Trends in Cognitive Sciences

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Letter

Prefrontal Cortex and Consciousness: Beware of the Signals

Theofanis I. Panagiotaropoulos,[1,*] Abhilash Dwarakanath,[1] and Vishal Kapoor[2]

During binocular rivalry (BR), incongruent, unchanged visual stimulation induces intrinsically generated transitions in conscious content. Due to this astonishing property, BR is commonly combined with functional magnetic resonance imaging (fMRI) or single neuron recordings to identify the neural correlates of consciousness (NCCs); namely, brain activity reflecting conscious contents and spontaneous transitions between them. No-report BR versions, where the perceived stimulus is decoded from objective markers like reflexive eye movements instead of active behavioral reports, can be used to discard activity related to motor and postperceptual processes that might contaminate the pure NCC. This is especially relevant for resolving an ongoing theoretical debate about the role of the prefrontal cortex (PFC) and posterior cortical areas in consciousness. Block recently suggested that no-report might still fail to eliminate postperceptual cognitive processes accompanying BR [1,2]. This could result in neural signals being incorrectly interpreted as reflecting conscious contents, under the strong assumption that postperceptual processes are systematically aligned to each of the competing percepts. He therefore calls for the development of no-post perceptual cognition paradigms and highlights the BR paradigm of Brascamp *et al.* [3], that uses unreportable transitions, to address this problem. We agree with Block that dissociating the NCCs from cognition is necessary. However, we caution against (i) Block's interpretation of the Brascamp *et al.* findings; and (ii) the criticism that our recent recordings during no-report BR in the PFC reflect postperceptual cognitive processing and show no evidence of transition processes.

Block's interpretation of the Brascamp *et al.* results relies on the assumption that the unnoticed and unreportable BR transitions in this elegant experiment are transitions in conscious perception. The validity of this interpretation depends on accepting the phenomenal consciousness concept, in which a stimulus can be consciously perceived without triggering the ability to report it. This view is opposed to the framework of access consciousness which would suggest that unreportable transitions fall into the category of unconscious perception, since consciousness is accompanied by the ability to report [4,5]. Indeed, transitions in phenomenal consciousness are more likely to reflect unconscious transitions, shown to induce neural activity fluctuations correlated with rivalry dynamics in primary visual cortex (V1) [6,7]. Similarly, alternating activation of V1 ocular dominance columns is observerd even when BR is presented during loss of consciousness induced by general anesthesia [8]. Unconscious BR transitions could therefore activate sensory visual cortex but are not access conscious, and therefore do not activate PFC. In other words, if no conscious transitions, and therefore changes in the consciously perceived content, occur, then PFC and other associational cortical areas will remain silent, as shown in the Brascamp *et al.* study.

Block also argues that our results [9,10], showing decoding of conscious contents from prefrontal neural ensembles using no-report BR are problematic due to the 'bored monkey problem': macaques participating in passive, no-report BR are bored during the experiment and therefore engage in postperceptual, higher-order thoughts reliably aligned to the rivaling stimuli and therefore decodable in cognitive brain areas such as the PFC. In this case, prefrontal populations could reflect postperceptual processing rather than pure conscious representations. However, this would suggest that postperceptual thinking is reproducible, and stimulus aligned across trials. This seems an unlikely combination of events in the brains of bored macaques, given also the absence of active reports that could associate stimuli with specific actions (e.g., button presses) and thoughts. It is unclear why the macaques would engage in such reliable postperceptual cognitive thinking to fight or due to boredom.

Block further argues that the absence of differences in content representations between externally induced stimulus alternations and endogenously driven BR transitions in the PFC suggests that this cognitively critical region does not causally initiate transitions, under the assumption that the neural bases of transitions and contents are linked. Therefore, failure to find differences between rivalrous and real transitions in cognitive areas disconfirms cognitive theories of conscious contents. Although we agree that PFC alone, most likely, does not cause the transitions and rather network interactions are necessary, Block's assumption is flawed (Box 1). Although the correlates of transitions in the PFC interact with conscious contents, it is likely that they are not the same. In our no-report experiments, we found that a spontaneous transition in the activity of feature specific neural ensembles reflecting conscious content representations is preceded by fluctuations in the PFC state, measured in the local field potential signals [10,11]. Similarly, conscious reports require a nonlinear ignition process that depends on ongoing neural activity in the PFC [12]. These findings, showing that spontaneous fluctuations precede conscious access, suggest a possible dissociation between the neural correlates of conscious contents and transitions in conscious perception.

Box 1. Perceptual Competition in BR and Transition Signals in the PFC

One of Block's major arguments against a PFC involvement in conscious perception derives from the premise that 'explanation of binocular rivalry is that pools of neurons that represent each of the stimuli are mutually inhibitory' [2]. Therefore, these interactions should be detectable and not finding them in PFC spiking activity between rivalry and nonrivalry conditions [9,10] is evidence against its involvement. Firstly, this is a theoretical assumption originally proposed as part of a mechanism, that BR results from competition between eyes and therefore depends on monocular neurons in early visual areas. However, only a minority of them were found to be perceptually modulated [6]. Therefore, Block's argument should take these findings into account. Secondly, such inhibitory interactions could still occur in earlier sensory regions (nonconsciously), with PFC, among other associational cortical areas, reflecting the resolution of competition, signaling ongoing perceptual content. Thirdly, such competition among stimulus representations does not necessarily imply interaction between neuronal ensembles mediating them, since the two processes could exist mutually exclusively. Indeed, neural activity preceding changes in conscious perception during rivalry but not during nonrivalrous conditions [11] suggests differential PFC modulation. Taken together, the (non)existence of differential activation requires careful scrutiny before considering it as evidence against the role of PFC in conscious perception.

We believe that current empirical findings from fMRI and electrophysiological BR studies may have a different interpretation and suggest that two mechanisms of intrinsically generated transitions might exist in the cortex. One mediating unconscious switches in sensory cortical areas, and another in association cortical areas that gates conscious access and therefore transitions between consciously perceived contents.

[1]Cognitive Neuroimaging Unit, CEA, DSV/I2BM, INSERM, Universite Paris-Sud, Universite Paris-Saclay, Neurospin Center, 91191 Gif/Yvette, France
[2]Department of Physiology of Cognitive Processes, Max Planck Institute for Biological Cybernetics, Tübingen 72076, Germany

*Correspondence:
theofanis.panagiotaropoulos@cea.fr (T.I. Panagiotaropoulos).

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References

1. Block, N. (2019) What is wrong with the no-report paradigm and how to fix it. *Trends Cogn. Sci.* 23, 1003–1013
2. Block, N. (2020) Finessing the bored monkey problem. *Trends Cogn. Sci.* Published online January 24, 2020. https://doi.org/10.1016/j.tics.2019.12.012
3. Brascamp, J. *et al.* (2015) Negligible fronto-parietal BOLD activity accompanying unreportable switches in bistable perception. *Nat. Neurosci.* 18, 1672–1678
4. Naccache, L. (2018) Why and how access consciousness can account for phenomenal consciousness. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* Published online July 30, 2018. https://doi.org/10.1098/rstb.2017.0357
5. Overgaard, M. (2018) Phenomenal consciousness and cognitive access. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* Published online July 30, 2018. https://doi.org/10.1098/rstb.2017.0353
6. Blake, R. and Logothetis, N. (2002) Visual competition. *Nat. Rev. Neurosci.* 3, 13–21
7. Zou, J. *et al.* (2016) Binocular rivalry from invisible patterns. *Proc. Natl. Acad. Sci. U. S. A.* 113, 8408–8413
8. Xu, H. *et al.* Rivalry-like neural activity in primary visual cortex in anesthetized monkeys. J. Neurosci. 36, 3231–3242.
9. Panagiotaropoulos, T.I. *et al.* (2012) Neuronal discharges and gamma oscillations explicitly reflect visual consciousness in the lateral prefrontal cortex. *Neuron* 74, 924–935
10. Kapoor, V. *et al.* (2020) Decoding the contents of consciousness from prefrontal ensembles. *bioRxiv* Published online January 28, 2020. https://doi.org/10.1101/2020.01.28.921841
11. Dwarakanath, A. *et al.* (2020) Prefrontal state fluctuations control access to consciousness. *bioRxiv* https://doi.org/10.1101/2020.01.29.924928
12. van Vugt, B. *et al.* (2018) The threshold for conscious report: Signal loss and response bias in visual and frontal cortex. *Science* 360, 537–542