

The rhythmic nature of visual perception

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Helfrich RF. The rhythmic nature of visual perception. *J Neurophysiol* 119: 1251–1253, 2018. First published December 20, 2017; doi:10.1152/jn.00810.2017.—Our continuous perception of the world could be the result of discrete sampling, where individual snapshots are seamlessly fused into a coherent stream. It has been argued that endogenous oscillatory brain activity could provide the functional substrate of cortical rhythmic sampling. A new study demonstrates that cortical rhythmic sampling is tightly linked to the oculomotor system, thus providing a novel perspective on the neural network underlying top-down guided visual perception.

neuronal oscillations; perceptual cycles; psychophysics

NEURONAL OSCILLATIONS AND HUMAN BEHAVIOR

For decades, it has been debated whether perception is continuous or discrete. One possibility is that our continuous experience of the world is the result of rapid, sequential sampling of the environment. Given that neuronal oscillations are ubiquitous in electrophysiological neural recordings and are thought to support sensory and cognitive processing (Helfrich and Knight 2016; Siegel et al. 2012), it has been hypothesized that endogenous neuronal oscillations could facilitate the periodic sampling of the environment, thus rendering perception discrete (for review see VanRullen 2016).

While numerous studies investigated the behavioral relevance of neuronal oscillations over the last three decades (for review see Siegel et al. 2012), a major shortcoming of many studies is that behavioral relevance was often only inferred from binary contrasts (e.g., correct vs. incorrect). Hence, it remained unclear how behavioral performance changes over time and how periodicities in behavior relate to endogenous ongoing oscillatory brain activity.

Recently, several groups began to investigate whether fluctuations in behavioral performance exhibit intrinsic oscillatory profiles when probed on a fine-grained temporal scale (for review see VanRullen 2016). Their results suggest that behavioral periodicities could potentially reflect oscillatory brain activity at the population level (Helfrich and Knight 2016; VanRullen 2016).

However, one potential confound is that rhythmic sampling and slow modulations of cortical excitability, especially in the visual cortex, could simply reflect eye movement artifacts. For

example, gamma-band activity (>40 Hz) is a proxy of cortical excitability that varies at a 3- to 4-Hz rhythm, which in turn is tightly linked to microsaccades (Lowet et al. 2016). Thus, it remains unclear whether the observed rhythmic patterns in behavior are directly linked to a cortical process or whether they simply reflect the quasi-periodic input induced by small eye movements during active exploration of the visual environment (Deouell 2016).

Interestingly, it has also been observed that microsaccades preferentially occur in the direction of behaviorally relevant objects and cues (Deouell 2016; Hafed et al. 2009; Lowet et al. 2016). This finding raises the question how the brain knows where to saccade to next if this object has not yet been overtly sampled. One hypothesis is that presaccadic covert rhythmic sampling could reflect a cortical mechanism of active exploration to inform subsequent overt behavior.

VISUAL PERCEPTION IS SAMPLED AT AN ALPHA RHYTHM

In a new study published in the *Journal of Neurophysiology*, Bellet et al. (2017) report data from three experiments, involving both humans and nonhuman primates, that collectively suggest that endogenous rhythmic sampling of the visual environment is not an artifact of microsaccadic eye movements. In contrast, they provide compelling evidence that microsaccades actually phase-reset endogenous oscillatory activity in the alpha/beta range (8–20 Hz).

Previous studies have demonstrated that visual perception cycles as a function of the posterior alpha phase (for review see VanRullen 2016). The majority of the studies used a high contrast cue to phase reset ongoing activity and then assessed behavior as a function of varying cue-target-intervals to reveal oscillatory dependent patterns in behavior (Fiebelkorn et al. 2013; Helfrich et al. 2017).

Nevertheless, several studies also failed to observe periodic patterns in behavioral time courses (for review see VanRullen 2016). In the present study, the authors also did not observe rhythmic fluctuations in behavior as a function of the cue-target interval. However, taking advantage of simultaneous eye tracking, they found that these perceptual cycles varied as a function of the microsaccade-target-interval with a peak frequency in the alpha/low-beta range (8–20 Hz). In particular, they observed that the microsaccade offset phase-aligned behavioral alpha oscillations across trials and across participants. Importantly, Bellet et al. (2017) only utilized trials where the microsaccade was not followed by a subsequent microsaccade, thereby ruling out the possibility that rhythmic fluctuations

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reflect periodic eye movements. This observation helps to reconcile previous unsuccessful attempts to demonstrate oscillatory patterns in behavior.

Importantly, the authors observed behavioral oscillations in two independent experiments assessing different behavioral outcome measures. In *experiment 1*, they demonstrated that reaction times fluctuated as a function of the microsaccade-target interval, and similar patterns were observed for time-resolved hit rates in a target detection task in *experiment 2*. They also provided data from nonhuman primate recordings demonstrating that 1) similar behavioral effects can be observed in monkeys and that 2) these behavioral effects might be a direct consequence of neural fluctuations at the level of the superior colliculus (SC). These results replicate and extend previous findings that the visual environment is sampled at the rate of endogenous alpha activity in states of controlled or constrained fixation.

RHYTHMIC PULSING OF ALPHA OSCILLATIONS MEDIATES TOP-DOWN CONTROL

Another intriguing observation was that rhythmic perceptual sampling was not evenly distributed across space but alternated between attended and unattended locations. In particular, the rhythmic sampling of the two spatial locations switched after ~300–400 ms, as indexed by a modulation of the instantaneous alpha amplitude. Bellet et al. (2017) refer to this comodulation as “rhythmic pulsing” across the two hemifields, which occurred at a slower 2- to 4-Hz rhythm and nicely parallels the findings of two recent EEG studies that suggested this low-frequency modulation might reflect long-range top-down control. The first study showed that visual attention is characterized by prominent alpha-band activity and that the instantaneous alpha power alternates between attended and unattended objects in anti-phase at a delta rhythm (<5 Hz; Jia et al. 2017). This observation suggests that attentional sampling of different spatial locations does not occur in parallel but instead occurs sequentially and is mediated via a modulation of the instantaneous alpha power (Jia et al. 2017). Importantly, these slow modulations of the alpha amplitude can also be observed when fixation is constrained to a single location and the spatial cue is replaced by an abstract contextual cue (Helfrich et al. 2017). Collectively, these findings indicate that top-down guided visual perception cycles as a function of multiple endogenous oscillations. While alpha oscillations may support rhythmic sampling within the visual system, delta- and theta-band oscillations (2–5 Hz) could reflect rhythmic top-down control, possibly emerging from the prefrontal cortex (PFC), and may determine the intrinsic timescale of cognition.

SPECTRAL ANALYSES OF BEHAVIORAL DATA

Discrete time series analysis of behavioral data has gained popularity in recent years. However, most available methods, such as wavelets, band-pass filtering, or the fast Fourier transformation, will force the signal into a sinusoidal shape, even though this might not appropriately capture nonsinusoidal time series features, such as sharp transients as often observed in beta oscillations (Zoefel and Sokoliuk 2014). While there is no consensus on how to implement spectral analyses on behavioral data, researchers do have multiple degrees of freedom when using these methods. For example, in the present study,

several data analysis parameters could have potentially affected the results. Even though unlikely, it is conceivable that high-pass filtering the data at 2 Hz is related to the observed rhythmic pulsing at ~2 Hz. Likewise, the authors observed a shift toward higher frequencies at the edges of the spectrograms, which is reminiscent of sharp edge artifacts (Helfrich and Knight 2016; Zoefel and Sokoliuk 2014). In addition, the increased phase consistency across subjects may be due to the increased power during that period, which provides a better signal-to-noise and resultant better phase estimates. Finally, the authors utilized randomly shuffled data to create surrogate time courses to establish statistical significance. While this is statistically sound, another option would have been to test microsaccadic-locked against cue-locked behavioral time courses to replicate and extend previous findings (VanRullen 2016). Critically, three independent studies utilizing variants of a cue-guided target detection task [varying the cue-target-interval (Helfrich et al. 2017), assessing the microsaccade-target-interval (Bellet et al. 2017), or using time-response functions (Jia et al. 2017)] all converged on two major findings: 1) evidence for rhythmic sampling at the alpha frequency and 2) a delta/theta comodulation (2–5 Hz) of the alpha envelope, reflecting top-down guided cues.

THE FUNCTIONAL ARCHITECTURE OF COGNITION IS RHYTHMIC

Taken together, the present study by Bellet et al. (2017) as well as two recently published studies (Helfrich et al. 2017; Jia et al. 2017) demonstrate that perception and cognition exhibit intrinsic temporal profiles, which are shaped by neural activity at the population level and do not constitute an eye movement artifact or an artifact due to sensory stimulation at the endogenous frequency (VanRullen 2016). In particular, the data by Bellet et al. (2017) clearly reveals a tight temporal interplay between rhythmic sampling and eye movements, where neuronal correlates of the rhythmic sampling could be detected even in the SC. These findings bring into question how the SC, visual cortex, and prefrontal areas precisely interact to support top-down guided visual perception.

While not explicitly tested in this paper, Bellet et al. speculated that “microsaccades ride on slow frequency rhythms,” which raises the important question of how cortical rhythms and oculomotor activity are coupled and interact (Deouell 2016). One testable hypothesis in primate models is whether PFC-dependent top-down signals modulate SC activity, which in turn resets rhythmic sampling in visual cortex. Hence, rhythmic sampling might inform the oculomotor system where to saccade to next, which might imply feedback connections within a large-scale network, including cortical (V1, posterior parietal, and frontal eye fields) as well as subcortical structures (SC, lateral geniculate nucleus, and visual thalamus, i.e., the Pulvinar). While the anatomical underpinnings and feedback connections are reasonably well understood, to date is unclear whether and how neuronal oscillations support feedback signaling in this network. This large-scale network hypothesis is also in line with the finding that fixation is better after a microsaccade than before (Bellet et al. 2017), which could imply that cortical association areas (e.g., the PFC) trigger microsaccades when the sensory input is suboptimal or deviations from fixation are detected.

Although the structural anatomy of this network is reasonably well understood, very little is known about their functional interactions and whether oscillations reflect a mechanism that precisely times information transfer in this system (Stitt et al. 2015). Thus, as noted by Bellet et al. (2017), it is remarkable that coherent effects, i.e., phase-aligned behavioral oscillations on a timescale of a few hundred milliseconds, emerge from the whole brain-processing cascade. These findings strongly support the notion that the functional brain architecture underlying these operations is rhythmic.

Other important future directions can focus on how and at which stage the brain fuses discrete snapshots into a coherent stream that constitutes our experience of the world (VanRullen 2016). While most of the research in this domain is cortico-centric, the study by Bellet et al. (2017) underscores the importance of cortical-subcortical networks interactions. Thus, understanding top-down guided cognitive processing will ultimately also require a better understanding of cortical-subcortical networks (Stitt et al. 2015). In addition, the approach by Bellet et al. exemplifies how the study of eye movement provides important insights into perception, action, and cognition.

Several additional key questions remain. For instance, how and why are covert and overt processes mutually dependent? Does covert rhythmic sampling guide overt behavior (Hafed et al. 2009)? Furthermore, do these mechanisms generalize to other sensory modalities, such as auditory or somatosensory domains (VanRullen 2016)?

In conclusion, an important implication of these findings is that behavior varies as a function of neural activity generated at the population level and not at the level of individual neurons. Hence, these findings support the notion that the units of cognition are neuronal cell assemblies and not the single neurons (Helfrich and Knight 2016; Siegel et al. 2012; VanRullen 2016). Taken together, these lines of research converge on the notion that the functional architecture of cognition is inherently rhythmic and neuronal activity at the population level determines the timescale of top-down guided visual perception.

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DISCLOSURES

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AUTHOR CONTRIBUTIONS

R.F.H. conceived and designed research, drafted manuscript, edited and revised manuscript, and approved final version of manuscript.

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