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DOI:
10.1016/j.neuron.2023.04.027

Neuron

Previews

Prefrontal cortex oscillations update and stabilize consciousness during binocular rivalry

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https://doi.org/10.1016/j.neuron.2023.04.027

In this issue of *Neuron*, Dwarakanath et al.[1] demonstrate that perceptual changes in binocular rivalry are predicted by low-frequency activity and beta-band oscillations in the prefrontal cortex, speaking to access consciousness being gated by oscillatory neuronal dynamics in the prefrontal cortex.

In real life settings, our senses are bombarded with a wealth of input; however, we are only consciously aware of a small fraction of what happens in our surroundings. Nevertheless, it is exactly this consciousness that determines how we perceive, interpret, and feel the world. Although it is commonly accepted that conscious awareness forms the basis for phenomenological experience, the neuronal correlates of consciousness are still debated.[2] The global neuronal workspace (GNW) theory has proposed the notion of "ignition," in which a given percept emerges because of a broadcast across the brain initiated in fronto-parietal areas.[3] However, many questions remain open on the neuronal implementation of the ignition in terms of both the neuronal network involved and the specific neurophysiological mechanisms. In natural settings, multiple visual objects are typically competing for awareness. At the network level, it is an open question whether this competition is primarily bottom up (i.e., due to the visual input competing at the sensory level after which a winner forming the dominant percept is broadcasted by parieto-frontal neurons). Alternatively, high-order areas, like the prefrontal cortex (PFC), might select between competing objects and then broadcast the winner by boosting the representations in sensory regions. A second major question pertains to the neuronal dynamics supporting the formation of the conscious percepts. Ignition undoubtedly requires a temporal organization of neuronal firing both within the PFC and across other brain regions. A prevalent idea is that neuronal oscillations can support such temporal coordination by synchronizing the activity of neuronal ensembles.[4]

The study by Dwarakanath et al.[1] investigates these questions, relying on multielectrode intracranial recordings in the PFC of non-human primates (NHPs). To this end, they employed a binocular rivalry (BR) paradigm. BR refers to the phenomenon where, when two different objects are presented to, respectively, the left and right eye, the percept switches back and forth between the two objects. This paradigm has been used for decades to study visual awareness and consciousness because it is able to produce changes in the visual percept, albeit the visual input remains unaltered. Micro-electrodes arrays (10 × 10 electrodes) were implanted in the inferior convexity of the lateral PFC of two rhesus macaques, allowing quantification of both the neuronal firing and local field potentials while the monkeys were engaged in the task. The BR paradigm employed visual gratings presented to the left and right eye while they moved in different vertical directions. The percept of the NHPs was inferred from the optokinetic nystagmus (OKN) associated with the up- or down-moving gratings recorded with an eye tracker. The OKN reflects the subtle tracking and reset of the eyes following one of the two moving directions. This is an elegant design as it does not require the NHPs to respond, thus ruling out potential explanations in terms of post-perceptual processing linked to reporting the conscious percept. Additionally, control conditions were performed in which the moving gratings were presented to either the left or the right eye. This was done to compare the spontaneous switching of BR with a forced physical alternation.

The key finding was that changes in percept were predicted by an increase in the power of low-frequency (LF) modulations (1–9 Hz), as well as by a decrease in beta-band power (20–40 Hz). While the LF modulation indicated a spontaneous switch of conscious content, the beta-band activity was associated with perceptual stability and decreased during perceptual switches. Importantly, the LF modulation co-occurred with negative field changes interpreted as cortical down states. This suggests that perceptual changes are more likely during spontaneous down states compared with up states when the percept is more stable. Furthermore, it was possible to decode which percept the NHPs maintained (in relation to the OKN patterns) from the spiking activity, but not from the LF or the beta-band activity.

These findings speak to a mechanism by which fluctuation of LF activity in the PFC gates conscious awareness during BR. These changes occur during down states and are associated with a decrease in beta-band activity. Although these signals are content agnostic, they can modulate perceptually related neuronal spiking. In particular, the spiking associated with the percept is locked to the phase of beta-band oscillations in the PFC, reflecting perceptually stable periods.

These exciting results provide important insight into the neuronal mechanisms associated with the formation of visual percepts and therefore awareness. In particular, they speak to a top-down-driven process in which changes in percepts originate in the PFC. This conclusion is in contrast to a mechanism in which gating to consciousness is the consequence of a bottom-up "winner-take-all" competition between monocular neurons in primary visual cortex, as was originally believed.[5] These switches are akin to the ignition mechanism proposed by GNW, in which emerging visual percepts are broadcasted within the brain.

Overall, these findings are aligned with GNW, which proposes that the PFC plays a key role in gating access to consciousness. However, other theories of consciousness, such as integrated information theory (IIT), place more emphasis on posterior brain regions. According to IIT, consciousness is determined by the cause-effect structure in the temporo-parietal-occipital "hot zone".[6] While evidence for a specific mechanism in primary visual cortex seems limited, other areas within the posterior hot zone may play a crucial role in resolving the competition during BR. In fact, it has been shown that the activity associated with a specific percept increases along the visual processing hierarchy.[7] Furthermore, in the context of IIT, activity in the PFC is thought to reflect the cognitive processes required to report the consciousness content. However, the BR paradigm used in the study did not require explicit reporting of the percept, as this was inferred from the NHPs' involuntary OKN, thus strengthening the evidence for a possible causal role of the PFC in conscious perception.

The novel insight on the role of the PFC in BR provided by Dwarakanath et al. forms the basis for a set of new investigations. As the PFC appears to drive changes in visual percept, it further begs the question of what prompts the PFC to update the gating. The authors point to a gating-like mechanism where intrinsically generated fluctuations in the PFC gate the access of competing perceptual representations to consciousness. However, are these intrinsic fluctuations purely stochastic, or are they driven be a so-far-not-identified mechanism possibly linked to arousal or attention? While purely stochastic fluctuations are possible, they do not provide a very satisfactory explanation, as they suggest that gating of consciousness is random, which seems unlikely given the processing demand on the visual system. As such, it would be of great interest to understand what drives the prefrontal fluctuations and how they might serve a behavioral or perceptual goal.

A second important question is on the communication between posterior sensory areas and the PFC. For instance, given that stable percepts seem to be reflected by increased beta-band activity, one could hypothesize that phase synchronization in the beta-band might reflect the communication between the PFC and visual regions. This is consistent with ideas suggesting that feedback mechanisms are supported by beta-band phase synchronization. Such studies could be conducted in NHPs employing simultaneous recordings in both visual and prefrontal regions. Measures of spectral Granger causality could then be used to confirm that ignition indeed involves a top-down drive from the PFC to posterior regions.

It would be of great interest to explore the causal role of the PFC for BR. This could be done by lesioning the PFC using cooling or pharmacological approaches in NHPs. Another possibility is to use repeated transcranial magnetic stimulation (TMS) to prefrontal regions in humans to address if such an intervention impacts the BR. While the TMS approach has provided insight on the role of the parietal cortex in BR, it has proven challenging in general to obtain reliable results when perturbing the PFC. Yet an exciting opportunity would be the application of transcranial photobiomodulation in which laser light is used to stimulate the metabolism in neurons in the PFC. Such interventions have shown to reliably increase working memory capacity[8] and thus have the potential of providing causal insight into role of the PFC for BR.

Finally, it would be interesting to replicate the study and findings in humans exploiting recent technical developments. While BR has been investigated using magnetoencephalography (MEG) and electroencephalography, more work could be done using multivariate approaches, and the innovation of "rapid invisible frequency tagging"[9] provides new opportunities. Furthermore, recent developments on optically pumped magnetometers have allowed for MEG systems to place sensors closer to the scalp. This advancement should allow for an increased signal-to-noise ratio when measuring the distributed activity from the PFC[10] and then relate it to posterior regions in BR-type paradigms.

ACKNOWLEDGMENTS

The authors are grateful for financial support from the Templeton World Charity Foundation, Inc. (no. TWCF0389).

DECLARATION OF INTERESTS

The authors declare no competing interests.

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