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Attention Cycles

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Current evidence challenges the traditional view of attention as a continuously active spotlight, suggesting instead a rhythmic operation at around 4–8 Hz. New intracranial recordings in monkeys and humans, including two papers in this issue of *Neuron*, by Helfrich et al. (2018) and Fiebelkorn et al. (2018), now validate this alternative notion and characterize its oscillatory neural bases.

Even when our eyes are still, our brains covertly explore the visual world, a process called visual attention. Attention is under voluntary control—though it may also be disrupted by salient events. Traditionally, sustained attention monitoring has been assumed to operate continuously over time: once attention is deployed at a cued location, it remains constant for as long as necessary. However, constancy is a difficult state to achieve in the brain, whose activity waxes and wanes rapidly under the effect of rhythmic oscillations spanning a wide range of frequencies. This is especially true of attention, which has been linked to various types of rhythmic neural activity. Therefore, an alternative view has emerged, in which attention—even in its sustained mode—dynamically fluctuates along with the underlying brain rhythms (Lakatos et al., 2008; VanRullen, 2013). Accordingly, a growing number of recent studies have revealed systematic periodicities in attention, peaking around the theta (4–8 Hz) frequency band (see VanRullen, 2016, for a recent review). Most of this ev-

idence, however, involved behavioral measurements or surface brain recordings (EEG or MEG), while the detailed neural underpinnings of rhythmic attention remained unknown and the topic controversial (VanRullen, 2016)...until now. In one fell swoop, a stream of new human (Helfrich et al., 2018) and monkey intracranial recording studies (Fiebelkorn et al., 2018; Kienitz et al., 2018; Spyropoulos et al., 2018) put the last nail(s) in the coffin of “sustained attention.” All studies present compelling evidence for theta-rhythmic fluctuations of attention that are not directly linked to overt eye movement behavior, saccades, or micro-saccades. Two of these studies are available in this issue of *Neuron* (Fiebelkorn et al., 2018; Helfrich et al., 2018), and their findings are summarized in Figure 1.

Fiebelkorn and colleagues recorded local field potentials (LFPs) from two key regions of the fronto-parietal network, FEF and LIP, while two monkeys performed an object attention task. On each trial, a cue marked the location of the upcoming target—a faint square. The mon-

keys’ ability to detect this target fluctuated rhythmically as a function of the time interval between cue and target, with a spectral maximum around 4 Hz. This theta-rhythmic behavior in monkeys mirrors that previously described for human subjects performing the same task (Fiebelkorn et al., 2013). In addition, it indicates a potentially rhythmic neural basis: as expected, in both FEF and LIP the 4–5 Hz LFP phase (as measured immediately before target onset) was predictive of target detection accuracy. This prompted the authors to define a “good” and a “poor” theta phase, and then to separately investigate behavior and brain responses for these two groups of trials. They observed that when the target occurred during the “good” theta phase in FEF, detection accuracy was also periodically modulated by beta-band oscillations (around 20 Hz); at the “good” theta phase in LIP, a similar periodic modulation of behavior encompassed beta- as well as gamma-band oscillations (30–40 Hz). In contrast, when the target appeared at the “poor” theta phase,



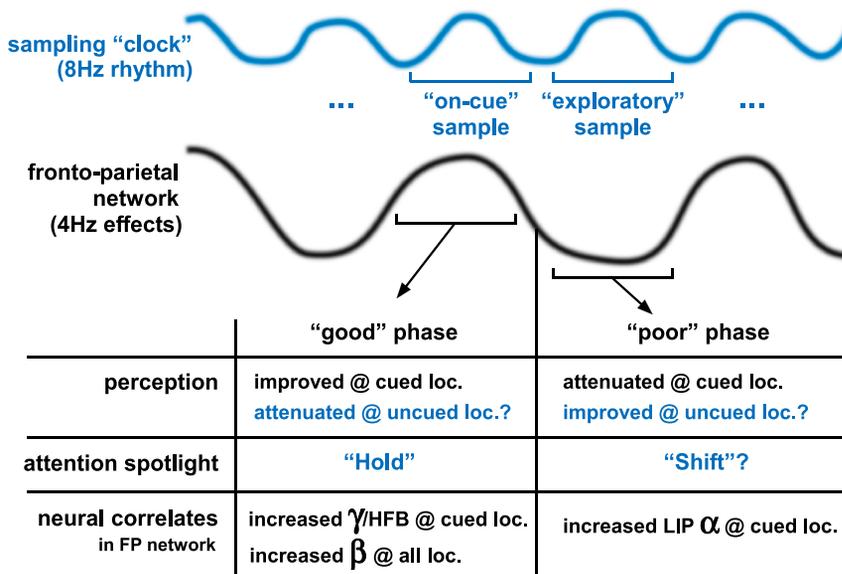


Figure 1. Summary Illustration

Findings directly drawn from [Fiebelkorn et al. \(2018\)](#) and [Helfrich et al. \(2018\)](#) are shown in black and additional speculations (discussed, but not directly tested in those studies) in blue. The exact brain network(s) responsible for the tentative 8 Hz sampling rhythm remain(s) an open question.

only alpha-band (10–15 Hz) LIP oscillations influenced behavioral performance. These results were corroborated by phase-amplitude coupling (PAC) analyses, which revealed that theta phase in both LIP and FEF modulated the oscillatory amplitude of other frequency bands across both regions. LIP and FEF theta phase were most strongly associated with gamma- and beta-band amplitudes, respectively. There was also a theta-phase dependence of alpha amplitude, specific to LIP. The broad theta-gamma and the LIP-specific theta-alpha PAC were strongest when the neural receptive fields overlapped the cued location, indicating an involvement in selective attentional processing. In contrast, the beta-band modulation occurred consistently at both cued and uncued locations. Since beta-band synchronization—often associated with sensorimotor suppression—was restricted to a population of so-called FEF “visual-movement” neurons typically involved in saccadic and attention shifts, Fiebelkorn and colleagues interpreted these beta-band fluctuations as a periodic “holding” of attention during the “good” theta phase, followed by a “release” at the “poor” theta phase, and thus an opportunity to shift attention to a new location. It is noteworthy that beta-band periodicity of visual attention

had been previously reported in monkey FEF recordings ([Buschman and Miller, 2009](#)). However, the theta-rhythmicity of attention described by [Fiebelkorn et al. \(2018\)](#), its interactions with other frequencies, and its correspondence with both monkey and human behavioral dynamics constitute an important breakthrough.

Helfrich and colleagues also contribute to this discovery. They employed a similar approach, but in human epileptic patients undergoing pre-surgical monitoring. Intracranial electrodes were inserted to record electro-corticography (ECoG, a brain signal comparable to LFPs; all recordings were made from brain tissue not affected by epilepsy). Some of their subjects ($n = 7$) performed the same object-attention task as in [Fiebelkorn et al. \(2018\)](#), where the detection of a faint target was the dependent behavioral variable. Another subject group ($n = 8$) performed a different attention task, with a high-contrast target appearing in the cued visual field (on most trials) and reaction time serving as the behavioral measure. For both tasks, the authors reported rapid behavioral fluctuations as a function of the cue-target interval, peaking on average around 4 Hz. Theta phase at target onset (4 Hz) was predictive of behavior (accuracy or reaction time) in a

number of channels covering the fronto-parietal network. This phase-detection relationship was stronger for electrodes responding to the cued location than those at the uncued location. Finally, Helfrich and colleagues measured high-frequency band brain signals (HFB, 70–150 Hz), meant to reflect the underlying spiking activity. Again, HFB signals were modulated at 4 Hz, and this modulation was stronger at the cued location. In summary, “sustained” monitoring actually involved rhythmic fluctuations of attention around 4 Hz. These fluctuations reflected spatially localized theta-band oscillations of the fronto-parietal network, and the concurrent modulation of neural excitability, as indexed by HFB. Importantly, Helfrich and colleagues observed compatible effects in two different attention tasks, and with two different behavioral variables (accuracy and reaction time), thereby confirming and extending the monkey results of [Fiebelkorn et al. \(2018\)](#).

Both of the above studies characterized the neural bases of theta-rhythmic attention in regions of the fronto-parietal network, responsible for the control and deployment of visual attention. It is natural to ask whether these theta-rhythmic fluctuations also percolate sensory regions of the visual system and what their neural signatures might be. Luckily, two other novel studies directly addressed these questions in monkeys.

[Kienitz et al. \(2018\)](#) recorded from area V4 during a divided attention task. Two competing stimuli were presented, one inside a neuron’s receptive field and one in its immediate suppressive surround. The antagonistic center-surround receptive field organization resulted in a clear 4 Hz modulation of firing rates, with each stimulus dominating responses at a separate theta phase. Behavioral response times to a flashed target also oscillated at 4 Hz, with an out-of-phase pattern depending on which of the competing stimuli the target had been flashed on. In other words, divided attention appeared to be resolved by alternating samples from the two competing objects, at an effective rate of 8 samples per second (i.e., two samples in each 4 Hz cycle).

In [Spyropoulos et al. \(2018\)](#), synchronized theta-band LFP oscillations were found in visually driven parts of primary visual cortex V1 and area V4. The theta

rhythm modulated gamma-band responses, a marker of visual processing, thus creating a succession of “good” and “poor” theta phases. Surprisingly, these fluctuations were much more prominent at the location of an uncued stimulus than in the very focus of attention. While this seems to contradict both the notion of rhythmic attention and much of the previously mentioned findings, one could tentatively interpret this situation as a form of divided attention where, despite the cue and instructions, some amount of attention would be (voluntarily or not) allocated to the uncued stimulus. This would result in alternating “on-cue” attention samples and “exploratory” samples (Figure 1, top). In this explanation, it remains mysterious why the theta modulation should be weaker at the cued site, under the focus of attention; speculatively, this could be attributed to a saturation of visual sensitivity and/or neural responses, whereby a further gain increase under the effect of attention would only result in minimal improvements. Regardless, the notion of alternating “on-cue” and “exploratory” samples, each location rhythmically modulated at opposite phases of a 4 Hz cycle, fits well with the divided attention findings by Kienitz et al. and suggests that the effective sampling rate of attention could be as high as 8 Hz (VanRullen, 2013, 2016). The origin of the postulated 8 Hz attention “sampling

clock” remains unknown: it could be produced directly in the visual system (e.g., by center-surround competitive interactions, as suggested by Kienitz et al.) or originate in attention control regions not investigated in the present studies, either within the fronto-parietal attention network or in other potentially subcortical regions such as the pulvinar.

The growing evidence for theta-rhythmic attention switching between competing visual representations begs the question of whether similar rhythmic dynamics could apply in other contexts. For instance, in the rodent medial temporal lobe, theta rhythms support spatial navigation and the localization of the animal in its environment. Competing signals encoding a rat’s head direction, for example, have been recorded on alternate cycles of the 8 Hz theta rhythm, each signal thus dominating the spatial representation in anti-phase at 4 Hz—a phenomenon called “theta-skipping” (Brandon et al., 2013). The temporal segregation or “multiplexing” of simultaneous neural representations across sequential theta cycles could turn out to be a brain-wide strategy for the management of cognitive resources.

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