for the phasic modulation of neural responses by alpha activity [26,27]. Figure 2d shows that neuronal firing decreases as alpha power increases and that the firing is modulated by the phase of the alpha rhythm [27]. In addition, our model (see Box 1) also predicts that not only spike activity but also gamma power is related to the phase of ongoing alpha oscillations [28,29] (Figure 2e). The phasic modulation of gamma activity should be interpreted

within the context that most electrophysiological studies have converged on the notion that gamma activity reflects neuronal processing [30,31]. This notion is supported, for instance, by attention studies demonstrating that the allocation of attention to a given visual field results in an increase in gamma power [26,32–34].

To summarize, these recent findings demonstrate that oscillatory activity in the alpha band phasically modulates neuronal excitability, gamma activity and perception. We predict that this phasic modulation, in particular, will become pronounced in unattended visual streams, where alpha activity is strong.

A case for pulsed inhibition

The data reviewed in the previous section demonstrate that alpha activity exercises a phasic force on neuronal excitability and perception. The model we propose predicts that this phasic force is manifested by pulses of inhibition rather than pulses of excitation. Numerous studies have demonstrated that alpha activity in sensory regions is linked to functional inhibition (for reviews see [7,8,35]). As shown in **Box 1** (Figure 1a), alpha activity is decreased in the hemisphere contralateral to the attended hemifield. Importantly, not only does the contralateral alpha decrease predict performance in working memory and detection tasks, so does the increase in the hemisphere ipsilateral to the attended hemifield [10,36,37]. A similar case has been made for somatosensory detection, where the somatosensory alpha activity is also hemispherically lateralized with respect to the attended hand [38,39]. In the presence of distracters on the unattended hand, the alpha activity ipsilateral to the attended hand is predictive of detection performance [40]. These findings are supported by combined EEG-TMS recordings which demonstrate that neuronal excitability is reduced when alpha activity is strong [41]. Furthermore, several combined EEG-fMRI studies point to a decrease in the BOLD signal with increasing alpha strength [42–44]. Intracranial single unit recordings in the sensorimotor system confirm that neuronal discharge is locked to the phase of the alpha rhythm and that spike probability decreases with alpha magnitude [27] (see Figure 2d). These and other findings have resulted in the notion that oscillatory alpha activity serves to actively inhibit task-irrelevant areas [7,8]. As a result, the alpha activity serves to phasically modulate processing by pulses of inhibition [20,45]. In this article, we further expand the putative mechanistic role of pulsed inhibition: we suggest that the gradual release from inhibitory pulses creates the sequential activation that constitutes the mechanism for prioritizing salient unattended inputs (Box 1).

A temporal phase code determined by saliency

The relation between spike timing and visual saliency has a history in the recent literature. It is well recognized that increased neuronal input strength results directly in shorter discharge latencies. As a result, the relative firing latency (or the order of neuronal discharge) across a population of neurons represents the relative strength of inputs to the population in question [46–48]. This provides a code for temporal order that operates much faster than what

can be achieved using coding schemes based on firing rates. This is consistent with multi-electrode recordings in cats demonstrating that short-lived spatiotemporal patterns of spiking defined by consistent delays can be reliably produced in the visual system [49]. Indeed, it has been suggested that spike-time-based codes could be key to understanding the remarkable speed of processing in the visual system [50–52]. Furthermore, the relative order of firing could even serve as a general code for representing visual saliency throughout the visual system [53]: at each level, the first neurons to discharge represent the most salient information. The notion of saliency itself is dependent on processing level. In early visual areas it is reflected by local contrast and in higher-level regions by more complex constructs. In support of this framework, neuronal excitability graded by saliency has been recorded in various regions, including early visual areas and higher areas such as temporal and parietal regions [54]. Finally, it has been suggested that spike-time-based codes need not depend on absolute latencies relative to external stimulation, but could also be referenced to internal brain events, such as the phase of specific oscillations [30,49,55].

To summarize, previous work has converged on the notion that the phase of discharge of ongoing oscillations can serve as a code for visual saliency. This conclusion is an important foundation for the present framework. In addition, however, we also propose that the relation between phase-of-discharge and saliency will be most consistent for unattended elements because of the large pulses of alpha inhibition that shape the temporal properties of unattended visual responses. Specifically, we hypothesize that the decreasing ramp of inhibition within an alpha cycle provides a mechanism that controls the timing and ordering of complex discharge patterns. Our proposal results in the prediction that, when recording from single units from unattended regions, the firing should be phase-locked to the alpha rhythm. This prediction has recently received experimental support from recording in the ventral visual stream of the monkey [26]. Moreover, one would predict a phase code in which neurons responding to the most salient representations would discharge at earlier alpha phases compared to neurons responding to less salient stimuli.

Concluding remarks

In this article, we have proposed a putative mechanism of how the processing of unattended visual information is prioritized. Key to this mechanism is the assumption that alpha activity helps to produce a temporal code, whereby neuronal representations are arranged according to saliency. This hypothesis can be tested using electrophysiological recordings in humans and non-human animals:

- The influence of alpha phase on perception is expected to be particularly strong in the unattended visual stream. This can be tested using spatial attention paradigms together with EEG or MEG. Multimodal approaches using TMS combined with EEG recordings, fMRI combined with EEG recordings and intracranial spike-field data will be informative as well.
- Neuronal spiking is predicted to occur earlier in the alpha cycle, as the respective visual stimulus increases in saliency. The possibility of an alpha phase code is best

Box 2. Outstanding questions

- Which physiological mechanisms are responsible for generating alpha activity? Existing models that account for the emergence of neuronal oscillations in the alpha band need to be further developed in conjunction with electrophysiological investigations.
- GABAergic interneurons are known to play an important role for the generation of gamma band activity [58]. However, the functional inhibition by alpha activity must also rely on GABAergic mechanisms. Future research is required to elucidate how these two different functional roles of GABAergic inhibition are implemented physiologically, for instance by different classes of interneurons [59] or by local feedback that depends on neuronal time constants (for gamma) vs. central generators that depend on circuit properties (for alpha).
- The involvement of thalamic regions such as the pulvinar and the lateral geniculate nucleus (LGN) remains to be further elucidated [60,61].
- On which spatial scale does the inhibitory role of alpha activity operate? For instance, it has been shown that movement of the hand results in an alpha power increase in the foot area in primary motor cortex and *vice versa* [62]. Does alpha activity also reflect inhibition between subregions of the same hemifield in the visual system?
- We have made a case for a specific functional role of alpha oscillations modulated by spatial attention in the visual system. Does the proposed role of alpha activity generalize to other modalities, such as the auditory and somatosensory system? Further, does the role of alpha oscillations in organizing a spatio-temporal code generalize to functions beyond the allocation of attention?
- Visual saliency has been shown to modulate neuronal excitability. However, top-down mechanisms, for instance, as a consequence of feature attention, are also likely to modulate neuronal excitability. What are the consequences of such top-down modulation for the putative alpha phase code?
- The proposed framework is inspired by models of the functional role of theta oscillations [1,6,16]. Theta activity is typically associated with active processing rather than functional inhibition. Nevertheless, the mechanistic role of the theta and alpha rhythms might be more related than previously assumed. Do theta and alpha oscillations serve the same function in terms of converting levels of excitability into a temporal phase code?
- The functional role of alpha oscillations for attention needs to be integrated with existing theories such as the normalization model of attention [63] and load theory [64]. The normalization model of attention relies on inhibition for divisive suppression. Does alpha activity play a role in implementing this inhibition? The load theory of attention holds that distracting stimuli are processed less as the perceptual load for attended stimuli increases [64]. EEG and MEG findings show that, when attention is allocated to one hemifield, alpha activity decreases in the contralateral hemisphere and increases in the ipsilateral hemisphere [36,65]. This hemispheric lateralization is parametrically dependent on how strongly attention is directed [66]. Does the alpha activity increase in the ipsilateral hemisphere reflect the physiological substrate of decreased distractor processing with load?

investigated by intracranial spike-field recordings in non-human primates.

- Alpha and gamma activity have recently been associated with deep and superficial cortical layers, respectively [26,56,57]. This would suggest that the phase of alpha oscillations in deeper layers exercises a phasic modulation on spiking and gamma activity in superficial layers. We predict that this modulation will change with attention. This can be tested in laminar animal studies.

In addition to these predictions, our framework prompts a set of theoretical and empirical questions for future research (see Box 2). Such work is likely to lead to a better understanding of the mechanistic role of oscillatory brain activity. In particular, the coupling between the phase of alpha oscillations and gamma activity could provide important novel insight into the neuronal dynamics that control visual attention.

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