What's up with Prefrontal Cortex?

A Commentary on John-Dylan Haynes

Caspar M. Schwiedrzik

The prefrontal cortex is perhaps one of the most intriguing areas of the brain, and considered by many to be involved in a whole battery of higher cognitive functions. However, evidence for a direct involvement in conscious perception, although often postulated, remains inconclusive. In his paper, John-Dylan Haynes presents results from experiments using multivariate decoding techniques on human functional magnetic resonance imaging data that speak against the assertion that prefrontal cortex broadcasts the contents of consciousness throughout the brain. I consider potential reasons for these null results, as well as where else we may look for the neural correlates of consciousness. Specifically, I propose that conscious perception arises when distributed neurons are bound into coherent assemblies—a process that does not require relay through specific brain areas.

Keywords
Multivariate pattern analysis | Neuronal correlates of consciousness | Neuronal synchrony | Prefrontal cortex

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1 Introduction

There is a striking parallel between the hierarchical organization of behavior and the hierarchical organization of the cerebral cortex (Botvinick 2008). It is thus tempting to assign consciousness, at least historically often considered to be one of our highest functions (Jackendoff 1987; Markowitsch 1995), to the prefrontal cortex (PFC), which is positioned at the top of the cortical hierarchy. While the idea that consciousness can be localized to a single brain area has now been discredited, many current theories of consciousness still consider the PFC a key player in the emergence of conscious perception (Dehaene & Changeux 2011; Lau & Rosenthal 2011). And indeed, a multitude of neuroimaging studies has shown differential activation for perceived vs. unperceived stimuli in various parts of the PFC (Dehaene et al. 2001; Lau & Passingham 2006; Sahraie et al. 1997; Schwiedrzik et al. 2014). A very prominent theoretical proposal on the neural correlates of consciousness, the Global Neuronal Workspace (GNW) model by Stanislas Dehaene and colleagues, posits that the PFC (in conjunction with parietal cortex) serves to distribute information that is processed in unconscious modules to the entire brain, and that it is this broadcasting of information that gives rise to conscious experience (Dehaene & Changeux 2011). The PFC may be particularly well equipped to

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do so, for example because it hosts an abundance of neurons with long-distance connections, so called "von Economo" neurons, which seem ideally suited to both receive and deliver information from all areas of the brain to all areas of the brain (Dehaene & Changeux 2011). A prediction that can be directly derived from this account and that has been eloquently put forward by John-Dylan Haynes is that the PFC should at least temporarily represent the information that we consciously perceive, i.e., it should directly encode the contents of consciousness (Haynes 2009; this collection). To test this idea, Haynes and his coworkers have used a neuroimaging technique that allows for exquisite access to perceptual content, namely multivariate pattern analysis (MVPA) of functional magnetic resonance imaging (fMRI) signals. In this technique, powerful machine learning algorithms are used to analyze spatially-distributed patterns of brain activity, and a brain region is said to represent the content of interest if its activity patterns allow the reliable classification—in the case of consciousness—of which stimulus the subject perceived on a given trial. This contrasts with previous fMRI studies not using MVPA: because these studies do not directly address content, activity in the PFC (and other regions) that differentiates perceived from not perceived trials could in principle reflect other aspects of conscious experience, for example the allocation of attentional resources or working memory. The stunning result of Haynes' investigations is that while MVPA shows that perceptual content can be decoded from higher sensory areas, PFC activity does not yield decoding accuracies higher than chance level. So what's up with PFC?

2 Neuronal representations in the PFC

Indeed, the inability to decode perceptual content from the PFC runs counter intuitions about PFC functions we have from animal models such as the macaque monkey, where representations of (perceptual) content can be even more directly assessed than with MVPA, by using electrophysiological recordings from single neurons. These studies show that PFC neurons are tuned for and thus represent perceptual features such as visual motion direction (Zaksas & Pasternak 2006) or somatosensory flutter frequency (Romo et al. 1999). Even more direct evidence for the representation of perceptual content in the PFC comes from a recent study by Theofanis Panagiotaropoulos et al. (2012), which shows that single PFC neurons exhibit stimulus-specific activity modulations as a function of subjective perception under flash suppression, a technique that can render visual stimuli temporarily invisible.

In the absence of direct electrophysiological recordings from human PFC, one possible explanation for this discrepancy is that the macaque brain is organized in a totally different way to the human brain. But while theoretically possible, this seems highly unlikely (Passingham 2009; Roelfsema & Treue 2014). Alternatively, one may consider whether certain properties of the neural representations in the PFC may pose limitations to the ability of the fMRI MVPA technique to decode their content. This is in light of the fact that decoding of content from human PFC has been unsuccessful not only in the context of conscious perception, but also in the context of working memory, which has led to a radical reinterpretation of the role of the PFC in this domain (Sreenivasan et al. 2014).

It has been hypothesized that successful decoding of stimulus features such as orientation or motion direction from sensory areas relies upon the presence of orderly spatial arrangements of these features in cortical columns or maps (Freeman et al. 2011; Kamitani & Tong 2005). It is thus worth asking the question whether PFC exhibits a similar map-like structure, or whether the spatial arrangement of features in the PFC already renders the likelihood of decoding any kind of information from its fMRI activity unlikely. For example, while maps representing space have been identified in the human PFC, they are much smaller than retinotopic maps in early visual areas, and intersubject variability in their location is much higher (Hagler & Sereno 2006). Furthermore, it is known from experiments in monkeys that only a subset of the neurons within the PFC subregions in which these maps have been found actually displays any spatial preference (Funahashi et al. 1989; Rainer et al. 1998). Importantly, the PFC also has a more complicated cytoarchitecture than sensory areas, with longer and more complex dendrites that allow for sampling of information from a wider range of inputs (Jacobs et al. 2001), which may affect the spatial scale at which information is represented and can be read out. Nevertheless, the overall picture that arises from studies employing optical imaging and microstimulation in monkeys is that at least several subregions of the PFC are topographically organized in a similar fashion as sensory areas (Roe 2010). However, while the topography of the PFC may be favorable to MVPA, neural representations in the PFC seem to exhibit more complex features and dynamics on a single neuron and population level than the representations in sensory areas where MVPA has been particularly successful. For example, recent studies in monkeys show that PFC representations are very high dimensional (Rigotti et al. 2013), that selectivity is not fixed but can be acquired (Bichot et al. 1996), that selectivity can change over time even within a trial (Stokes et al. 2013), and that populations of PFC neurons represent multiple stimulus dimensions at the same time even if one dimension is unattended (Mante et al. 2013). Thus, the dimensionality and temporal instability of neural representations in the PFC may pose a serious challenge to fMRI MVPA experiments, given that they rely on an inherently slow, hemodynamic signal that integrates neural activity over time.

Putting these and other (Anderson & Oates 2010; Vilarroya 2013) potential limitations of the MVPA approach aside, what other evidence do we have that the PFC is actually involved in conscious perception? In particular, is there *causal* evidence for a role of the PFC in conscious perception?

3 Beyond decoding: Causal evidence for a role of the PFC in conscious perception?

Early studies in macaque monkeys have found that lesions to the PFC can increase the luminance threshold (Latto & Cowey 1971) and degrade detection performance (Kamback 1973). More recently, studies in humans using transcranial magnetic stimulation have similarly found that stimulation of the PFC can impair the visibility of stimuli (Rounis et al. 2010), but also improve detection rates during visual masking (Grosbras & Paus 2003). Finally, Antoine Del Cul et al. have shown that perceptual thresholds are increased in patients with relatively small prefrontal lesions even when attentional effects are tightly controlled for (2009). However, none of these studies has shown dramatic impairments, but rather modulations of performance or perception. Total blindness has only been reported after removing the entire frontal cortex including (parts of) the underlying cingulate cortex in monkeys, and only lasted for a few days in several cases (Nakamura & Mishkin 1986). Importantly, other lesion studies in humans have not reported perceptual deficits at all (Heath et al. 1949; Markowitsch & Kessler 2000). Taken together with the fact that the PFC is also active during unconscious processing (Diaz & McCarthy 2007; Lau & Passingham 2007; van Gaal et al. 2008), not deactivated under Thiopental anesthesia (Veselis et al. 2004), but deactivated during rapid eye movement sleep when vivid (non-lucid) dreams can be experienced (Braun et al. 1998; Desseilles et al. 2011; Muzur 2002), this indicates that the evidence for a direct, specific involvement of the PFC in conscious perception is currently inconclusive at best.

4 An alternative to localization

Luckily, we can do without PFC, at least for the purposes of explaining conscious perception, while still maintaining many of the other, more compelling aspects of the GNW model. One central component that the GNW model shares with several other proposals about the neural correlates of consciousness (for example Melloni & Singer 2010; Tononi 2004; von der Malsburg 1997) is the concept of global integration of information. In light of the modular organization of the brain, a mechanism is required that brings information together such that an integrated, coherent percept

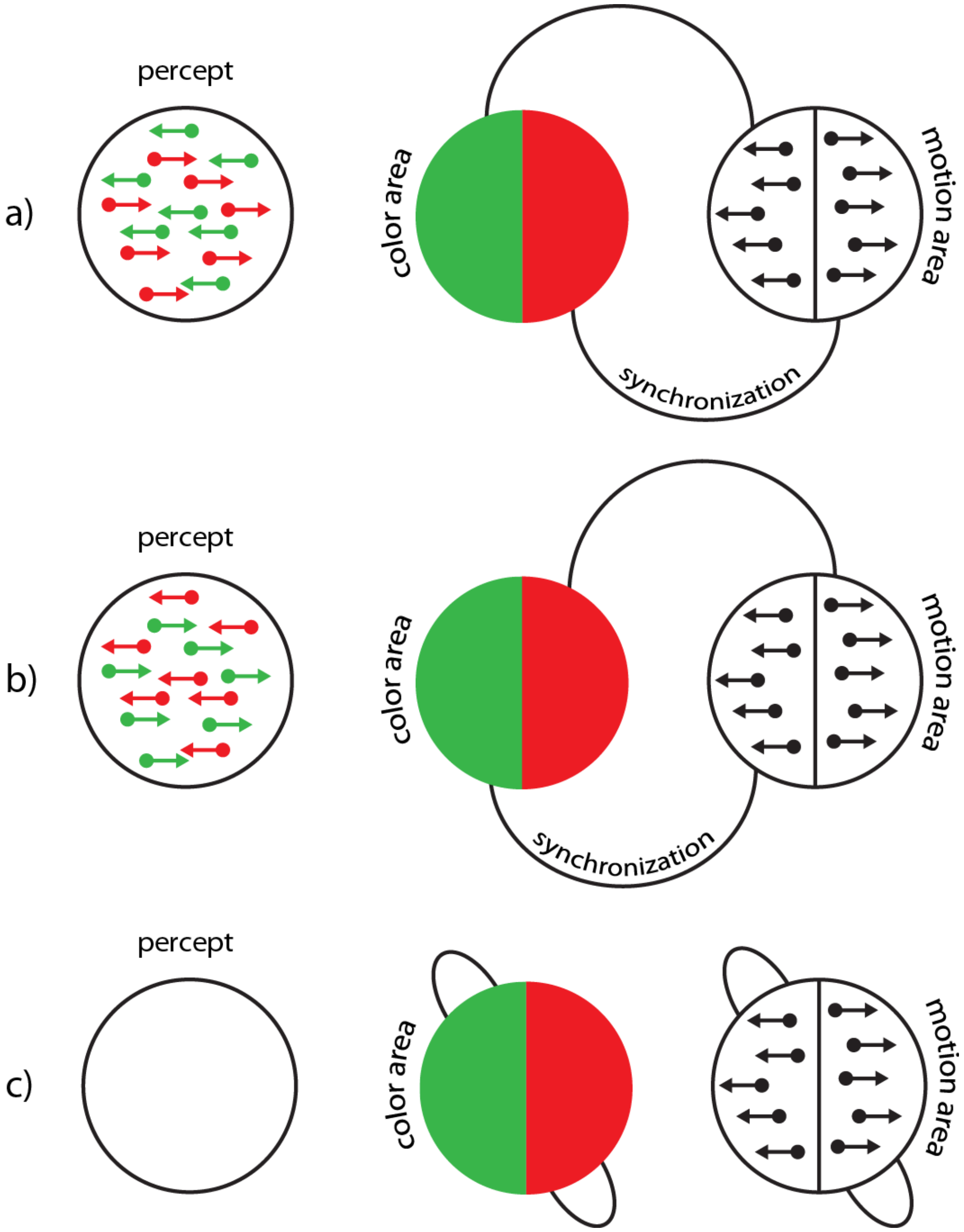

Figure 1: Neuronal synchrony binds distributed neurons into coherent assemblies, giving rise to conscious experience. Consider an experiment in which the subject is confronted with two superimposed, transparent surfaces of moving dots, as shown in the first column. **(a)** The dots on one surface are green and move to the left, and the dots on the other surface are red and move to the right. The two colors of dots are represented in a brain area coding for color, while the two motion directions are represented in an area coding for motion. If the neurons coding for green in the color area synchronize with the neurons coding for motion to the left in the motion area, and the neurons coding for red synchronize with the neurons coding for motion to the right, the two surfaces are consciously perceived. **(b)** A change in experience does not require a change in activity levels within areas, but a change of which neurons are synchronized. The opposite percept of (a) arises if neurons coding for green are synchronized with neurons coding for motion to the right, and if neurons coding for red are synchronized with neurons coding for motion to the left. Such content-specific synchronization between neurons has for example been observed in working-memory tasks in monkeys (Salazar et al. 2012). **(c)** Even when activity is synchronized within the color or motion area, respectively, a coherent conscious percept does not arise unless the areas are synchronized with each other.

can be formed. One attractive neural mechanism that can account for this requirement is neuronal synchrony (Bosman et al. 2012; Bressler et al. 1993; Salazar 2012). As has been discussed in greater detail elsewhere (Melloni & Singer 2010; Melloni this collection; Singer this collection), areas can be brought into *direct* contact with each other by synchronizing their neuronal activity, for example by phase alignment of neuronal oscillations, thus binding them into a functionally coherent assembly that forms a distributed representation of perceptual content. This self-organizing process can flexibly create and dissolve assemblies on top of a fixed anatomical architecture and does so without the need for anatomical convergence or broadcasting bottlenecks.

For example, imagine that a subject is confronted with two superimposed, transparent surfaces of moving dots (Figure 1). The dots on one surface are green and move to the left, and the dots on the other surface are red and move to the right. The two colors of dots are represented in a brain area coding for color, while the two motion directions are represented in an area coding for motion. For the subject to become conscious of the two surfaces, the neurons coding for green in the color area would need to synchronize their activity with the neurons coding for motion to the left in the motion area, and the neurons coding for red would need to synchronize with the neurons coding for motion to the right (Figure 1a). If the dots change direction, a new state of synchronization needs to be established, this time linking neurons coding for green with neurons coding for motion to the right, and neurons coding for red with neurons coding for motion to the left (Figure 1b). Hence, while the contents of the subject's experience are determined by the specific neuronal assemblies being active, conscious perception would be an emergent property of the state of synchronization. Recent tracing and modelling work in the macaque brain suggests that the kind of direct connectivity required to flexibly instantiate numerous, high-dimensional combinations of features is indeed afforded by high-density, reciprocal connections between brain areas (Markov et al. 2013).

Theoretical considerations and empirical evidence further suggest that the critical feature differentiating conscious from unconscious processing is the spatial scale at which information is exchanged: while the integration of information in local modules, even in higher sensory areas (Sterzer et al. 2008), does not give rise to conscious experience by itself, large-scale integration over long distances does (Del Cul et al. 2007; Melloni et al. 2007). In the example of the transparent surfaces, this implies that even when activity is synchronized within the color or motion area, respectively, a coherent conscious percept cannot arise unless the areas are synchronized with each other (Figure 1c). Taken together, functional connectivity between distributed brain areas (i.e., connectivity that does not imply that one drives or controls the other) is an attractive alternative to localization in PFC as a candidate for the neural correlate of consciousness.

Coming back to the MVPA technique, this proposal makes a clear prediction that could be tested using decoding algorithms: specifically, one would predict that the large-scale connectivity patterns *between* brain regions for different percepts should differ, even if only slightly, for different conscious contents, and hence that conscious content should be decodable from them. This may well be the case in light of the fact that, at a much coarser scale, the neural correlates of auditory and visual awareness involve different brain networks (Eriksson et al. 2007), and that higher decoding accuracy for a subject's percept can be achieved if the joint activity patterns of several areas are considered instead of only singular patterns (Pessoa & Padmala 2007). The MVPA technique could in principle also be applied to other neuroimaging techniques that afford higher time resolution, such as electro- or magnetoencephalography or electrocorticography, thus potentially resolving the problem that arises because the representational carriers of perceptual content are highly dynamic and thus require a time-resolved analysis.

5 Conclusions

In summary, a complete theory for the neural correlates of consciousness should be able to account for the neural implementation of the contents of consciousness. John-Dylan Haynes has proposed a clever experimental approach to localizing the contents of consciousness in the human brain, and has found that the PFC does not seem to be involved in this representation. Although surprising at first sight, this null result lines up well with the overall inconclusive evidence for a direct involvement of the PFC in conscious perception. However, it remains to be seen whether localization is the most fruitful approach to identifying the neural correlates of consciousness, or whether a more dynamic view that embraces the importance of communication between brain areas will bring us closer to solving the enigma of consciousness in the brain.

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