



Published in final edited form as:

Trends Cogn Sci. 2019 February ; 23(2): 87–101. doi:10.1016/j.tics.2018.11.009.

A rhythmic theory of attention

Ian C. Fiebelkorn¹ and Sabine Kastner^{1,2}

¹Princeton Neuroscience Institute, Princeton University, Princeton, NJ 08544, USA.

²Department of Psychology, Princeton University, Princeton, NJ 08544, USA.

Abstract

Recent evidence has demonstrated that environmental sampling is a fundamentally rhythmic process. Both perceptual sensitivity during covert spatial attention and the probability of overt exploratory movements are tethered to theta-band activity (3–8 Hz) in the attention network. The fronto-parietal part of this network is positioned at the nexus of sensory and motor functions, directing two tightly coupled processes related to environmental exploration: preferential routing of sensory input and saccadic eye movements. We propose that intrinsic theta rhythms temporally resolve potential functional conflicts by periodically re-weighting functional connections between higher-order brain regions and either sensory or motor regions. This rhythmic re-weighting alternately promotes either sampling at a behaviorally relevant location (i.e., sensory functions) or shifting to another location (i.e., motor functions).

Keywords

attention; motor; vision; saccades; oscillations; theta

A rhythmic pattern of sampling and shifting

Imagine searching for a child's favorite toy on the floor of a cluttered playroom. Environmental sampling is the means through which the brain directs its limited resources to first select and then boost the processing of behaviorally relevant stimuli. It occurs through a combination of preferential sensory processing—broadly referred to as selective attention—and exploratory movements. Selective attention establishes prioritization of stimuli and enhances neural processing of behaviorally relevant stimuli, while at the same time suppressing neural processing of irrelevant stimuli. In contrast, exploratory movements—such as saccadic eye movements in primates and whisking in rodents—orient the sensory organs toward behaviorally relevant stimuli.

In primates, a common network (i.e., the “attention network”) of brain regions directs sensory and motor aspects of environmental sampling [1]. Here, we describe recent evidence

Correspondence: ianfc@princeton.edu (Ian C. Fiebelkorn).

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

that rhythmic neural activity shapes both these aspects of environmental sampling. We specifically propose that theta rhythms in the attention network resolve potential functional conflicts by temporally organizing sensory and motor functions. Even under conditions that promote sustained attention at a behaviorally relevant location, there are alternating periods of either enhanced or diminished perceptual sensitivity [2–4]. Whereas theta-dependent periods of enhanced perceptual sensitivity reflect attention-related sensory sampling, theta-dependent periods of diminished perceptual sensitivity provide opportunities to shift attention. We propose that the presently attended location is periodically re-assessed (every ~250 ms) to confirm that it is still the most important location. In the following sections, we will elaborate on the neural basis and the functional consequences of this rhythmic pattern of sampling and shifting. We refer to this new, theta-rhythmic characterization of environmental sampling as the “rhythmic theory of attention.”

Environmental sampling involves both sensory and motor processes

The present discussion focuses on sampling in visual space, through spatial attention and saccadic eye movements (or saccades). These sampling processes are closely related. Spatial attention can be either coupled to eye position, during overt sampling, or uncoupled from eye position, during covert sampling (but see [5] for evidence of a link between covert sampling and small eye movements). We will synthesize recent findings that shed light on the relationship between attention-related boosts in sensory processing (i.e., spatial attention) and saccades, leading to a new theory for how a shared network of brain regions organizes and directs these two sampling processes.

The brain’s sensory and motor systems have historically been studied in isolation. The sensory system is considered the point of input, processing environmental stimulation, while the motor system is considered the point of output, generating reactions to environmental stimulation. But this is clearly an oversimplification. The sensory and motor systems evolved together and are functionally integrated [6–10]. For example, given limited processing resources, saccades largely determine the targets for preferential sensory sampling. On the other hand, a sensory analysis of stimulus properties (e.g., salience) largely determines the end points for saccades [11, 12]. Environmental sampling thus involves an integrative loop of motor-guided sensory processing and sensory-informed exploratory movements [6].

In addition to this functional interplay between the sensory and motor systems, there is anatomical overlap among the brain regions that direct enhanced processing of sensory information (i.e., selective attention) and saccades [1, 13, 14]. That is, a large-scale network has been linked to both preferential processing of spatial locations and exploratory eye movements. This network, known as the attention network, includes cortical structures, such as the frontal eye fields (FEF) [15] and the lateral intraparietal area (LIP) [16], as well as subcortical structures, such as the superior colliculus [17] and the pulvinar nucleus of the thalamus [18, 19]. These structures are positioned at the nexus of sensory and motor functions, playing a role in both.

Such functional and anatomical overlap has previously led researchers to debate whether neural responses in hubs of the attention network are related to either spatial attention [20] or the intention to make a saccade [21], with some arguing that spatial attention and saccades are inseparably coupled [22, 23]. The influential but controversial “premotor theory of attention” posits that covert spatial attention arises from a weaker activation of the same neural circuits that typically guide saccades and primarily reflects saccadic preparation [24]. That is, this theory posits that there is a single control mechanism guiding environmental sampling through both spatial attention and saccades.

There was initially considerable enthusiasm for the “premotor theory of attention,” with supporting evidence from electrophysiological studies. A series of seminal studies, for example, demonstrated that electrically stimulating an oculomotor region of frontal cortex, below the level that evokes eye movements, has attention-like consequences for behavioral performance [25] and sensory processing in visual cortex [26, 27]. That is, weakly stimulating a frontal region that contributes to the generation of saccades [28], led to behavioral and neural effects that mimicked covert spatial attention [25–27]. These results were therefore initially interpreted as supporting evidence for the “premotor theory of attention.” However, frontal cortex contains neurons with different functionally defined response profiles: visual (i.e., only sensory-related responses), visual-movement (i.e., both sensory- and saccade-related responses), and movement (i.e., only saccade-related responses) cell types. Only neurons with visual-sensory responses (i.e., visual and visual-movement neurons) demonstrate increased firing rates during the deployment of spatial attention [4, 29, 30]. Electrical stimulation of frontal cortex activates multiple cell types, making their unique contributions to subsequent attention-like effects unclear. That is, although imaging studies have broadly linked frontal cortex to the generation of both spatial attention and saccades [13, 14], there is a microstructure in frontal cortex comprised of functionally dissociable cell types. These functionally dissociable cell types—also present in other hubs of the attention network [31]—might make it possible to separately engage either attention-related boosts in sensory processing or exploratory eye movements. On the other hand, the presence of neurons with both sensory and motor responses provides a potential neural basis for integrating sensory and motor processing.

In addition to functionally dissociable cell types, there are specific neural circuits and patterns of anatomical connectivity associated with sensory and motor functions of the attention network. For example, neurons in frontal cortex that project to visual-sensory cortex are predominantly located in the supragranular layers, while neurons that project to the superior colliculus—a structure often associated with the motor output of attention—are exclusively located in the infragranular layers (i.e. layer 5) [32]. Future research needs to determine the precise neural circuits involved in deployments of covert and overt attention, determining the extent to which those neural circuits are the same or different.

Perhaps more critical to challenging the “premotor theory of attention,” clever experimental manipulations have shown that spatial attention and saccades can be uncoupled, both in monkeys [33] and in humans [34]. Rather than a single control mechanism, there seem to be separate control mechanisms for spatial attention and saccades. Based on these findings, the “premotor theory of attention” has seemingly been disproven, at least in its strictest form

[35]. However, it remains undeniable that the sensory and motor dimensions of environmental sampling typically operate in lockstep [36]. full understanding of how an overlapping network of brain regions (i.e., the attention network) directs both attention-related boosts in sensory processing and exploratory eye movements therefore remains a critical goal for cognitive neuroscience.

Here, we will discuss evidence that potential functional conflicts in the attention network are partly resolved through temporal isolation of the neural activity that promotes either preferential sensory processing (i.e., spatial attention) or exploratory eye movements. We propose that intrinsic brain rhythms—specifically theta rhythms (3–8 Hz)—organize neural activity into alternating attentional states associated with either sampling at the presently attended location or shifting to another location.

Rhythmic sampling during spatial attention

Spatial attention is the process through which behaviorally relevant locations receive boosts in sensory processing [37], leading to better behavioral outcomes at the selected location [38]. Classic studies of spatial attention largely ignored its temporal dynamics, assuming that associated neural and behavioral effects were continuous over time and persisted for the duration of attentional deployment. Several recent studies, however, have provided compelling behavioral evidence—in both humans and monkeys—that spatial attention is instead discontinuous (Figure 1A, B) [2, 4, 39–41]. That is, spatial attention fluctuates, sampling the visual environment in theta-rhythmic cycles (3–8 Hz). These attention-related theta rhythms are associated with alternating periods of either enhanced or diminished perceptual sensitivity [2, 40, 42]. Whether a visual target is detected therefore depends not only on its stimulus properties, such as contrast and brightness, but also on when it occurs relative to ongoing brain rhythms. Some of the first work on this topic elegantly demonstrated that attention-related neural activity could rhythmically sample information by entraining to rhythmic stimulation in the environment [43, 44]. In comparison, the theta-rhythmic sampling described here is intrinsically generated and does not depend on environmental rhythms.

Spatial attention has sometimes been compared to a spotlight [38], scanning the visual environment and pausing to illuminate potentially relevant stimuli. We now know that this metaphorical spotlight of spatial attention blinks [2, 39, 40], but what is the neural basis of this blinking? As a first step, electroencephalographic (EEG) and magnetoencephalographic (MEG) studies broadly linked attention-related effects to intrinsic brain rhythms [45, 46]. Researchers, for example, used EEG and brief light flashes to correlate the phase of neural oscillations with detection performance [45]. The phase of fronto-central theta rhythms, just prior to stimulus onset, was predictive of successful visual-target detection. But this phase-detection relationship only occurred when targets were presented at the attended location. These results therefore established that perceptual fluctuations are linked to theta rhythms, specifically during the deployment of spatial attention.

An MEG study similarly linked theta rhythms with detection performance, but during a task that instead promoted attentional shifting between two equiprobable target locations [46].

Whereas the previously described EEG study showed that fluctuations in sensory processing at a single location are linked to theta rhythms [45], this MEG study showed that boosts in sensory processing can also alternate (or shift) between locations at a theta rhythm [46]. Their results specifically demonstrated theta-dependent changes in gamma-band activity (30–90 Hz), with increased gamma-band activity in the contralateral hemisphere being associated with better visual-target detection (see Box 1 for further discussion of the functional significance of gamma-band activity). Theta-dependent increases in gamma-band activity alternated between hemispheres, and attention-related boosts in visual processing likewise alternated between visual hemifields. Combined, these EEG and MEG studies revealed that both attentional sampling and attentional shifting are rhythmic [47]. While these studies clearly demonstrated that attention-related theta rhythms are correlated with behavioral outcomes, neither EEG nor MEG has the spatial resolution necessary to more precisely identify the neural basis of theta-rhythmic sampling.

In contrast, electrocorticography (ECoG), with recording electrodes placed directly on the cortical surface, has the spatial resolution both to localize signals within specific cortical regions and to resolve functional networks. We therefore used ECoG in pharmacoresistant epilepsy patients to investigate the neural basis of theta-rhythmic sampling during two different spatial-cueing tasks [3]. The phase of theta-band activity was predictive of behavioral performance (i.e., hit rates and reaction times) across multiple cortical regions, with the strongest relationships between oscillatory phase and behavioral performance being measured at electrodes placed on frontal and parietal cortices (Figure 1C). Theta phase was not only predictive of behavioral performance but also of cortical excitability [3]—as measured by high-frequency broadband band activity, which is a known proxy for population spiking [48]. That is, perceptual fluctuations during spatial attention were associated with theta-rhythmic changes in cortical excitability, primarily localized in frontal and parietal cortices. By replicating these findings across two experimental tasks, we further demonstrated that theta-rhythmic sampling is not context specific. Theta-rhythmic sampling is a fundamental property of spatial attention, operating regardless of the specific task requirements. While previous studies have demonstrated coupling between theta phase and higher-frequency power during various cognitive tasks [49–52], we were able to specifically link such coupling in frontal and parietal cortices (i.e., the attention network) with theta-rhythmic sampling during spatial attention.

To study the neural mechanisms underlying theta-rhythmic periods of either enhanced or diminished perceptual sensitivity, we recorded local field potentials (LFPs) and single-unit activity (SUA) in monkeys performing a spatial-cueing task [4]. Here, we employed one of the two experimental tasks used in our human ECoG study [2, 3], thereby providing complementary results in two primate species. We specifically targeted well-established cortical hubs of the macaque attention network: the frontal eye fields (FEF) and the lateral intraparietal area (LIP). Our results first demonstrated that theta rhythms in both cortical regions were predictive of behavioral performance (i.e., hit rates; Figure 1D). Combined with our previous findings in humans [2, 3], these results thus revealed that theta-rhythmic sampling has been evolutionarily preserved across at least two primate species, again indicating that theta-rhythmic sampling is a fundamental property of spatial attention.

We next demonstrated that theta rhythms organize neural activity into alternating attentional states, characterized by both differences in neural dynamics and differences in perceptual sensitivity. These attentional states were revealed through phase-amplitude coupling between the phase of theta-band activity and higher-frequency power. Phase-amplitude coupling is defined as a modulation of higher-frequency power by the phase of a lower frequency [49, 53, 54], and has been proposed as a mechanism for temporally coordinating cognitive functions [43].

The first theta-dependent attentional state, associated with periods of enhanced perceptual sensitivity (i.e., the “good” theta phase), was defined by FEF-dominated beta-band activity (15–35 Hz) and LIP-dominated gamma-band activity (> 35 Hz; Figure 2A). Both the specific frequencies and the cell types associated with those frequencies (i.e., beta and gamma) provided evidence of the functional roles attributable to this first attentional state. Increased gamma- and beta-band activity have been repeatedly associated with sensory enhancement [46, 55–60] and motor suppression [30, 61, 62], respectively. In line with these functional interpretations, gamma-band activity in our data was primarily associated with visual-sensory neurons, while beta-band activity was primarily associated with visual-movement neurons (Figure 2B). We therefore propose that the first attentional state is characterized by both the enhancement of sensory processing and the suppression of attentional shifts (either covert or overt).

The second theta-dependent attentional state, associated with periods of diminished perceptual sensitivity (i.e., the “poor” theta phase), was defined by LIP-specific alpha-band activity (Figure 2A). Fittingly, alpha-band activity has been repeatedly linked to the attenuation of sensory processing [63–66]. Thus, this second attentional state is characterized by a periodic attenuation of visual processing—specifically occurring at the presently attended location—together with a temporary release from beta-related motor suppression. These combined effects on sensory and motor processing periodically increase the likelihood of attentional shifts to other locations.

Our recordings in the macaque attention network thus revealed dynamic interactions between frontal and parietal cortices that seemingly shape attention-related sampling [4]. These theta-rhythmic interactions were not, however, restricted to cortical hubs of the attention network. Theta rhythms in the mediodorsal aspect of the pulvinar, which is interconnected with frontal and parietal cortices [67], were also predictive of behavioral performance (i.e., hit rates; Figure 1D) and regulated functional connectivity with higher-order cortex [31]. We recently demonstrated that the mediodorsal pulvinar specifically regulates neural activity in FEF and LIP during the theta-dependent state associated with enhanced perceptual sensitivity, while LIP regulates neural activity in the pulvinar during the attentional state associated with diminished perceptual sensitivity (Figure 2C). Theta-rhythmic sampling is therefore also associated with a reweighting of functional connections between cortical and subcortical hubs of the attention network [31]. We propose that this rhythmic reweighting reflects functional dissociations within the attention network, with some hubs and pathways promoting sampling (i.e., preferential sensory processing) at the presently attended location and others promoting shifting to another location.

Here, we have synthesized evidence that theta rhythms in the attention network shape sensory sampling during spatial attention, leading to alternating periods of either enhanced or diminished perceptual sensitivity (Figure 1). Attention-related theta rhythms have also been identified in visual cortex [68]. It remains unclear, however, whether these theta rhythms in visual cortex are functionally related to theta rhythms in the attention network (Box 2) and/or linked to fluctuations in perceptual sensitivity (i.e., rhythmic sampling).

Theta-rhythmic sampling may provide critical flexibility for attention function, offering windows of opportunity when it is easier to disengage from the presently attended location and shift to another location (i.e., during periods of relative disengagement). Importantly, these periodic windows are merely opportunities for shifting, meaning that an attentional shift does not necessarily occur. That is, we would only expect an attentional shift if warranted by stimulus properties (e.g., the salience of stimuli at other locations) and behavioral goals. For example, attentional shifts should be less likely to occur during tasks that promote sustained attention at a single location and more likely to occur during tasks that promote the monitoring of multiple locations (Figure 3, Key Figure). Yet even under conditions of sustained attention at a single location, windows of opportunity for potential shifts continue to occur, interrupting detection and leading to theta-rhythmic sampling [2–4]. These periodic disruptions in attention-related sampling may have provided our ancestors with an evolutionary advantage, e.g., allowing them to detect and therefore avoid predators while foraging.

Rhythms during exploratory eye movements

We have thus far focused on evidence of links between covert attentional sampling and theta rhythms, which set up alternating periods of either enhanced or diminished perceptual sensitivity. In this section we will describe complimentary evidence of links between exploratory eye movements and theta rhythms. Attentional shifts can occur covertly (i.e., independent of eye position) but are often accompanied by an eye movement. Similar to recent studies focusing on the temporal dynamics of covert spatial attention, studies focusing on the temporal dynamics of exploratory eye movements have demonstrated theta-rhythmic sampling [69–73].

For example, an electrophysiological investigation in macaques demonstrated that the phase of theta-band activity (at ~3.3 Hz) in visual cortex predicted the occurrence of microsaccades [70]. These small, fixational eye movements have the same underlying neural circuitry as saccades [69, 74], and have been associated with attention-like changes in visual processing [5, 70, 75, 76] and behavioral performance [70, 76, 77]. It has been shown that there is a microsaccade-related enhancement in the neuronal response to peripheral stimuli—even when those stimuli are behaviorally irrelevant—similar to effects observed under conditions of selective attention [75]. Based on these findings, one might posit that theta-rhythmic sampling during covert spatial attention results from the theta-rhythmic generation of microsaccades. However, several recent studies investigating the neural basis of attention-related theta rhythms have shown that accounting for microsaccades does not eliminate theta-rhythmic behavioral and neural effects [4, 46, 68]. Both attention-related boosts in sensory processing and microsaccades are linked to the phase of theta rhythms. But as with

studies suggesting that spatial attention and exploratory eye movements have separate control mechanisms [33, 34], these sampling processes seem to be independently linked to theta rhythms. That is, microsaccades are not the source of theta-rhythmic fluctuations in covert attentional sampling.

Our “rhythmic theory of attention” (Figure 2) predicts a higher probability of exploratory eye movements during the theta phase associated with diminished perceptual sensitivity at the cued location. We therefore propose that microsaccades are more likely to occur during these theta-dependent periods of disengagement, regardless of whether they are directed away from the cued location or toward the cued location (Figure 3, Key Figure). With microsaccades away from the cued location being indicative of an attentional shift [78], and microsaccades toward the cued location being indicative of the cued location being selected for another round of sampling [79]. Even sustained attention at a behaviorally relevant location is thus discontinuous, characterized by interdigitated periods of diminished perceptual sensitivity, when the presently attended location must be re-selected based on stimulus properties and behavioral goals.

Theta rhythms are not only linked to fixational eye movements, but also to larger saccadic eye movements that are employed during overt exploration [10, 71, 72, 80–82]. Studies linking saccades to theta rhythms have provided evidence that the sensory and motor aspects of environmental sampling are tethered to the same theta rhythms. For example, a couple of recent studies have demonstrated that theta-rhythmic fluctuations in perceptual sensitivity are time-locked to motor responses [10, 82]. A third study, on the other hand, reported periodicity in perceptual sensitivity both prior to a saccade (at its origin) and after the saccade (at its destination) [71]. Importantly, saccades did not seem to change (or reset) the phase of perceptual rhythms, with the eyes instead moving during troughs in the perceptual rhythm. That is, the eyes moved during periods typically associated with diminished perceptual sensitivity at the saccade origin, with the perceptual rhythm then continuing when the eyes reached their destination. This final detail is consistent with our “rhythmic theory of attention” (Figure 2), which proposes alternating periods of either engagement at the presently attended location (and therefore enhanced perceptual sensitivity) or relative disengagement (and therefore diminished perceptual sensitivity), with periods of disengagement being associated with a higher likelihood of covert or overt attentional shifts (Figure 3, Key Figure). Thus, there is emerging behavioral evidence that saccades are initiated during periods of diminished perceptual sensitivity (i.e., during the theta phase associated with worse visual-target detection) [71].

It should be noted that only a few studies have used intracortical—rather than behavioral or EEG/MEG data—to link exploratory eye movements and theta rhythms. Those studies have measured electrophysiological data in visual cortex [70, 73] and the superior colliculus [76]. Future research will therefore need to (i) further investigate the neural basis of theta rhythms underlying exploratory eye movements in primates and (ii) determine the extent to which this neural basis is shared with theta-rhythmic sampling during covert spatial attention. We predict that attention-related boosts in sensory processing and exploratory eye movements will be linked to opposite phases of the same theta rhythms (Figure 2). It has yet to be

determined whether these theta rhythms originate in sensory cortex [68, 83], the attention network [3, 4], or elsewhere [84], such as the hippocampus [85].

Attentional rhythms as a basis of cognitive flexibility

Theta rhythms seemingly provide a clocking mechanism for both attention-related boosts in sensory processing and exploratory eye movements. We propose that these theta rhythms share a neural basis in the attention network. We further propose that **theta-rhythmic sampling resolves functional conflicts by temporally isolating sensory and motor processes during environmental sampling**. That is, **sensory (i.e., sampling) and motor (i.e., shifting) processes are linked to opposite phases of the same theta rhythm, which organizes neural activity into two alternating states** (Figure 2). These theta-dependent states promote either sampling at a behaviorally relevant location or shifting, covertly or overtly, to another location [4, 31].

The first theta-dependent state is associated with both the suppression of saccades [4, 30] and the opening of feedforward sensory channels [86], reflecting engagement at the presently attended location and therefore enhanced perceptual sensitivity [4]. That is, **the first theta-dependent state promotes sensory sampling at a behaviorally relevant location, by both suppressing attentional shifts [4, 30] and increasing functional connectivity between hubs of the attention network and sensory regions (e.g., visual cortex)**. **Enhanced sensory processing during spatial attention is associated with increased gamma synchronization (Box 1) between hubs of the attention network and visual cortices [60, 87]**. We hypothesize that the strength of attention-related functional connections increases during periods of sensory sampling (i.e., during the first theta-dependent state).

The **second theta-dependent state is associated with the attenuation of sensory processing at the presently attended location [4], reflecting preparation for a potential shift, either covert or overt, to another location**. Importantly, this theta-dependent **state does not necessarily result in a shift, but rather primes the attention network should such a shift be warranted based on either stimulus properties across the visual scene and/or behavioral goals**. A **priority map—informed by stimulus properties and behavioral goals—** generally guides environmental sampling [16, 88]. We propose that rhythmic attenuations in visual processing at the presently attended location reweight the priority map to increase the likelihood of other locations being selected for further processing. This prevents the observer from being overly focused on any given location and promotes a more active sampling of the visual environment. Regardless of whether a shift occurs, there is a consistent decrease in perceptual sensitivity during the second theta-dependent state, specific to the presently attended location [2–4]. **We predict that this decrease in perceptual sensitivity co-occurs with an increase in functional connectivity between the attention network and regions typically associated with the initiation of covert or overt attentional shifts, such as the superior colliculus [17, 36, 89–91]**.

Concluding Remarks

Spatial attention and exploratory eye movements are linked both functionally and anatomically. However, these sampling processes can be functionally dissociated, demonstrating that they have separate control mechanisms [33, 34]. Here, we synthesized recent research that ties both attention-related boosts in sensory processing and exploratory eye movements to theta rhythms, indicating that environmental sampling is fundamentally rhythmic. This recent research provides the basis for a “rhythmic theory of attention,” whereby theta rhythms in the attention network organize neural activity into alternating states that promote either sampling or shifting. That is, we propose that sensory and motor processes are temporally isolated during environmental sampling, helping to resolve potential functional conflicts in the attention network. A disruption in these coordinating rhythms might contribute to atypical attentional function in neurological or psychiatric disorders. Rather than a temporal balance between sampling and shifting, the attention network might, for example, be biased toward remaining in the state that promotes shifting.

While some aspects of this “rhythmic theory of attention” are already strongly supported by empirical data, others will require verification through future experiments (see Outstanding Questions). We are intrigued by the possibility that theta-rhythmic sampling contributes to well-known attentional phenomena, such as inhibition of return [92] and the attentional blink [93]. Inhibition of return is characterized by the suppression of a previously attended location [92]. Approximately four times per second, theta-rhythmic sampling leads to a relative attenuation of visual processing at the presently attended location [2, 4], accompanied by a proposed increase in the likelihood of attentional shifts away from that location [71]. If an attentional shift occurs, attenuation (or suppression) at the previously attended location might persist, contributing to inhibition of return. Future studies need to re-examine such well-known attentional phenomena in the context of theta-rhythmic sampling, perhaps revealing novel insights into their underlying neural basis.

The “rhythmic theory of attention” also has far-reaching implications for how the brain prioritizes stimuli for preferential processing. For example, theta-rhythmic sampling during spatial attention indicates that the biased competition for limited processing resources [37] unfolds over time and therefore that time is an important variable when studying cognitive processes. Specifically, a periodic attenuation of visual processing indicates that there is an intrinsic bias toward shifting away from the presently attended location (or object). Theta-rhythmic sampling thus promotes an active exploration of the visual environment.

While the neural mechanisms underlying theta rhythms in the attention network remains largely unknown, theta rhythms in sensory cortex have been linked to the competition between neural populations representing simultaneously presented stimuli [83, 94, 95]. As a result of this competition, representations of the stimuli alternate over time between responses typically associated with the first stimulus when shown in isolation, and responses typically associated with the second stimulus when shown in isolation (Box 2). These local changes in sensory cortex might be accompanied by the re-weighting of functional connections across a larger network [31], including hubs in higher-order areas of the

attention network. Future studies need to establish whether theta rhythms in sensory cortex and the attention network share the same neural basis (see Outstanding Questions).

Finally, it is important to note that the proposed role of low-frequency oscillations in the present theory—resolving functional conflicts within a large-scale network—might not be specific to the attention network. Rather, this could be a more general mechanism for providing functional flexibility in large-scale networks [52]. similar process might occur, for example, when multiple items are held in working memory [96–98]. That is, the brain might rhythmically cycle through stronger neural representations of each to-be-remembered item, rather than fully processing the items simultaneously. Lower-frequency oscillations might be generally employed to organize and disassociate functionally distinct, large-scale networks that have shared (or overlapping) hubs.

Acknowledgements:

This work was supported by a training fellowship to I.C.F. (F32EY023465), and by grants from NIMH (R01MH064063, Silvio O. Conte Center (21560-685), NEI (R01EY017699, R21EY023565), and the James S. McDonnell Foundation to S.K.

References

1. Corbetta M et al. (1998) A common network of functional areas for attention and eye movements. *Neuron* 21 (4), 761–73. [PubMed: 9808463]
2. Fiebelkorn IC et al. (2013) Rhythmic sampling within and between objects despite sustained attention at a cued location. *Curr Biol* 23 (24), 2553–8. [PubMed: 24316204]
3. Helfrich RF et al. (2018) Neural mechanisms of sustained attention are rhythmic. *Neuron* 99 (4), 829–841. [PubMed: 30100255]
4. Fiebelkorn IC et al. (2018) A dynamic interplay within the frontoparietal network underlies rhythmic spatial attention. *Neuron* 99 (4), 842–853. [PubMed: 30138590]
5. Lowet E et al. (2018) Enhanced Neural Processing by Covert Attention only during Microsaccades Directed toward the Attended Stimulus. *Neuron* 99 (1), 207–214 e3. [PubMed: 29937279]
6. Schroeder CE et al. (2010) Dynamics of Active Sensing and perceptual selection. *Curr Opin Neurobiol* 20 (2), 172–6. [PubMed: 20307966]
7. Gutteling TP et al. (2011) Grasping preparation enhances orientation change detection. *PLoS One* 6 (3), e17675. [PubMed: 21408131]
8. Schubotz RI (2007) Prediction of external events with our motor system: towards a new framework. *Trends Cogn Sci* 11 (5), 211–8. [PubMed: 17383218]
9. Rolfs M et al. (2013) Reach preparation enhances visual performance and appearance. *Philos Trans R Soc Lond B Biol Sci* 368 (1628), 20130057. [PubMed: 24018719]
10. Tomassini A et al. (2015) Rhythmic oscillations of visual contrast sensitivity synchronized with action. *J Neurosci* 35 (18), 7019–29. [PubMed: 25948254]
11. Itti L and Koch C (2000) A saliency-based search mechanism for overt and covert shifts of visual attention. *Vision Res* 40 (10–12), 1489–506. [PubMed: 10788654]
12. Parkhurst D et al. (2002) Modeling the role of salience in the allocation of overt visual attention. *Vision Res* 42 (1), 107–23. [PubMed: 11804636]
13. Corbetta M (1998) Frontoparietal cortical networks for directing attention and the eye to visual locations: identical, independent, or overlapping neural systems? *Proc Natl Acad Sci U S A* 95 (3), 831–8. [PubMed: 9448248]
14. Nobre AC et al. (2000) Covert visual spatial orienting and saccades: overlapping neural systems. *Neuroimage* 11 (3), 210–6. [PubMed: 10694463]
15. Squire RF et al. (2013) Prefrontal contributions to visual selective attention. *Annu Rev Neurosci* 36, 451–66. [PubMed: 23841841]

16. Bisley JW and Goldberg ME (2010) Attention, intention, and priority in the parietal lobe. *Annu Rev Neurosci* 33, 1–21. [PubMed: 20192813]
17. Krauzlis RJ et al. (2013) Superior colliculus and visual spatial attention. *Annu Rev Neurosci* 36, 165–82. [PubMed: 23682659]
18. Saalmann YB and Kastner S (2011) Cognitive and perceptual functions of the visual thalamus. *Neuron* 71 (2), 209–23. [PubMed: 21791281]
19. Halassa MM and Kastner S (2017) Thalamic functions in distributed cognitive control. *Nat Neurosci* 20 (12), 1669–1679. [PubMed: 29184210]
20. Colby L and Goldberg ME (1999) Space and attention in parietal cortex. *Annu Rev Neurosci* 22, 319–49. [PubMed: 10202542]
21. Andersen RA and Buneo CA (2002) Intentional maps in posterior parietal cortex. *nnu Rev Neurosci* 25, 189–220.
22. Kowler E et al. (1995) The role of attention in the programming of saccades. *Vision Res* 35 (13), 1897–916. [PubMed: 7660596]
23. Hoffman JE and Subramaniam B (1995) The role of visual attention in saccadic eye movements. *Percept Psychophys* 57 (6), 787–95. [PubMed: 7651803]
24. Rizzolatti G et al. (1987) Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention. *Neuropsychologia* 25 (1A), 31–40. [PubMed: 3574648]
25. Moore T and Fallah M (2001) Control of eye movements and spatial attention. *Proc Natl Acad Sci U S A* 98 (3), 1273–6. [PubMed: 11158629]
26. Moore T and Armstrong KM (2003) Selective gating of visual signals by microstimulation of frontal cortex. *Nature* 421 (6921), 370–3. [PubMed: 12540901]
27. Armstrong KM et al. (2006) Changes in visual receptive fields with microstimulation of frontal cortex. *Neuron* 50 (5), 791–8. [PubMed: 16731516]
28. Goldberg ME and Bushnell MC (1981) Behavioral enhancement of visual responses in monkey cerebral cortex. II. Modulation in frontal eye fields specifically related to saccades. *J Neurophysiol* 46 (4), 773–87. [PubMed: 7288464]
29. Thompson KG et al. (2005) Neuronal basis of covert spatial attention in the frontal eye field. *J Neurosci* 25 (41), 9479–87. [PubMed: 16221858]
30. Gregoriou GG et al. (2012) Cell-type-specific synchronization of neural activity in FEF with V4 during attention. *Neuron* 73 (3), 581–94. [PubMed: 22325208]
31. Fiebelkorn IC et al. (2018) Thalamo-cortical interactions characterize rhythmically alternating attentional states. *Nature Communications*
32. Pouget P et al. (2009) Visual and motor connectivity and the distribution of calcium-binding proteins in macaque frontal eye field: implications for saccade target selection. *Front Neuroanat* 3, 2. [PubMed: 19506705]
33. Juan CH et al. (2004) Dissociation of spatial attention and saccade preparation. *Proc Natl Acad Sci U S A* 101 (43), 15541–4. [PubMed: 15489272]
34. Juan CH et al. (2008) Segregation of visual selection and saccades in human frontal eye fields. *Cereb Cortex* 18 (10), 2410–5. [PubMed: 18326522]
35. Smith DT and Schenk T (2012) The Premotor theory of attention: time to move on? *Neuropsychologia* 50 (6), 1104–14. [PubMed: 22306518]
36. Kustov AA and Robinson DL (1996) Shared neural control of attentional shifts and eye movements. *Nature* 384 (6604), 74–7. [PubMed: 8900281]
37. Desimone R and Duncan J (1995) Neural mechanisms of selective visual attention. *Annu Rev Neurosci* 18, 193–222. [PubMed: 7605061]
38. Posner MI (1980) Orienting of attention. *Q J Exp Psychol* 32 (1), 3–25. [PubMed: 7367577]
39. VanRullen R et al. (2007) The blinking spotlight of attention. *Proc Natl Acad Sci U S A* 104 (49), 19204–9. [PubMed: 18042716]
40. Landau AN and Fries P (2012) Attention samples stimuli rhythmically. *Curr Biol* 22 (11), 1000–4. [PubMed: 22633805]

41. Song K et al. (2014) Behavioral oscillations in attention: rhythmic alpha pulses mediated through theta band. *J Neurosci* 34 (14), 4837–44. [PubMed: 24695703]
42. Dugue L et al. (2015) Theta oscillations modulate attentional search performance periodically. *J Cogn Neurosci* 27 (5), 945–58. [PubMed: 25390199]
43. Schroeder CE and Lakatos P (2009) Low-frequency neuronal oscillations as instruments of sensory selection. *Trends Neurosci* 32 (1), 9–18. [PubMed: 19012975]
44. Lakatos P et al. (2008) Entrainment of neuronal oscillations as a mechanism of attentional selection. *Science* 320 (5872), 110–3. [PubMed: 18388295]
45. Busch NA and VanRullen R (2010) Spontaneous EEG oscillations reveal periodic sampling of visual attention. *Proc Natl Acad Sci U S A* 107 (37), 16048–53. [PubMed: 20805482]
46. Landau AN et al. (2015) Distributed Attention Is Implemented through Theta-Rhythmic Gamma Modulation. *Curr Biol* 25 (17), 2332–7. [PubMed: 26279231]
47. Dugue L et al. (2016) Attention Reorients Periodically. *Curr Biol* 26 (12), 1595–1601. [PubMed: 27265395]
48. Ray S and Maunsell JH (2011) Different origins of gamma rhythm and high-gamma activity in macaque visual cortex. *PLoS Biol* 9 (4), e1000610. [PubMed: 21532743]
49. Canolty RT et al. (2006) High gamma power is phase-locked to theta oscillations in human neocortex. *Science* 313 (5793), 1626–8. [PubMed: 16973878]
50. Szczepanski SM et al. (2014) Dynamic changes in phase-amplitude coupling facilitate spatial attention control in fronto-parietal cortex. *PLoS Biol* 12 (8), e1001936. [PubMed: 25157678]
51. Tort AB et al. (2009) Theta-gamma coupling increases during the learning of item-context associations. *Proc Natl Acad Sci U S A* 106 (49), 20942–7. [PubMed: 19934062]
52. Lisman JE and Jensen O (2013) The theta-gamma neural code. *Neuron* 77 (6), 1002–16. [PubMed: 23522038]
53. Lakatos P et al. (2005) An oscillatory hierarchy controlling neuronal excitability and stimulus processing in the auditory cortex. *J Neurophysiol* 94 (3), 1904–11. [PubMed: 15901760]
54. Jensen O and Colgin LL (2007) Cross-frequency coupling between neuronal oscillations. *Trends Cogn Sci* 11 (7), 267–9. [PubMed: 17548233]
55. Fries P (2009) Neuronal gamma-band synchronization as a fundamental process in cortical computation. *Annu Rev Neurosci* 32, 209–24. [PubMed: 19400723]
56. Fries P et al. (2001) Modulation of oscillatory neuronal synchronization by selective visual attention. *Science* 291 (5508), 1560–3. [PubMed: 11222864]
57. Womelsdorf T et al. (2006) Gamma-band synchronization in visual cortex predicts speed of change detection. *Nature* 439 (7077), 733–736. [PubMed: 16372022]
58. Bichot NP et al. (2005) Parallel and serial neural mechanisms for visual search in macaque area V4. *Science* 308 (5721), 529–34. [PubMed: 15845848]
59. Womelsdorf T et al. (2007) Modulation of neuronal interactions through neuronal synchronization. *Science* 316 (5831), 1609–12. [PubMed: 17569862]
60. Gregoriou GG et al. (2009) High-frequency, long-range coupling between prefrontal and visual cortex during attention. *Science* 324 (5931), 1207–10. [PubMed: 19478185]
61. Pogosyan A et al. (2009) Boosting cortical activity at Beta-band frequencies slows movement in humans. *Curr Biol* 19 (19), 1637–41. [PubMed: 19800236]
62. Zhang Y et al. (2008) Response preparation and inhibition: the role of the cortical sensorimotor beta rhythm. *Neuroscience* 156 (1), 238–46. [PubMed: 18674598]
63. Foxe JJ and Snyder AC (2011) The Role of Alpha-Band Brain Oscillations as a Sensory Suppression Mechanism during Selective Attention. *Front Psychol* 2, 154. [PubMed: 21779269]
64. Worden MS et al. (2000) Anticipatory biasing of visuospatial attention indexed by retinotopically specific alpha-band electroencephalography increases over occipital cortex. *J Neurosci* 20 (6), RC63. [PubMed: 10704517]
65. Haegens S et al. (2011) Alpha-Oscillations in the monkey sensorimotor network influence discrimination performance by rhythmical inhibition of neuronal spiking. *Proc Natl Acad Sci U S A* 108 (48), 19377–82. [PubMed: 22084106]

66. Jensen O and Mazaheri A (2010) Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Front Hum Neurosci* 4, 186. [PubMed: 21119777]
67. Gutierrez C et al. (2000) Neurochemical and connectional organization of the dorsal pulvinar complex in monkeys. *J Comp Neurol* 419 (1), 61–86. [PubMed: 10717640]
68. Spyropoulos G et al. (2018) A theta rhythm in macaque visual cortex and its attentional modulation. *Proc Natl Acad Sci U S A* 115 (24), E5614–E5623. [PubMed: 29848632]
69. Otero-Millan J et al. (2008) Saccades and microsaccades during visual fixation, exploration, and search: foundations for a common saccadic generator. *J Vis* 8 (14), 21 1–18.
70. Bosman CA et al. (2009) A microsaccadic rhythm modulates gamma-band synchronization and behavior. *J Neurosci* 29 (30), 9471–80. [PubMed: 19641110]
71. Hogendoorn H (2016) Voluntary Saccadic Eye Movements Ride the Attentional Rhythm. *J Cogn Neurosci* 28 (10), 1625–35. [PubMed: 27243615]
72. Wutz A et al. (2016) Temporal Integration Windows in Neural Processing and Perception Aligned to Saccadic Eye Movements. *Curr Biol* 26 (13), 1659–68. [PubMed: 27291050]
73. Lowet E et al. (2016) Areas V1 and V2 show microsaccade-related 3–4-Hz covariation in gamma power and frequency. *Eur J Neurosci* 43 (10), 1286–96. [PubMed: 26547390]
74. Otero-Millan J et al. (2013) An oculomotor continuum from exploration to fixation. *Proc Natl Acad Sci U S A* 110 (15), 6175–80. [PubMed: 23533278]
75. Chen CY et al. (2015) Neuronal Response Gain Enhancement prior to Microsaccades. *Curr Biol* 25 (16), 2065–74. [PubMed: 26190072]
76. Bellet J et al. (2017) Sequential hemifield gating of alpha- and beta-behavioral performance oscillations after microsaccades. *J Neurophysiol* 118 (5), 2789–2805. [PubMed: 28794193]
77. Hafed ZM (2013) Alteration of visual perception prior to microsaccades. *Neuron* 77 (4), 775–86. [PubMed: 23439128]
78. Hafed ZM and Clark JJ (2002) Microsaccades as an overt measure of covert attention shifts. *Vision Research* 42 (22), 2533–2545. [PubMed: 12445847]
79. Engbert R and Kliegl R (2003) Microsaccades uncover the orientation of covert attention. *Vision Res* 43 (9), 1035–45. [PubMed: 12676246]
80. Benedetto A and Morrone MC (2017) Saccadic Suppression Is Embedded Within Extended Oscillatory Modulation of Sensitivity. *J Neurosci* 37 (13), 3661–3670. [PubMed: 28270573]
81. Tomassini A et al. (2017) Theta oscillations locked to intended actions rhythmically modulate perception. *Elife* 6.
82. Benedetto A et al. (2016) Rhythmic modulation of visual contrast discrimination triggered by action. *Proc Biol Sci* 283 (1831).
83. Kienitz R et al. (2018) Theta Rhythmic Neuronal Activity and Reaction Times Arising from Cortical Receptive Field Interactions during Distributed Attention. *Curr Biol*
84. Colgin LL (2013) Mechanisms and functions of theta rhythms. *Annu Rev Neurosci* 36, 295–312. [PubMed: 23724998]
85. Jutras MJ et al. (2013) Oscillatory activity in the monkey hippocampus during visual exploration and memory formation. *Proc Natl Acad Sci U S A* 110 (32), 13144–9. [PubMed: 23878251]
86. Bastos AM et al. (2015) Visual Areas Exert Feedforward and Feedback Influences through Distinct Frequency Channels. *Neuron* 85 (2), 390–401. [PubMed: 25556836]
87. Saalmann YB et al. (2007) Neural mechanisms of visual attention: how top-down feedback highlights relevant locations. *Science* 316 (5831), 1612–5. [PubMed: 17569863]
88. Fecteau JH and Munoz DP (2006) Saliency, relevance, and firing: a priority map for target selection. *Trends Cogn Sci* 10 (8), 382–90. [PubMed: 16843702]
89. Wurtz RH and Goldberg ME (1972) Activity of superior colliculus in behaving monkey. 3. Cells discharging before eye movements. *J Neurophysiol* 35 (4), 575–86. [PubMed: 4624741]
90. Wurtz RH and Goldberg ME (1972) Activity of superior colliculus in behaving monkey. IV. Effects of lesions on eye movements. *J Neurophysiol* 35 (4), 587–96. [PubMed: 4624742]
91. Posner MI et al. (1982) Neural systems control of spatial orienting. *Philos Trans R Soc Lond B Biol Sci* 298 (1089), 187–98. [PubMed: 6125970]

92. Posner MI et al. (1985) Inhibition of Return - Neural Basis and Function. *Cognitive Neuropsychology* 2 (3), 211–228.
93. Raymond JE et al. (1992) Temporary suppression of visual processing in an RSVP task: an attentional blink? *J Exp Psychol Hum Percept Perform* 18 (3), 849–60. [PubMed: 1500880]
94. Rollenhagen JE and Olson CR (2005) Low-frequency oscillations arising from competitive interactions between visual stimuli in macaque inferotemporal cortex. *J Neurophysiol* 94 (5), 3368–87. [PubMed: 15928064]
95. Caruso VC et al. (2018) Single neurons may encode simultaneous stimuli by switching between activity patterns. *Nat Commun* 9 (1), 2715. [PubMed: 30006598]
96. Lisman J (2010) Working memory: the importance of theta and gamma oscillations. *Curr Biol* 20 (11), R490–2. [PubMed: 20541499]
97. Lundqvist M et al. (2011) Theta and gamma power increases and alpha/beta power decreases with memory load in an attractor network model. *J Cogn Neurosci* 23 (10), 3008–20. [PubMed: 21452933]
98. Lundqvist M et al. (2016) Gamma and Beta Bursts Underlie Working Memory. *Neuron* 90 (1), 152–164. [PubMed: 26996084]
99. Fries P (2015) Rhythms for Cognition: Communication through Coherence. *Neuron* 88 (1), 220–35. [PubMed: 26447583]
100. Buschman TJ and Miller EK (2007) Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science* 315 (5820), 1860–2. [PubMed: 17395832]
101. Foxe JJ et al. (1998) Parieto-occipital approximately 10 Hz activity reflects anticipatory state of visual attention mechanisms. *Neuroreport* 9 (17), 3929–33. [PubMed: 9875731]
102. Liebe S et al. (2012) Theta coupling between V4 and prefrontal cortex predicts visual short-term memory performance. *Nat Neurosci* 15 (3), 456–62, S1–2. [PubMed: 22286175]
103. Siegel M et al. (2009) Phase-dependent neuronal coding of objects in short-term memory. *Proc Natl Acad Sci U S A* 106 (50), 21341–6. [PubMed: 19926847]
104. Killian NJ et al. (2012) A map of visual space in the primate entorhinal cortex. *Nature* 491 (7426), 761–4. [PubMed: 23103863]
105. Moser EI et al. (2008) Place cells, grid cells, and the brain's spatial representation system. *Annu Rev Neurosci* 31, 69–89. [PubMed: 18284371]
106. Fanselow EE and Nicolelis MA (1999) Behavioral modulation of tactile responses in the rat somatosensory system. *J Neurosci* 19 (17), 7603–16. [PubMed: 10460266]
107. Moldakarimov S et al. (2005) Competitive dynamics in cortical responses to visual stimuli. *J Neurophysiol* 94 (5), 3388–96. [PubMed: 15944239]

Box 1.**Functions of oscillatory synchronization**

Neural oscillations are comprised of rhythmic shifts between high- and low-excitability states, occurring at the level of neural populations. In our account, theta oscillations in the attention network act as a clocking mechanism, temporally isolating the potentially conflicting functions of sampling versus shifting. This role is notably different from that typically attributed to higher-frequency oscillations, such as gamma (35–90 Hz) or beta (15–35 Hz) [4]. For example, the “communication through coherence” theory proposes that the between-region synchronization of neural oscillations, particularly gamma oscillations, works to facilitate interregional communication [99]. That is, the synchronization of presynaptic neurons maximizes their influence on postsynaptic neurons, with a shared, phase-locked gamma rhythm optimally aligning output from presynaptic neurons with the high-excitability state (or phase) of postsynaptic neurons. Such between-region gamma synchronization increases under conditions of spatial attention and is generally thought to enhance sensory processing, by amplifying feedforward sensory signals [56, 59, 60]. In comparison, synchronization in the beta range is thought to amplify feedback signals [86, 100]. For example, an electrophysiological investigation in macaques showed that increased gamma synchronization between FEF and LIP was associated with an attention task that emphasized stimulus-driven (or feedforward) processing, while beta synchronization was associated with an attention task that emphasized goal-directed (or feedback) processing [100].

In addition to proposed roles in organizing and facilitating communication between neural populations, specific oscillatory frequencies have been repeatedly associated with specific functions or brain states. We partly relied on these associations in interpreting the functional roles of the theta-dependent attentional states that promote either sampling or shifting. These attentional states are characterized by nested, higher-frequency oscillations (i.e., alpha, beta, and gamma). Whereas gamma oscillations are associated with enhanced sensory processing, alpha oscillations (9–15 Hz) are associated with attenuated sensory processing [63], reflected in changes to both the timing and the rate of spiking activity [65]. That is, alpha synchronization increases in cortical regions representing, for example, to-be-ignored spatial locations [64] or to-be-ignored sensory modalities [101]. Beta oscillations, on the other hand, are generally associated with the attenuation of motor processing [30, 61, 62]. Beta synchronization in sensorimotor cortex, for example, increases during periods of motor inactivity and decreases during periods of motor preparation [61, 62].

Changes in the brain’s spatiotemporal dynamics can thus provide clues regarding its functional state. The functional significance of specific frequencies is likely linked to the cell types associated with the generation of those frequencies (e.g., excitatory vs. inhibitory and sensory vs. motor). The frequency itself might also contribute to function. For example, spikes occurring at higher frequencies (e.g., gamma) are more likely to be integrated by postsynaptic neurons.

Box 2.**The neural basis of attention-related theta rhythms**

Theta rhythms occur in multiple regions of the primate and rodent brains. In the context of memory [52, 102, 103] and environmental navigation [104, 105], theta rhythms have most frequently been reported in the medial temporal lobe and prefrontal cortex [84]. In the context of environmental sampling, theta rhythms have primarily been reported in sensory cortices [68, 70, 83, 94, 106] and higher-order cortical [3, 4, 50] and subcortical [31] hubs of the attention network. While it has yet to be established whether attention-related theta rhythms in sensory and higher-order brain regions are synchronized during environmental sampling, at least one study—investigating short-term memory—has shown that such functional connectivity in the theta range does occur between frontal and visual cortices [102].

The specific neural circuitry and mechanisms that produce attention-related theta rhythms are largely unknown. There are a few studies, however, indicating that theta rhythms can arise from competition for limited processing resources when the environment includes multiple, behaviorally relevant stimuli [83, 94, 95, 107]. An electrophysiological investigation in macaques, for example, investigated whether theta-rhythmic spiking activity among neurons in inferotemporal cortex might depend on competitive interactions between neurons selective for different stimuli [94]. The study employed two stimuli: one displayed at central fixation and a second displayed in the periphery (i.e., a flanker). When displayed alone, only the stimulus presented at central fixation elicited an excitatory neuronal response. When displaying the stimulus at central fixation in the presence of the flanker, there was a stronger oscillatory component in the neuronal response. This oscillatory activity, occurring when both stimuli were displayed, seemed to be dependent on attention being allocated to the flanker. Associated modeling work proposed that theta rhythms associated with such competitive interactions might arise from (i) the strength of inhibition between competing neuronal pools and (ii) neuronal fatigue [107].

A couple of recent papers have now reported similar findings in visual area V4 [83] and the inferior colliculus [95], suggesting that competitive interactions might induce low-frequency neural oscillations. It has yet to be demonstrated, however, that competition-driven theta rhythms occur in the attention network. It is noteworthy that studies investigating theta-rhythmic sampling have typically employed experimental tasks with multiple target locations [2, 39, 40], which promotes competitive interactions. Competition among different locations (and/or stimuli) in the environment might therefore be a prerequisite for theta-rhythmic sampling, or at least strengthen neural oscillations associated with theta-rhythmic sampling. Future studies need to examine the extent to which attention-related sampling stems from a competition among multiple behaviorally relevant stimuli, and whether the number of stimuli, for example, influences the sampling frequency (see Outstanding Questions).

Outstanding Questions:

Are there additional behavioral consequences of theta-rhythmic sampling? We have established that theta rhythms during attentional deployment are associated with fluctuations in perceptual sensitivity and therefore signal detection. Our theory further predicts theta-dependent fluctuations in the likelihood of attentional shifts, with a greater likelihood (and/or faster attentional shifts) specifically occurring during the theta phase associated with diminished perceptual sensitivity.

Do theta rhythms associated with preferential sensory processing and exploratory eye movements share the same neural basis? Whereas attention-related boosts in sensory processing have been linked to theta rhythms in the attention network, studies linking exploratory eye movements to theta rhythms have mostly recorded from sensory cortex. Future studies need to determine (i) whether exploratory eye movements are also linked to theta rhythms in the attention network, and (ii) whether there is a functional link between theta rhythms in the attention network and theta rhythms in sensory cortex.

Does the attention network alternately increase its engagement with either sensory or motor regions during theta-rhythmic sampling? We have provided evidence that theta rhythms in the attention network organize neural activity into alternating attentional states, which are associated with either sampling at the presently attended location or shifting to another location. Future studies need to examine whether these alternating attentional states are characterized by a rhythmic re-weighting of functional connections between the fronto-parietal attention network and brain regions that are typically associated with either sampling (e.g., visual cortex) or shifting (e.g., the superior colliculus).

Is the specific frequency of rhythmic sampling flexible? For example, the frequency might change based on the number of behaviorally relevant locations (or objects). Alternatively, the frequency could be fixed; with half a cycle of theta being approximately the time it takes for the visual system to process a complex natural scene.

Highlights

- Spatial attention and saccadic eye movements are typically coupled but can be uncoupled.
- Spatial attention samples the environment in theta-rhythmic cycles, leading to alternating periods of either enhanced or diminished perceptual sensitivity. The likelihood of saccades similarly fluctuates at a theta rhythm.
- Rhythmic attentional sampling is linked to theta-band activity in the large-scale network that directs both spatial attention and saccades.
- Theta rhythms organize neural activity into alternating attentional states associated with either sampling at a behaviorally relevant location or shifting to another location.
- Theta rhythms might resolve temporal conflicts between processes that promote either sampling (sensory function) or shifting (motor function), by periodically altering functional connectivity between higher-order brain regions and sensory or motor regions.

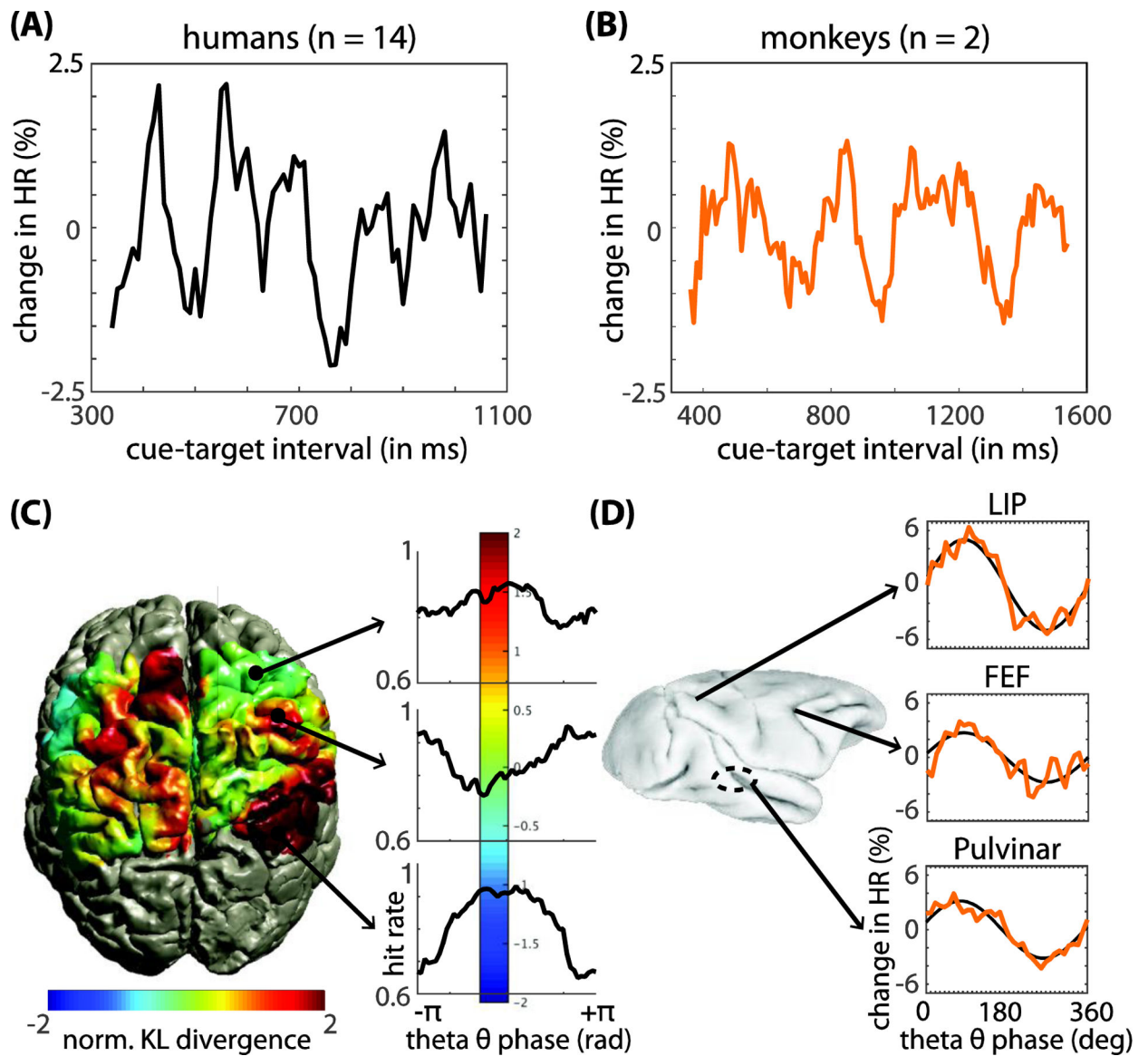


Figure 1. Attention-related theta rhythms shape behavioral performance.

(A, B) Behavioral performance (i.e., change in hit rate) as a function of time from the cue (i.e., at different cue-target intervals), for (A) humans (adapted from Fiebelkorn, Saalman and Kastner [2]) and (B) monkeys (adapted from Fiebelkorn, Pinsk and Kastner [4]). For both species, behavioral performance under conditions of spatial attention is associated with significant theta rhythmicity. (C, D) Behavioral performance was linked to neural oscillations and is plotted as a function of theta phase, for humans (adapted from Helfrich, Fiebelkorn, Szczepanski, Lin, Parvizi, Knight and Kastner [3]) and monkeys (adapted from Fiebelkorn, Pinsk and Kastner [4] and Fiebelkorn, Pinsk and Kastner [31]). Theta rhythms in hubs of the network that directs both spatial attention and saccadic eye movements seem to shape attentional sampling.

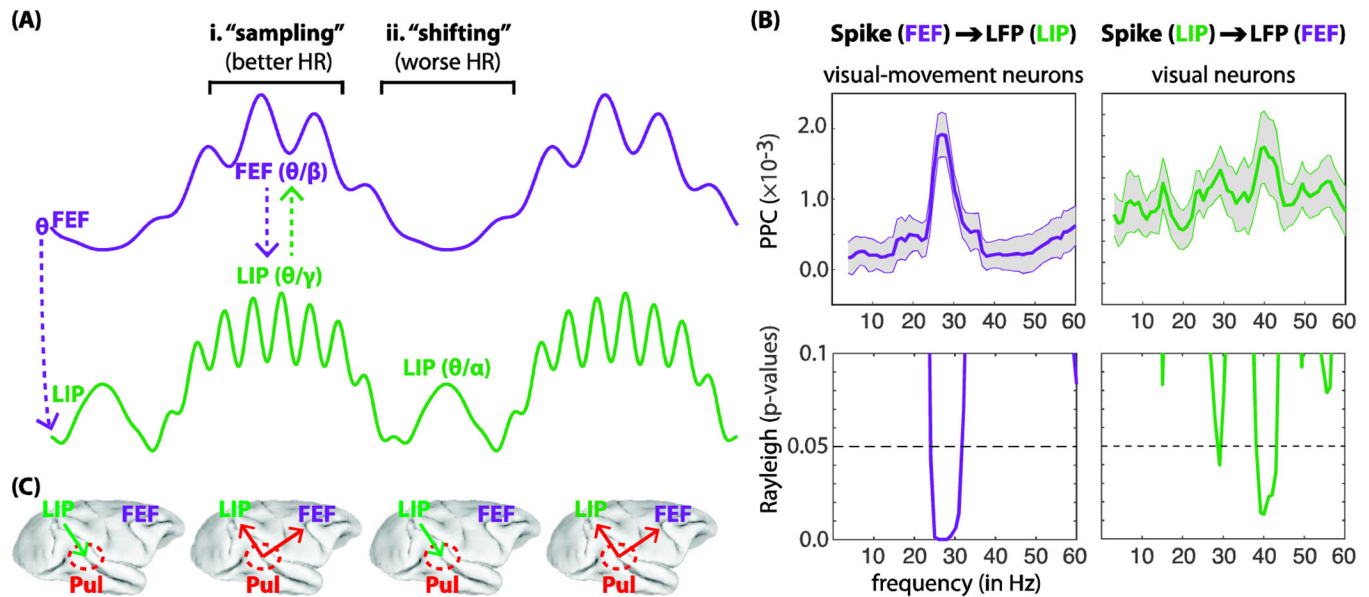
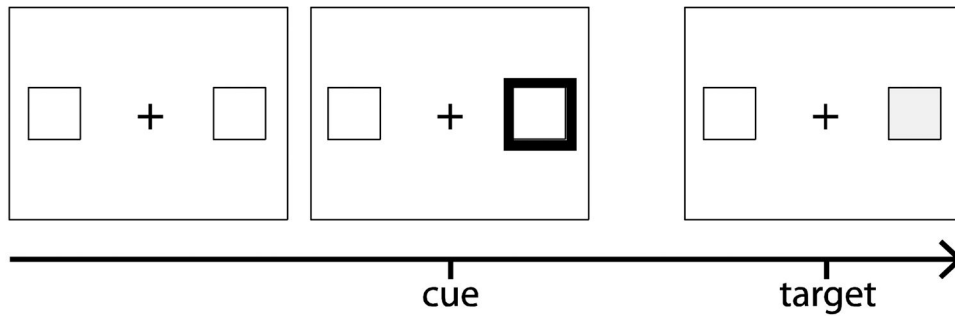
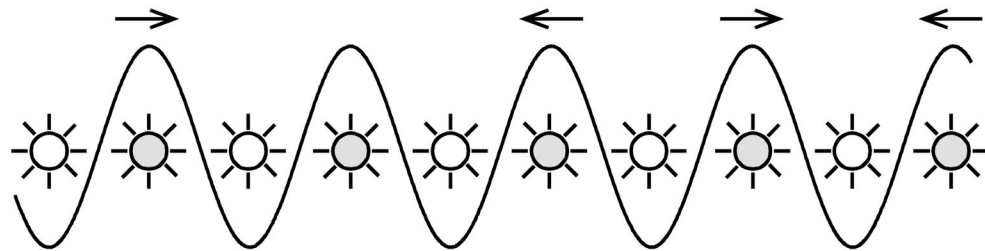
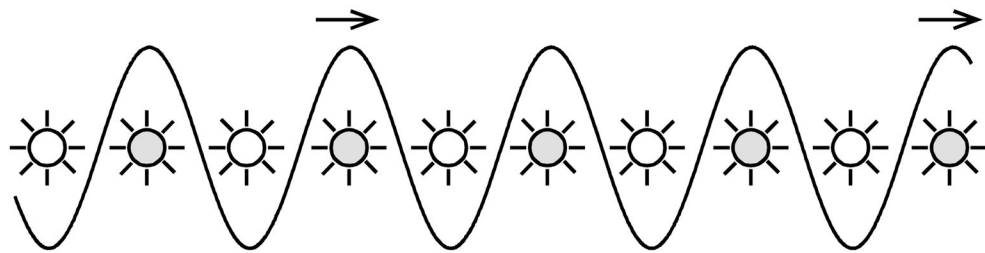


Figure 2. Theta rhythms organize two rhythmically alternating attentional states.

These attentional states are characterized by changes in oscillatory activity across multiple, functionally defined frequency bands and cell types. **(A)** The first state (i.e., “sampling”) is characterized by (i) increased beta-band activity from FEF, associated with the suppression of attentional shifts (and/or eye movements) and (ii) increased gamma-band activity from LIP, associated with the enhancement of sensory processing and therefore better signal detection at a behaviorally relevant location. The second state (i.e., shifting) is characterized by an increase in alpha-band activity in LIP, associated with attenuated visual processing, perhaps in anticipation of a potential attentional shift (either covert or overt) to another location. The arrows, indicating directionality, are based on interpretations of spike-LFP phase coupling and Granger causality. **(B)** Oscillatory frequency bands are further linked to specific cell types. Spiking activity from visual-movement neurons (i.e., from neurons with both a visual and a motor response) in FEF, for example, is coupled to beta-band activity in LIP, while spiking activity from visual neurons in LIP (i.e., from neurons with only a visual response) is coupled to gamma-band activity in FEF. **(C)** Theta-rhythmic sampling is also associated with a rhythmic re-weighting of functional connectivity between higher-order cortical regions and the mediodorsal pulvinar (Pul), with that connectivity specifically occurring in the alpha/low-beta range (10–20 Hz) (9). LIP specifically coordinates Pul activity during the attentional state associated worse visual-target detection (i.e., shifting), while Pul specifically coordinates cortical activity during the attentional state associated with better visual-target detection (i.e., sampling). Adapted from Fiebelkorn, Pinsk and Kastner [4] and Fiebelkorn, Pinsk and Kastner [31].

(A) covert attention task**(B) non-informative spatial cue (i.e., 50% cue validity)****(C) informative spatial cue (i.e., 80% cue validity)**

☀ enhanced perceptual sensitivity

→ microsaccade toward right stimulus location

⬛ diminished perceptual sensitivity

← microsaccade toward left stimulus location

Figure 3. A rhythmic theory of attention: sampling versus shifting.

In our account, environmental sampling is characterized by alternating attentional states that promote either sampling at the presently attended location or shifting to another location.

(A) An example of a standard covert attention task. Participants are asked to maintain central fixation, while monitoring two target locations. Spatial attention is deployed during a variable cue-target interval. **(B)** When the cue is non-informative (i.e., the subsequent target is equally likely to occur at either location), there are alternating periods of either enhanced or diminished perceptual sensitivity at the cued location. Periods of diminished perceptual

sensitivity are associated with a greater likelihood of covert or overt attentional shifts. Here, microsaccades are equally likely to occur toward or away from the cued location. (C) When the cue is spatially informative (i.e., it indicates where the visual-target is most likely to occur), microsaccades still occur during periods of diminished perceptual sensitivity at the cued location. However, microsaccades are now more likely to occur toward the cued location, indicative of the cued location being selected for another round of sampling. Even sustained attention is thus discontinuous, characterized by interdigitated periods of diminished perceptual sensitivity, when the presently attended location is re-selected based on stimulus properties and behavioral goals.