Journal Club

Editor's Note: These short, critical reviews of recent papers in the *Journal*, written exclusively by graduate students or postdoctoral fellows, are intended to summarize the important findings of the paper and provide additional insight and commentary. For more information on the format and purpose of the Journal Club, please see http://www.jneurosci.org/misc/ifa_features.shtml.

Late EEG Responses Are Absent for Conscious But Task-Irrelevant Stimuli

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Review of Shafto and Pitts

Thousands of neural circuits are activated in our brains each second, but only some of them (quite mysteriously) give rise to conscious perception (Koch, 2004). The neuroscience of consciousness is the quest to identify these processes: a crucial pursuit with a wide range of applications, such as assessing consciousness in comatose patients and animals and restoring conscious sensory functions in brain-damaged patients.

A first step toward solving the ambitious problem of explaining consciousness is recognizing the brain regions and the temporal dynamics of neural processes involved in generating conscious perceptions. For this problem, two conflicting views have been proposed. One theory, the global neuronal workspace (Dehaene and Naccache, 2001), suggests that consciousness arises with a global late ignition (~300–500 ms) across different cortical regions (Dehaene and Changeux, 2011). Another view asserts that recurrent cortical activity at earlier latencies (150–250 ms) corresponds more closely to con-

scious perception (Lamme, 2000; Koivisto and Revonsuo, 2010).

To distil the neural processes associated with conscious perception from those present in the absence of awareness, previous research has relied on contrastive analysis (Baars, 1988). This method involves presenting subjects with stimuli that are consciously seen on only some trials (for example, 50% of the time), and comparing the brain activity associated with each perceptual state ("seen" vs "unseen" conditions). For more than a decade, contrastive analysis has been considered the gold standard in the search for the neural correlates of consciousness (NCCs). Recently, however, several researchers have argued that this method is unable to disentangle conscious from nonconscious neural activity (Aru et al., 2012; de Graaf et al., 2012). One of these criticisms resides in the impossibility of distinguishing NCCs from (1) the neural correlates of the prerequisites for consciousness (pre-NCCs, i.e., the neural events occurring before the NCCs) and (2) the neural correlates of the consequences of consciousness (co-NCCs, the neural events following the NCCs) (Aru et al., 2012; de Graaf et al., 2012). According to this view, "seen" and "unseen" trials might differ in several aspects besides the perceptual state of the subject. For example, the NCCs could be mixed up with the correlates of reporting one's perception (Pitts et al., 2014) after the NCC has taken place (co-NCC) or with the allocation of attentional resources (Lamme,

2003) before the occurrence of the NCC (pre-NCC). These potential confounds have led researchers to ask what the appropriate methods to study conscious perception are (Navajas et al., 2014; Aru and Bachmann, 2015).

Building upon these observations, several studies have tried to disentangle the NCCs from the neural correlates of reporting one's perception, regarded as a co-NCC. The challenge, of course, is to design an experiment in which the experimenter can assess participants' subjective awareness without asking subjects for an explicit report. To meet this challenge, Pitts et al. (2012) adapted the inattentional blindness paradigm to record event-related potentials (ERPs) with scalp electroencephalography (EEG). The main novelty of this experimental design is that it allowed the researchers to identify neural signals modulated by conscious perception independently of whether the content of conscious perception was task-relevant. To do so, the authors compared the ERPs elicited on a block of trials in which participants reported their perception with those on another set of trials in which subjects were aware of the critical stimuli but were performing a different task (for a detailed review on the experimental design, see Pitts et al., 2014).

In a recent paper, Shafto and Pitts (2015) adapted this paradigm to specifically study the N170, an occipito-temporal component of EEG that was

previously shown to be associated with conscious face perception (Fisch et al., 2009; Navajas et al., 2013; Sandberg et al., 2013). The goal of the study was to dissociate the neural correlates of conscious face perception from the neural correlates of reporting a face (Shafto and Pitts, 2015). The authors showed that the N170, and a later EEG component peaking at ~250 ms [known as the visual-awareness negativity (VAN)], correlated with conscious perception independently of the task relevance of the faces. In contrast, a later component, P3b, was absent when faces were consciously perceived but task-irrelevant. Altogether, their results challenge theoretical accounts predicting a late (>300 ms) emergence of conscious perception (Dehaene et al., 2003). In particular, the results suggest that previous studies could have confounded consciousness with task relevance.

The findings of Shafto and Pitts (2015) add to the evidence against proposals linking late (>300 ms) EEG components with the NCC. For example, P3 components (either P3a or P3b) are absent in a range of conditions in which participants are aware of stimuli that are irrelevant to their task: when subjects passively observe a sequence of distractor images appearing on the screen (Sutton et al., 1965), and when they actively fixate on distractors during a free eye-movement visual scene exploration (Kaunitz et al., 2014). In both cases, subjects pay attention and consciously recognize those stimuli as distractors as opposed to targets, but the P3 component is absent. Similarly, the P3 component associated with task-relevant stimuli disappears when those stimuli (still consciously perceived) become task-irrelevant (Pitts et al., 2012; Shafto and Pitts, 2015). All this evidence suggests that, in tasks requiring subjects to identify a target that was present in a fraction of trials, the P3 component might reflect task-relevant target detection rather than conscious perception.

One could speculate that there is a range of consciousness (Navajas et al., 2014). It seems plausible that participants could stop processing a stimulus after determining that it was task-irrelevant without being fully conscious of it. For example, participants may be aware that a distractor stimulus is not a face, but still be unable to recognize or name it. Similarly, they could consciously perceive a face without being able to tell its identity, gender, or age. But even in these situations, participants must be conscious of some properties of those distractor faces (at least the properties that make distractor stimuli differ from target stimuli). In fact, they are able to recall those distractors after the task is finished, a phenomenon known as incidental memory (Castelhano and Henderson, 2005; Williams et al., 2005). Incidental memory of faces is an indicator that task-irrelevant stimuli can be consciously perceived in the absence of late EEG components (Kaunitz et al., 2014; Shafto and Pitts, 2015) and retrieved as episodic memories after the task.

One intriguing aspect of the evidence presented by Shafto and Pitts (2015) is that both early components (the N170 and the VAN) failed to show an all-or-none correlation with awareness. In fact, task-relevant faces elicited larger N170/VAN components than task-irrelevant faces, even though in both conditions faces were consciously perceived. This is in clear conflict with proposals arguing that the all-or-none nature of consciousness (i.e., the idea that one can be aware or unaware that a given stimulus is a face, but not half-aware) should be reflected in an all-or-none NCC (Dehaene and Changeux, 2011). The authors' interpretation is that these early components might very well represent another cognitive process, e.g., visual attention. While this possibility cannot be ruled out because attention and awareness were not independently manipulated in Shafto and Pitts (2015) (for a review on the experimental manipulations used to manipulate awareness and attention, see Koch and Tsuchiya, 2007), an alternative interpretation could also explain their results. In the task-irrelevant condition, Shafto and Pitts (2015) assessed awareness by retrieving the subjective reports after the entire block of trials had concluded. With this experimental manipulation, the authors could establish that, overall, faces were consciously perceived in that set of trials. This assessment, however, cannot ensure that participants perceived all presented faces. As most attentional resources were deviated to a different task (thus yielding faces as task-irrelevant), it is reasonable to expect that faces were missed in some trials. This would lead to a smaller N170/VAN in the task-irrelevant condition as a consequence of averaging all trials: those that were consciously perceived and those that were not. Further research should aim to test this possibility to disambiguate the role played by the N170/VAN in eliciting conscious perception at the single-trial level (Navajas et al., 2013).

The most important theoretical implication of Shafto and Pitts (2015) is that distinguishing NCCs from the correlates of reporting one's perception can pose constraints on models of consciousness. The evidence provided by Shafto and Pitts (2015) favors the view that conscious face perception might arise earlier than 300 ms (Fisch et al., 2009; Navajas et al., 2013; Sandberg et al., 2013) and that the P3 component might correlate better with stimulus task relevance than with conscious perception. The quest to identify the spatiotemporal dynamics of consciousness in the brain is, however, still far from complete. In the future, it will be interesting to see if new versions of this paradigm can evaluate awareness on a trial-by-trial basis and, at the same time, disambiguate NCCs from other cognitive processes, such as attention.

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