Conscious Perception and the Prefrontal Cortex: A Review

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Author's version. Published in the *Journal of ConsciousnessStudies*. Please cite the published version.

Abstract: Is perceptual processing in dedicated sensory areas sufficient for conscious perception? Localists say 'Yes—given some background conditions.' Prefrontalists say 'No: conscious perceptual experience requires the involvement of prefrontal structures.' I review the evidence for prefrontalism. I start by presenting correlational evidence. In doing so, I answer the 'report argument', according to which the apparent involvement of the prefrontal cortex in consciousness stems from the requirement for reports. I then review causal evidence for prefrontalism and answer the 'lesion argument', which purports to show that prefrontalism is wrong because lesions to the prefrontal cortex do not abolish consciousness. I conclude that multiple sources of evidence converge toward the view that the prefrontal cortex plays a significant role in consciousness.

Introduction

Suppose that I unconsciously perceive an apple—assuming unconscious perception exists[1]. Some neural activity is responsible for my being in this unconscious perceptual state. What is the minimal kind of neural activity that you would need to add for me to *consciously* perceive the apple, given that I already perceive it unconsciously? Answering that question amounts to finding the *neural correlate of consciousness*(Chalmers, 2000).

The debate over the neural correlate of consciousness (NCC) has crystallized around two main views. Prefrontalists surmise that activity in the prefrontal cortex (PFC) is a component of the NCC (Brown et al. 2019; Mashour et al. 2020; Michel & Morales, 2019; Odegaard et al. 2017). Localists hold that PFC is irrelevant for (at least visual) consciousness (Block, 2007; Boly et al. 2017; Lamme, 2010, 2015; Malach, 2021). Given some background conditions, local activity in sensory areas is sufficient for consciousness.

Let me give two reasons to take this debate seriously. First, if prefrontalism is correct, consciousness (probably) involves cognition—prefrontal areas are often regarded as 'higher cognitive' areas. This has consequences for several debates, including which perceptual or cognitive functions (if any) are associated with consciousness, as well as consciousness in non-human animals, infants, and non-communicating patients. Second, identifying NCCs is a way of testing theories of consciousness. If localism is correct, popular theories such as global workspace theory and (most) higher-order theories are probably wrong (Mashour, 2020; Lau & Rosenthal, 2011). If prefrontalism is correct, local recurrence theory (Lamme, 2015), micro-consciousness theory (Zeki, 2003), the 'local ignition' theory (Malach, 2021), and integrated information theory (Oizumi et al. 2014), are probably wrong.

The debate is far from settled. Nevertheless, I hold that, as things currently stand, prefrontalism is more likely to be correct than localism. I start by distinguishing between two kinds of prefrontalism (Section 1). I then present evidence indicating that PFC is involved in consciousness. I discuss correlational evidence in sections 2.1. and 2.2., and causal evidence in sections 2.3. and 2.4.

Before we come to this, two caveats are in order. First, I will often talk about 'PFC' in general instead of specific sub-regions of PFC. I am not happy with this level of anatomical vagueness. But I have to do this for two reasons. First, given the nature of PFC representational

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[1] I consciously perceive an apple if there's something it's like for me to perceive it. I unconsciously perceive an apple if I mentally represent that there is an apple but there's nothing it's like for me to do so. In that case, mentally representing that there is an apple doesn't feel any different from not representing that there is an apple.

codes—'dense coding' rather than 'sparse coding' (e.g., Rigotti et al. 2013; Safavi et al. 2018)—conscious representational contents could be distributed throughout PFC rather than represented in a single sub-region. The second reason is somewhat less glorious: prefrontalists don't have a good idea of the specific components of PFC that are supposed to play a role for consciousness. Dorsolateral prefrontal cortex is mentioned as a key area (Brown et al. 2019; Mashour et al. 2020), but so are other parts of PFC such as the frontal pole, the ventro-lateral and ventro-medial prefrontal cortices (e.g., LeDoux, 2019).

Second, I focus on conscious *perception*—primarily *visual* perception. There's a strong case for the view that prefrontal structures are involved in other kinds of conscious experiences, such as emotions (LeDoux & Brown, 2017; LeDoux & Pine, 2016). While I believe that this should bring inductive support for the role of PFC in perceptual experience as well, I will not discuss this. Similarly, I do not focus on pain, olfactory, interoceptive, and gustatory experiences, the experience of agency, and 'cognitive phenomenology'. That's for a simple reason: the localist stance on conscious vision is clear, but it is not clear that localists should be committed to denying a role for PFC mechanisms in all these other cases.

1. Two kinds of prefrontalism

Let me start by distinguishing between two versions of prefrontalism: re-representationalist and relationalist theories[2]. That's important since the two versions make slightly different predictions.

Suppose again that I *unconsciously* perceive an apple. Some neuronal population signals the presence of an apple—carries a representation with the content 'there is an apple'. Suppose now that I see it consciously. Is *that* representation—which was previously involved in my *unconscious* percept—now constitutively involved in my *conscious* percept? Relationalists say 'Yes'. Re-representationalists say 'No'.

An analogy will help. Suppose that the army decides to recruit me[3]. I now have a new functional role. Having that functional role is what makes me a member of the army. Relationalists believe that consciousness is a bit like that. A representation is *recruited* in consciousness by taking a functional role that it didn't previously have. PFC mechanisms operate the recruitment: whether the representation takes the functional role required for consciously representing or not depends on what PFC mechanisms do with that representation.

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[2] This distinction is inspired from Brown's distinction between two kinds of higher-order theories of consciousness (e.g., Brown, 2015).

[3] I borrow the recruitment analogy from van Gulick (2004).

Re-representationalists reject the recruitment analogy. An unconscious representation of an apple might be *causally* involved in my consciously perceiving it. But at no point does *that* representation become constitutively involved in a conscious experience. Instead, what constitutes the experience is another representation, which could have a different representational format and a different functional role. And that representation is carried by neuronal vehicles in the PFC.

Prefrontalists are not always clear about whether their view is re-representationalist or relationalist in nature[4]. But the distinction matters because these views make different predictions. Let me give two examples.

Relationalists are not necessarily committed to the view that contents of consciousness can be decoded in PFC. Looking at PFC is a bit like looking at a (very complicated!) light switch. That tells you whether the light is on or off, but doesn't tell you anything about the objects thereby illuminated. Re-representationalists, on the other hand, are committed to the in-principle-decodability of conscious contents in PFC.

In the same way, re-representationalists are not necessarily committed to the view that some interactions between PFC and the relevant 'lower-order' areas—such as feedback from PFC to visual cortex, or neural synchrony—are constitutive of conscious experience. But relationalists should be committed to something like that.

2. Some evidence for prefrontalism

Part of the evidence for prefrontalism comes from the 'contrastive analysis' methodology (Baars, 1988). I discuss this evidence in the first sub-section (2.1). I discuss confounding factors involved

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[4] Global workspace theory has an interesting ambiguity here (to the best of my knowledge, it has only been mentioned by Wu, 2014). One can think of the global workspace as a 'blackboard': a separate memory buffer where modules can store and access relevant information (Newell, 1990). Following that view, representations in sensory modules are never globally accessible. What is globally accessible is the content of the 'blackboard'. This interpretation is re-representationalist. The blackboard architecture involving re-representation was the main source of inspiration for global workspace theory (Baars, 1988). But other comments from global workspace theorists indicate otherwise. For instance, Mashour et al. (2020) write: "the GNW hypothesis is not a localizationist approach to conscious access, nor is conscious access posited to exist solely in a given node of the GNW … Rather, the GNW acts as a distributed "router" associated with millions of neurons distributed in many brain regions through which information can be amplified, sustained, and made available to specialized sensory processors and thalamocortical loops." (p.777). No 'central blackboard', then. This suggests a relationalist interpretation. A representation is made globally available when its vehicle is connected, or the content it carries is 'routed', in the right way to consumer systems. In sum, according to re-representationalists, representations are copied in the global workspace. According to relationalists, they are recruited in the global workspace. That makes a pretty big difference. Given the similarities between global workspace and working memory, these two interpretations can be compared to the two main hypotheses about the locus of working memory storage (Postle, 2016; Xu, 2020, 2021).

in these studies in Section 2.2. I present causal evidence for prefrontalism in section 2.3. And I discuss issues with lesion cases in section 2.4.

2.1. Correlational Evidence

To discover the neural correlates of consciousness, scientists often rely on a 'contrastive analysis' method—comparing neural activity when subjects consciously perceive a stimulus and when they perceive it unconsciously (Baars, 1988). The contrast between the two should reveal the activity associated with consciousness of the stimulus.

There are, of course, confounding factors one should take care of. Consciousness is not the only difference between the relevant conditions: they also differ in stimulus parameters, attention, confidence, reports, working memory encoding and maintenance, thoughts about the stimulus, and task performance, to name just a few confounding factors. In Section 2.2. I explain why I believe that many of these confounding factors are somewhat overrated.

Researchers have a variety of methods for suppressing consciousness of the stimuli. Breitmeyer (2015) counted twenty-four. Scientists carried out contrastive analysis with nearly all of these. Those studies have revealed that PFC is the main area distinguishing conscious from unconscious perception. I will review some of them next. The fact that most of them point to the same conclusion is evidence that this finding is not simply due to our reliance on specific consciousness-suppression methods. Meanwhile, early visual areas are typically activated both when participants are conscious of the stimuli and when they are not. Activity in these areas also generally tracks the physical presence of the stimulus instead of subjective experience. This research program has been going on for more than twenty years, so I cannot aim for exhaustivity. I will only mention some of the findings that, in my opinion, are representative of the literature and relevant.

Visual Masking

Dehaene et al. (2001) showed that words masked with forward-backward patterns activated word-processing areas in the visual cortex. This activity drove a priming effect even when the words could not be detected or identified (objectively invisible), and participants reported no visual awareness (subjectively invisible). Dehaene et al. found a small increase in local activity measured with fMRI between masked vs. unmasked conditions. But PFC activity was the main difference. Several confounds could explain this result. Notably, differences in report demands and performance. Still, it is of historical importance, as it triggered a wave of experiments investigating the neural correlates of consciousness with visual masking.

Three similar studies are particularly relevant. Del Cul et al. (2007) compared brain activity measured with electroencephalography (EEG) (combined with source reconstruction) with different levels of masking strengths. They report that early visual activity scales linearly with stimulus strength but does not distinguish between seen versus not seen reports. Prefrontal activity and late local activity, from 300 milliseconds onwards, track conscious perception.

Similarly, Salti et al. (2015) trained pattern classifiers on EEG and magnetoencephalography (MEG) data to determine where and when conscious visual information could be decoded. They conclude: "Seen and unseen stimuli are initially encoded identically, but after ~270 ms, the information is selectively amplified on 'seen' trials." (p.12), with parietal and prefrontal cortices showing the first clear signs of difference between conscious and unconscious trials.

Gaillard et al. (2009) report essentially the same result with intracranial encephalography, using a masking paradigm similar to that of Dehaene et al. (2001). They write: "None of our four analyses … ever detected any event specifically associated with conscious reportability before 150 ms, and in most of them, the main differences were found after 300 ms." (p.485). Again, prefrontal cortex activity and late local sensory activity track conscious perception. Early local activity doesn't.

This sits well with prefrontalism and some versions of localism. One problem for the latter view—aside from the slightly late timing relative to what most localists believe (e.g., Lamme, 2015)—is that late local activity could correlate with attention instead of conscious perception (Macknik & Martinez-Conde, 2007).

Wyart et al. (2012) showed that late prefrontal activity (measured with MEG) correlates with conscious perception in masking. Again, early activity in sensory areas correlates with objective stimulus presence, not subjective reports. Late activity in sensory areas correlates with reported visibility. Wyart et al. controlled for the effect of endogenous attention by combining their task with a cueing paradigm. They showed that the correlate of visibility in PFC does not *result* from attention to the stimulus. Instead, it might be involved in re-orienting attention. Following the Wyart et al., this effect "runs opposite to the usual view according to which spatial attention controls conscious access" (p.10). Meanwhile, a re-orienting of attention on conscious trials might partly explain the late increase in local activity.

Together, these results suggest that early local activity—before 150 milliseconds—scales with stimulus presence and signal strength. Late activity, both local and prefrontal, correlates with conscious perception (see also Fisch et al. 2009 for a similar result combining visual masking with electrocorticography (ECoG)). Late local activity could, in turn, reflect feedback from prefrontal structures—consistent with relationalist prefrontalist views, could result from uncontrolled experimental confounds such as the re-orienting of attention on conscious trials, or could result from late recurrence loops within visual areas.

In line with relationalist views, studies from Thompson & Schall (1999, 2000) suggest a role for feedback from PFC to visual cortex in masking. Their electrophysiological recordings showed that 'visual cells' in the Frontal Eye Field (FEF)—cells that do not project to oculomotor structures—track conscious visual perception in a detection task with masked stimuli. According to Thompson & Schall, these neurons, in turn, modulate activity in extrastriate visual areas through feedback connections. Huang et al. (2020) also conclude that feedback from FEF and dorsolateral PFC (dlPFC) to early visual areas mediates awareness-dependent figure-ground segregation in a masking task.

A visual masking study by Lau & Passingham (2006) controlling for the 'performance capacity confound' confirms that local activity scales with signal strength and performance rather than conscious perception (Lau, 2008; Morales et al. 2015, 2022). By controlling for differences in performance between two conditions of a discrimination task that differed in reported visibility, Lau & Passingham (2006) found that the only activity (measured with fMRI) tracking conscious perception was in dlPFC. This experiment reproduced an early result from Sahraie et al. (1997) comparing conscious and non-conscious perception with similar performance levels in blindsight patient G.Y.

Caveat: a failure to find a difference in local activity between conscious and non-conscious conditions does not imply that there is no difference. Measurement tools like fMRI have relatively low sensitivity, and we should expect false negatives (Cremers et al. 2017). In addition, the evidence presented so far is mostly problematic for local views according to which the NCC is both *local* and *early* (Zeki, 2003)[5]. But this empirical evidence does not clearly distinguish between prefrontalist views and local views positing that consciousness correlates with (relatively) late local activity (Lamme, 2010, 2015).

Three questions will have to be settled: (1) whether late local activity results from experimental confounds or correlates with consciousness; (2) whether late local activity is driven

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[5] See also Stein et al. (2021) for a visual masking experiment indicating that activity in early visual areas representing stimulus properties is not, by itself, sufficient for conscious experience.

by feedback from PFC or recurrence loops within visual areas; and (3) if feedback from PFC turns out to be important, whether is *constitutive* of the neural state sustaining conscious experience, or whether its contribution is merely *causal*.

Binocular Rivalry and Bistable Perception

In binocular rivalry an image presented to one eye is unconscious because it competes with an incompatible image shown to the other eye—causing conscious perception to alternate between the two images every few seconds. PFC relationalists predict that a switch in conscious perception is constituted by a switch in recruited percept: one percept is recruited in the conscious state, then the other percept is recruited. They should thus (presumably)[6] predict an increase in PFC activity corresponding to the occurrence of the switch. PFC re-representationalists not only (presumably) predict an increase in activity accompanying the switch, but also that conscious contents are (re-)represented in PFC.

The typical finding from binocular rivalry studies is that neurons early in the visual processing hierarchy tend to track the physical stimuli, while anterior visual regions tend to be more selective to the conscious percept (Hesselmann et al. 2011; Leopold & Logothetis, 1999; Sheinberg & Logothetis, 1997). This is not to say that these neuronal populations do not track the unconscious percept. Studies by Hesse & Tsao (2021) and Cao et al. (2021) provide strong evidence that neurons in the fusiform face area (FFA) track the identity of faces even when participants do not report seeing them and cannot report their identity. Again, extreme forms of localism cannot account for these results.

Several reviews indicate that PFC activity—especially in the inferior frontal cortex—correlates with perceptual transitions in binocular rivalry and bistable perception, mostly based on fMRI results (Brascamp et al. 2018; Rees, 2007). But this evidence does not clearly distinguish between three possibilities: (1) a *causal influence* of PFC over perceptual transitions—for instance, attention signals from PFC might contribute to perceptual switches; (2) PFC *constitutes* the conscious percept—either together with early sensory activity, or by re-representing the relevant content; (3) PFC activity is a *consequence* of the perceptual switch (e.g., Block, 2020).

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[6] Why 'presumably'? Because from the 'perspective' of PFC, there's nothing so special about the switch in contents that occurs during binocular rivalry. Switching between one content and another in binocular rivalry could be just as demanding as any other switch in the contents of consciousness. Since this is commonly assumed in the literature, I wrote this section as if prefrontalists were committed to an increase in activity during rivalry and bistable perception switches. But I don't think prefrontalists should necessarily predict a detectable increase, for instance in BOLD signals, each time the contents of consciousness change.

A recent study by Weilhammer et al. (2021) provides some initial evidence for arbitrating between these alternative hypotheses in the case of bistable perception. Long story short, Weilhammer et al. combined Bayesian computational modeling with fMRI, and their result validated the following model: conflicting interpretations of the stimulus generate prediction errors that progressively accumulate in inferior frontal cortex (IFC) until a peak is reached and a feedback signal is sent back to visual areas to resolve the perceptual conflict by selecting a winning (conscious) interpretation. They further validated this model by showing that (theta-burst) transcranial magnetic stimulation (TMS) to IFC could reduce the frequency of switches in perceptual experience. Watanabe (2021) obtained a very similar result using a different TMS method, and could shorten the duration of perceptual alternations by inhibiting IFC (see also Vernet et al. (2015) for another convergent result). These results provide clear evidence against the view that PFC activity is only a consequence of the perceptual switches. Not only do prediction error signals start accumulating in IFC *before* the transitions, but Weilhammer et al. (2021) and Watanabe (2021) also provided *causal* evidence for a role of IFC activity in the occurrence of perceptual transitions. Dwarakanath et al. (2020) obtained converging evidence in the case of binocular rivalry.

Again, there is still an important unresolved issue. As in studies relying on visual masking, it is currently unclear whether PFC activity *causally* contributes to selecting the conscious percept or whether it (perhaps partly) *constitutes* the relevant conscious percept.

Motion Induced Blindness

In motion-induced blindness (MIB), a salient visual target on a moving background spontaneously disappears from visual consciousness and subjectively reappears a few seconds later. One can use this phenomenon to disentangle the effects of consciousness and attention since it is one of the few phenomena exemplifying an *adverse effect* of attention on consciousness—cases where attention to a target makes it more likely to subjectively disappear (Lou, 1999; Schölvinck and Rees, 2009).

Schölvinck and Rees (2010) report that local activity in sensory areas—specifically in areas V1 and V2 that retinotopically represent the targets—*increases* as targets subjectively *disappear*. By contrast, physically removing the targets decreases activity in these areas. Schölvinck and Rees thus show that local activity can either increase (in the case of subjective disappearance) or decrease (in the case of physical disappearance) between phenomenologically matched conditions. Davidson et al. (2020) pushed this a step further. They presented participants with a MIB setting where targets and backgrounds flickered at different frequencies while measuring brain activity with EEG. With this method, Davidson et al. recorded the SSVEP (steady-state visually evoked potentials)—which reflect neural oscillations in response to rhythmic stimuli, induced by the target and background, before and during stimulus disappearance. They found that SSVEPs for target and background *increased* before the illusory disappearance of targets—a result that did not occur for phenomenally matched physical disappearances[7]. Meanwhile, Libedinsky and Livingstone (2011) reported that activity in the FEF closely tracked reports of disappearance, irrespective of whether the disappearance was physical or subjective. These MIB results indicate a dissociation between at least some kinds of local activity and visual consciousness (but see Donner et al. 2008), while PFC activity reliably tracks conscious perception. As a side note, a role for prefrontal structures in MIB fits well with the 'perceptual scotoma' account (New & Scholl, 2008). This account hypothesizes that MIB results from a process of perceptual inference—the system discards activity generated in visual cortex by the non-moving target on a moving background because this activity is akin to a perceptual scotoma (Dijkstra et al. 2022; New & Scholl, 2008, 2018).

Attentional effects

It is worth mentioning studies investigating attentional effects: the attentional blink, inattentional blindness, and change blindness. I only mention them in passing because localists often hold that these effects do not abolish conscious perception but simply the ability to notice and report about one's conscious experiences (Block, 2007; Lamme, 2015, 2018). Somewhat unsurprisingly given the nature of these effects, evidence indicates that PFC is systematically associated with conscious perception in those instances as well, while local activity is often engaged in similar ways irrespective of whether the targets are reported or not (e.g. Beck et al. 2001; Turatto et al. 2004; Sergent & Dehaene, 2004; Sergent et al. 2005; Mashour et al. 2020).

Detected versus missed

Perhaps the easiest contrast one can draw to learn more about conscious perception is between 'hits' and 'false alarms' versus 'miss' and 'correct rejections' in detection tasks. Simple 'yes/no' detection is indeed intuitively associated with consciousness. van Vugt et al. (2018) conducted what is perhaps the most relevant study in this context. They taught monkeys to detect and report the presence of a circle by making a saccade to its location (if detected), or making a saccade to a dot (if the target is absent). During this task, they recorded multiunit activity in

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[7] See also Smout & Mattingley (2018) for a case where attention to a subjectively invisible stimulus increases visual activity in response to this stimulus.

visual areas V1, V4, as well as in the ventral and dorsal PFC. Focusing specifically on target-present trials, van Vugt et al. computed an index measuring the difference in activity between hits (stimulus present detected) and misses (stimulus present undetected). Of the three areas, PFC showed the greatest difference between hits and misses (Figure 1B). Meanwhile, activity in V1 and V4 seemed to track objective stimulus presence much more reliably than subjective reports. These areas remained highly activated on miss trials, and showed virtually no difference between false alarms (in which the monkey erroneously reported stimulus presence) and correct rejections (in which the monkey correctly reported stimulus absence) (Figure 1A).

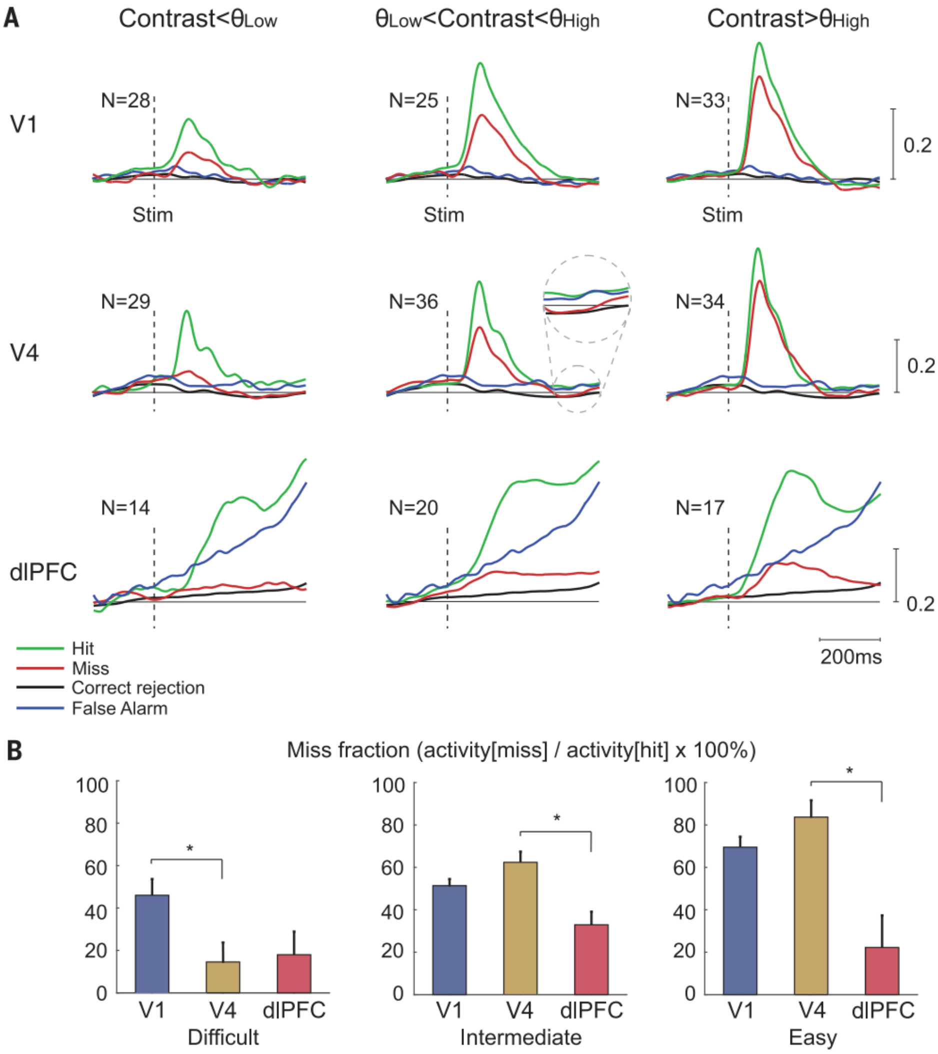

Figure 1. Source: van Vugt et al. (2018). (A) Averaged activity in areas V1, V4 and dlPFC across three contrast levels, separated for hits, miss, correct rejection, and false alarm trials. Visual activity correlates with stimulus presence, while PFC activity correlates with the decision. (B) Index of the difference in activity between hits and misses.

This result is consistent with several studies in the tactile domain (de Lafuente and Romo 2005, 2006; see Romo and Rossi-Pool (2020) for a review). Using electrophysiological recordings in monkeys during a tactile detection task, de Lafuente and Romo (2005) showed that early sensory activity scales with stimulus strength irrespective of whether the stimulus is detected. Meanwhile, PFC activity (in particular, in the pre-supplementary motor area, which is densely connected with dorsolateral and dorsomedial PFC) correlates with the decision. de Lafuente and Romo complemented this study with a control task to show that this activity is not associated with the report, or motor preparation. In this task, the correct response button is illuminated at the start of every trial. So, monkeys know which button they have to press even before stimulus presentation. In this control task, if PFC activity correlates with the decision to report, or motor preparation, we should observe it before stimulus presentation. This is not what de Lafuente and Romo found. PFC activity is virtually identical in the standard detection task and in this control task, which suggests that it correlates with perception and not just with the decision to report.

Conscious and unconscious flicker detection

I finish this overview by discussing a group of results comparing conscious versus non-conscious flicker detection. Neurons in the visual cortex can track visual flickers at rates well above the flicker fusion threshold—where no flicker is detected at all (Gur & Snodderly, 1997; Shady et al. 2004; Vul & MacLeod, 2006). Using chromatic red-green flickers perceived as uniform yellow, Jiang et al. (2007) showed that chromatic flickers lead to broad activations of visual areas without any associated consciousness of the red-green flicker. Similarly, Carmel et al. (2006) presented participants with a flickering light at the fusion threshold such that the flicker was sometimes consciously perceived and sometimes not. In this case, the main difference between consciousness of flicker and no consciousness of flicker occurred in frontal and parietal areas (measured with fMRI). They did not find a significant difference associated with consciousness of flicker in early visual areas. Zou et al. (2016) used red-green flickering gratings perceived as uniform yellow and obtained essentially the same result. Invisible chromatic flickers significantly increased V1, V2, V3, and lateral occipital cortex activity, while prefrontal areas only responded to subjectively visible flickers. Prefrontal activity thus seems to be the main difference between unconscious tracking of flicker and conscious perception of flicker.

Interim conclusion on contrastive analysis

This is a small sample of the work done in the past twenty years with the contrastive analysis method (for more, see Morales & Lau, 2020; Mashour et al. 2020). Undoubtedly, many of these studies have confounding factors. But together they paint a broad picture of the research on the neural correlates of consciousness obtained with contrastive analysis. Local activity—especially *early* local activity—does not discriminate very well between conscious and non-conscious conditions, whereas PFC activity does. The fact that the same result has been obtained with so many experimental paradigms further indicates that it does not stem from the specific paradigms used in these studies (e.g., visual masking). Localists have to account for these results. They typically do this by pointing to a set of confounding factors at the heart of the contrastive analysis itself (Koch et al. 2016; Tsuchiya et al. 2015). I discuss these confounding factors in contrastive analysis next before turning to causal sources of evidence.

2.2. Confounding factors in contrastive analysis

What confounding factor?

The main problem with contrastive analysis is that it's difficult to distinguish between pre-requisites, correlates, and consequences of consciousness (Aru et al. 2012; de Graaf et al. 2012). In particular, some have argued that PFC activity *seems* to correlate with consciousness only because of task-related demands, such as the requirement for subjective reports (Koch et al. 2016; Tsuchiya et al. 2015)—a view that I used to hold (Michel, 2017).

With Jorge Morales, we have provided a detailed response to this argument (Michel & Morales, 2019), and I cover some of the most recent developments below. But let me start by noting that task-related confounding factors are a problem for everyone. For instance, the fact that late local activity often seems to correlate with consciousness might be due to top-down attention directed to the stimulus on conscious trials. Macknik & Martinez-Conde (2009) have notably argued that feedback within the visual system—often considered by localists as a correlate of consciousness (Lamme, 2010, 2018)—is mainly dedicated to attentional facilitation and suppression. In the same way, general increases in activity in visual areas between conscious and unconscious trials might reflect a higher capacity for performing visual tasks between these two conditions, or signal strength differences—as we saw earlier (Lau & Passingham, 2006; Lau, 2008; Morales et al. 2015, 2022).

Now, part of the report-related activity is matched between conscious and non-conscious conditions. That's for the simple reason that participants provide subjective reports in both conditions. If the increase in PFC activity were due to reports themselves, we should find it in the unconscious condition too. But we don't. So what, exactly, are the confounding factors supposed to be? In a nutshell: extra cognitive processing, including noticing that the stimulus is present, sub-vocal naming, associative thinking, and above all, maintenance of stimulus properties in working memory.

Sub-vocal naming, thoughts about the stimuli, or associative thinking, can't constitute significant confounding factors. That's again because these factors are presumably matched between the conscious and non-conscious conditions. There's no reason to expect that subjects only have thoughts, associative thinking, and sub-vocal naming in response to consciously perceived stimuli. Perhaps they're also thinking things like: "I'm sure I didn't see any flicker this time". But, most likely, participants don't think much about the task at all—psychophysics experiments aren't that interesting, especially after a few hundred trials.

The main confounding factor then seems to be the asymmetry in working memory maintenance. With Jorge Morales, we have argued that subjects do not have to maintain stimulus identity in working memory (especially in detection tasks). All they need to maintain is an abstract decision, such as 'seen' or 'not seen'—and maintenance of that decision is matched between conscious and non-conscious conditions (Michel & Morales, 2019).

In response, Pitts & Ortego (2020) remarked that just because participants don't need to maintain stimulus identity in working memory doesn't mean they don't do it. Participants could maintain 'incidental memory'. They write:

> if we were to pause the experiment at any moment (or even wait until the experiment is over) and ask the subject surprise questions about the color, shape, or location of the stimulus, they would almost always be able to report these basic stimulus properties. This is called "incidental memory", and even in more cognitively-demanding tasks … memory performance is fairly good even for task-irrelevant stimuli (p.2)

But if incidental memory, rather than *active* working memory maintenance, is the culprit, then there's hardly anything we can do about it. This is unfortunately true of 'no-report' paradigms too. And if it weren't true that participants maintained incidental memories of the stimuli, one could legitimately doubt that the participants consciously perceived them. That's at least what I would think if participants were unable to answer a single question about the stimuli.

Fortunately for us, incidental memory maintenance might not significantly affect measurements of brain activity. Several studies have reported an absence of persistent stimulus-related activity during the maintenance of items in memory (Masse et al. 2020; Rose et al. 2016; Sreenivasan et al. 2014; Stokes, 2016). This kind of 'activity-silent' memory maintenance doesn't constitute a confounding factor. In addition, the idea that representations of visual properties are *maintained* in PFC is currently controversial, given some evidence indicating that these representations are instead maintained in visual areas (for a review on the 'sensory recruitment model' of working memory, see D'Esposito & Postle, 2015).

Ultimately, we will learn a lot from controlling for report-and-cognition-related confounding factors. But we are also entitled to strong arguments before throwing away the past twenty years of hard work based on the suspicion that all these results are so severely confounded that they don't tell us anything about the neural bases of conscious perception[8].

Contrastive analysis without reports

Several studies have conducted contrastive analysis in 'no-report' paradigms (Tsuchiya et al. 2015). We have previously reviewed these results with Jorge Morales (Michel & Morales, 2019). In the interest of space, I only cover some of the most recent developments.

Some of these recent developments concern binocular rivalry. A study by Frässle et al. (2014) has been quite influential. They compared brain activity in binocular rivalry versus replay (i.e., 'fake' rivalry where stimuli actually alternate) during perceptual transitions, in two conditions—one with and one without reports. PFC activity compared to replay was severely decreased in the no-report condition (even if the superior frontal gyrus and the inferior frontal gyrus remained more active compared to replay even without report (Zaretskaya & Narinyan, 2014)). Passingham (2021) provides a good explanation for this result:

> The reason why there was no activation in the contrast of the passive condition with replay is presumably that the PF cortex was activated in both conditions. The explanation for why it was more activated in the active condition than replay is presumably that it was more difficult for the subjects to decide on their reports during rivalry. The lesson is that the results of no report studies are not valid unless the images are compared against baseline. In too many studies the comparison is with another condition, and this means that there is a danger that the activation of the PF cortex is subtracted out. (p.400-401).

A more recent study using intracranial recordings in monkeys did find neural activity in PFC representing the conscious stimulus during binocular rivalry alternations in a no-report paradigm (Kapoor et al. 2022). Block (2020) noted that post-perceptual cognition could account for this result: "subjects whose only task is fixating a dot may have thoughts about the noticeably different stimuli, causing prefrontal differences" (p.1). The debate is far from settled, but I agree with Panagiotaropoulos et al.'s response (2020):

> 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

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[8] Other confounding factors that do constitute a genuine problem for contrastive analysis, such as the performance capacity confound, have unfortunately not attracted nearly as much attention (Lau, 2008; Morales et al. 2015, 2022).

> 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. (p.1)

Thoughts about the stimulus explain Kapoor et al.'s finding only if *stimulus-specific thoughts systematically occur for each subjective switch*. Without stimulus-specific thoughts, decodability of specific contents is unexplainable. So, for the argument to work, monkeys aren't allowed to entertain thoughts (in their language of thought, no less) that are not stimulus-specific, such as 'Oh there's the change again' or 'How many of those switches will I have to look at before getting a reward?!' While it could be true that bored monkeys could entertain systematic, stimulus-specific thoughts in a way that would lead to decodable contents, that seems unlikely[9].

A success story among no-report paradigms is a series of experiments by Pitts et al., indicating that the P3b wave detected with EEG—long thought to correlate with consciousness[10]—is likely not a correlate of conscious perception (Pitts et al. 2012, 2014; Cohen et al. 2020). These experiments manipulated task relevance and found that conscious perception correlates with the P3b only when the stimuli are task-relevant. Why is that important? Because global workspace theorists (used to) predict that the P3b wave is a correlate of consciousness (Dehaene & Changeux, 2011). A popular account of the P3b is that it correlates with working memory updating (Polich, 2007). Given the proximity between global workspace and working memory, finding conscious perception without P3b could be evidence against global workspace.

So what, then? Sergent et al. (2021) bring some clarity. They confirmed Pitts et al.'s finding by contrasting report and no-report auditory detection tasks. But they also note:

> we could demonstrate that the late sustained waveform that signs conscious access in the absence of a task … is included in the P3-like waveform observed in the active condition. In other words, the P3-like waveform observed when making this very general contrast of stimulus presence versus absence during active sessions, is actually a composite waveform that includes two overlapping components: the signature of conscious access *per se*, with its bilateral positivity, and an additional central positivity that corresponds to the P300 in a strict sense, which specifically reflects decision processes. (p.12)

As a bonus, PFC activity inferred from source reconstruction analyses performed on the EEG signal still correlates with consciousness even without reports. Additional investigations of the

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[9] A more obvious confound is that if confidence in favor of each stimulus is computed automatically in PFC, even when no confidence ratings are required, the activity tracked by Kapoor et al. in PFC could reflect confidence in the (subjectively) perceived stimulus.

[10] For the anecdote, Posner (1986) suggested that the P3 wave could "be thought of as being related to conscious awareness of a stimulus" (p.168), and dated this view back to an article by Goff (1969). So, the P300 has indeed been hypothesized as a correlate of consciousness for quite some time.

nature of the P3b wave further indicate that it could simply correlate with the detection of a relevant target (Nieuwenhuis et al., 2005), or with task-relevant categorization (Kok, 2001), instead of working memory encoding itself (see Rac-Lubashevsky & Kessler, 2019 for a review). Failing to find a correlate of task-relevant categorization for task-irrelevant stimuli is somewhat unsurprising, but it's still good to know that P3 doesn't correlate with consciousness[11].

I refer the readers to Michel & Morales (2019) for a more complete take on this 'report argument'. Long story short: we concluded that the no-report literature indicates that PFC is a NCC. Still, the increase in activity associated with consciousness might be somewhat more subtle than assumed by global workspace theorists (see Dellert et al. (2021) for a similar conclusion).

I am ultimately quite skeptical about many of these paradigms. Confounding factors such as 'cognition' (Block, 2020), automatic confidence computations, the *disposition* to re-orient attention, or incidental memory (Pitts & Ortego, 2020), are likely to remain confounding factors even without reports. PFC also receives fast direct visual inputs from FEF that will naturally spread in PFC (Bellett et al. 2022; Thompson & Schall, 1999, 2000), and will appear to correlate with consciousness (of course, they *could* be NCCs) if signal strength is unequal between the conscious and non-conscious conditions. Under such conditions, signals from visual areas will also naturally spread farther in the processing hierarchy in the conscious compared to non-conscious condition, *perhaps for no particular reason*—even under conditions of passive viewing, when stimuli are task-irrelevant, or unattended. Attempting to completely suppress these signals by manipulating task demands seems unfeasible, and any no-report paradigm using sufficiently sensitive measurement methods will likely find such signals, which will appear to correlate with consciousness, even without reports or tasks. Approaching NCCs from different research angles might be the way to go: these studies can be complemented with experiments attempting to match confounding factors across conditions. *Ceteris paribus*, not *ceteris absentibus*.

2.3. Causal Evidence

Correlational evidence from contrastive analysis is not the only source of evidence for prefrontalism. Causal evidence also provides an increasingly consistent picture in which feedback from PFC is critical for consciousness, and has the potential to reveal mechanisms down to the cellular level (Almeida, 2022; Aru et al. 2020; Klatzmann et al. 2022; Mashour et al. 2020).

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[11] While this is clearly a fruitful application of no-report paradigms, prefrontal theories other than global workspace have no business to do with the P3b wave. Its source is more commonly located in the parietal cortex, or temporo-parietal junction, than prefrontal cortex (e.g., Bledowski et al., 2004; Linden, 2005). And higher-order theories predict that it can be elicited unconsciously—as seems to be the case (Silverstein et al., 2015; but see Naccache et al., 2016).

Neglect

Several studies demonstrate visual neglect and visual extinction—a failure to respond to a stimulus presented in the contralesional hemifield when presented at the same time as an ipsilesional stimulus—resulting from lesions to PFC, including the FEF and dlPFC (Adam et al. 2019; Crowne et al. 1981; Deuel & Farrar, 1993; Johnston et al. 2016; Latto & Cowey, 1971; Lawler and Cowey, 1987; Passingham, 2021, p.169-171). For instance, Crowne et al. (1981) showed that, following unilateral lesions to FEF, monkeys presented with two threatening stimuli, one in each hemifield, only responded to the stimulus presented on the ipsilesional side—a case of visual extinction. Many studies have also induced neglect across modalities in rats with lesions to dorsomedial PFC (Christakou et al., 2005; Corwin & Vargo, 1993; Cowey and Bozek, 1974; King & Corwin, 1993; Vargo et al., 1988, 1989).

These results from lesion studies are consistent with causal manipulations of FEF. Grosbras & Paus (2003) improved the detection of an otherwise subliminal stimulus by applying a single pulse of transcranial magnetic stimulation (TMS) to FEF 40 milliseconds prior to stimulus presentation (see also Moore & Fallah, 2001). Several subsequent studies replicated this effect and showed that rhythmic 30 Hertz TMS pulses to FEF, which drive oscillatory neuronal activity, are particularly effective for improving visual detection (Chanes et al. 2012; Vernet et al. 2019). Stengel et al. (2021) pushed this further by showing that increased phase synchrony between prefrontal and parietal neuronal populations drives the effect. Finally, Quentin et al. (2015) showed that the strength of this effect correlates with the volume of the superior longitudinal fasciculus white matter pathway—in particular, its dorsal component connecting PFC to the parietal cortex, a result consistent with global workspace theory.

Of note, de Schotten et al. (2005) induced visual neglect in a human patient—assessed on a line bisection task—by electrical stimulation of the superior occipitofrontal fasciculus, a pathway terminating in the lateral prefrontal cortex. The integrity of this pathway is a good predictor of neglect following strokes (Bartolomeo, 2007; de Schotten et al. 2014). Herbet et al. (2017) also induced neglect by electrically stimulating the inferior occipitofrontal fasciculus. These results are important since extensive visual processing in the ventral visual pathway can be preserved in neglect and visual extinction, thus indicating that local processing is not sufficient for consciousness (Driver et al. 2001; Driver & Vuilleumier, 2001; Rees et al. 2000, 2002; Sackur et al. 2008; Vuilleumier et al. 2001, 2002).

Object Recognition

An essential role for PFC in visual perception is during object recognition. This idea is not new (Bar, 2006; Hochstein & Ahissar, 2002), and has more recently been bolstered by mental architectures positing a significant role for prediction in perception (e.g., Dürschmid et al. 2019). Representations of occlusion relations and occluded objects are interesting cases for our discussion. Using electrophysiological recordings in monkeys, Fyall et al. (2017) found that ventrolateral PFC (vlPFC) neurons represent the occlusion relation. The activity of shape-selective neurons in V4 is modulated accordingly by feedback from vlPFC, thus suggesting that vlPFC participates in the phenomenon of amodal shape completion. Choi et al. (2018) further validated a model postulating that vlPFC does this by feeding back predictions about the shapes of occluded objects. This is a pretty important role for PFC: what we see in ordinary life is often occluded, thus rendering amodal completion omnipresent in naturalistic settings. Kar & DiCarlo (2021) also demonstrated the relevance of vlPFC for object recognition by showing that pharmacological inactivation of this area selectively degraded recognition performance and modulated object representations in the inferior temporal cortex, especially for 'challenging' images (see also Bichot et al. 2019; Ciaramelli et al. 2007).

'But what does object recognition have to do with consciousness', you ask. At this point our discussion intersects with a debate in the philosophy of perception about whether or not experience presents us only with 'thin' properties. As Siegel puts it (Siegel & Byrne, 2016), the list of thin properties includes "colors, textures, spatial relations, shapes (including volumes), luminance, and motion … according to the Thin View, the only properties presented in experience are limited to the ones on the list" (p.1). According to the Rich View, on the other hand, visual experience presents us with properties that are not on this list, including *kinds*, such as being an anchovy or a volcano; *causal* properties; *affordances*, and *relations*, such as the relation of occlusion mentioned above (e.g., Hafri & Firestone, 2021). If we *do* experience some of these 'rich' properties—if representing these properties makes a phenomenological difference, then a kind of modest prefrontalism becomes somewhat irresistible given the role of PFC in object recognition and the representation of other 'rich' properties. PFC would thus be involved in a variety of visual experiences—those complex experiences presenting us with the rich properties we know and love[12]. This is not to say that PFC is not involved in representing thin properties.

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[12] This kind of 'modest prefrontalism' could be exemplified in the literature by the 'level of processing' approach, according to which PFC might be involved in some visual experiences, but not all of them, depending on the required level of processing (e.g., Windey et al., 2013; Derda et al., 2019). This view is worth noting as a middle path between localism and prefrontalism. But localists are likely to insist that in those cases the contribution of PFC is only causal, and not constitutive. Meanwhile, prefrontalists are

For instance, Liu et al. (2019) found that illusory movement in the double drift illusion is represented in PFC, while visual areas only track physical movement that does not correspond to the reported illusory percept.

Feedback from PFC: Anesthesia, NMDA receptors, and schizophrenia

If feedback from PFC is involved in all instances of conscious perception—as relationalist theories would have it—deficits impacting these feedback connections should affect conscious perception while also sparing unconscious perceptual effects which depend on feedforward activity. This prediction, or something close to it, can be tested partly because feedforward and feedback propagations of activity rely on somewhat different neurobiological mechanisms (Froudist-Walsh et al. 2021; Goulas et al. 2021; Klatzmann et al. 2022; Self et al. 2012; Yang et al. 2018). Fast excitatory feedforward transmission seems to depend in large part on AMPA receptors. Slower feedback transmission depends in large part on NMDA receptors. Accordingly, neuronal firing in response to visual stimuli in visual areas like V1 mostly depends on AMPA receptors, while firing in prefrontal areas like dlPFC primarily depends on NMDA receptors (Dawson et al. 2013; Wang et al. 2013; Yang et al. 2018).

At high doses, NMDA receptor antagonists such as ketamine cause loss of consciousness. Several studies suggest that they do so by disrupting fronto-parietal communication and feedback from PFC (Bonhomme et al., 2016; Hudetz & Mashour, 2016; Lee et al. 2013; Palanca et al. 2015). These results are consistent with studies using other anesthetics, most notably sevoflurane anesthesia (see Mashour, 2019 for a review). Imas et al. (2005) showed that feedforward signals from visual cortex to PFC were preserved in anesthetized rats, while feedback signals from PFC were suppressed. This conclusion was later corroborated in humans with various anesthetics, including ketamine (Jordan et al. 2013; Lee et al. 2013; Ranft et al. 2016). In a groundbreaking study, Pal et al. (2018) showed that cholinergic manipulation of PFC—but not of two parietal targets—could *reverse* anesthesia in rats (see also Tasserie et al. 2022). As noted by Knotts et al. (2018) in reaction to this study, "the importance of restoring consciousness from anesthesia cannot be denied lightly." (p.571).

At lower doses, NMDA receptor antagonists such as ketamine can reproduce the symptoms of schizophrenia (Krystal et al. 1994). This is consistent with the finding that schizophrenia itself is associated with abnormal regulation of NMDA receptors (Abi-Saab et al. 1998; Coyle, 2006; Olney & Farber, 1995).

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likely to insist that, without PFC, *none* of the local representations—not just those representing rich properties—would be recruited for consciousness.

The study of schizophrenia is thus doubly relevant for investigating the role of feedback from PFC in conscious perception. Not only because abnormal NMDA regulation is involved, but also because PFC is one of the regions most affected by schizophrenia, as indicated in imaging studies (Hill et al. 2004), but also by behavioral performance on executive tasks recruiting PFC (e.g., Joyce et al. 2002; Salgado-Pineda et al. 2007). Multiple experiments have confirmed the predicted dissociation between preserved unconscious feedforward processes and impaired conscious processing (for a review, see Berkovitch et al. 2017).

Backward masking thresholds for conscious perception are higher in schizophrenia: patients need much longer intervals between the onset of the target and the onset of the mask—or stimulus onset asynchrony (SOA)—to achieve performance levels similar to controls (Green et al. 2011; Herzog & Brand, 2015). This is not due to medication: healthy relatives of patients also need longer SOAs compared to controls (Chkonia et al. 2010; Green et al. 1997). Berkovitch et al. (2021) found that variations in masking threshold correlate with long range connectivity in the inferior fronto-occipital pathway (see also Lefebvre et al. 2021), and not with connectivity in the inferior longitudinal fasciculus, which connects the occipital and temporal lobes.

Meanwhile, subliminal processing seems to be preserved in schizophrenia. In an early experiment by Dehaene et al. (2003), patients and controls compared whether a target number appearing after a prime was higher or lower than five. The prime was either congruent with the target (both higher or lower than five) or incongruent, and either masked or unmasked. The priming effect in the masked condition was identical for patients and controls: faster responses on congruent trials; slower responses on incongruent trials. But the priming effect disappeared in the unmasked condition for patients, while it was preserved for controls. Unconscious priming is preserved, while conscious priming is affected.

Similarly, Grandgenevre et al. (2015) tracked the eye movements of patients and controls as they detected changes in a change blindness task. Consistent with an increased threshold for consciously detecting whether a change occurs or not, patients took longer to detect changes, and their detection performance was lower than control participants. But, astonishingly, implicit detection of the change—indicated by eye movements towards its location—occurred *faster* in patients compared to control subjects[13]. Again, unconscious detection of the change is preserved, while conscious detection is impaird.

Many similar priming results have been reported, suggesting that these effects are quite robust (Del Cul et al. 2006; Grave et al. 2021; Huddy et al. 2009; Seymour et al. 2016; See Berkovitch et al. (2017) for a review). Morgan et al. (2006) and Stefanovic et al. (2009) induced similar dissociations in healthy subjects with low doses of ketamine. All in all, conscious processing seems impaired in schizophrenia and with low doses of NMDA receptor antagonists like ketamine, while subliminal processes are preserved. Relationalist prefrontalist theories account for these results.

2.4. Prefrontal lesions: what's going on?

As you can see there's some causal evidence for prefrontalism. But you might also think that there is causal evidence against it. Some have argued that significant prefrontal lesions leave consciousness untouched, as indicated by the patients' reports about their experiences following the lesions (e.g., Boly et al. 2017; Kozuch, 2014). This stands in stark contrast with some of the evidence reviewed above. So what's going on?

The case studies mentioned by Boly et al. (2017) or Kozuch (2014) do not provide evidence against prefrontalist theories. In fact, it is unclear whether case studies relying on spontaneous reports from patients can provide such evidence, even in principle.

For lesions to PFC to count as evidence against prefrontalist theories, one would need to find a case where (1) a patient reports having an experience; and yet (2) the prefrontal mechanisms hypothesized as being relevant for that experience are impaired. But here's the thing: (1) counts as evidence against (2).

Let's take an example. Global workspace theory says that I have a phenomenal experience of red when a mental representation of red is cognitively accessed. Phenomenal consciousness and cognitive access are co-extensive. If a patient reports experiencing red, that means that the relevant representation is cognitively accessed. But if the relevant representation is cognitively accessed, that's evidence that cognitive access mechanisms are not relevantly

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[13] This is just one of many dissociations between conscious perception and the sensory representations influencing eye movements (see Spering & Carrasco (2015) and Zhaoping (2019) for reviews). The result obtained by Grandgenevre et al. (2015) has interesting similarities with what Kato et al. (2021) found in blindsight monkeys. In this eye-tracking, visual search experiment, monkeys had to look for a target presented in the blind visual field. Once you've found something you're searching for, the normal thing to do is to stop looking for it. Here, the monkeys' eyes were attracted to the target in the blind field, but even after stopping right on the target, monkeys just *kept looking for it*, indicating that they had no idea that they had found the target.

impaired. Had these mechanisms been relevantly impaired, the relevant representation would not have been accessed. And had the relevant representation not been accessed, the patient would not have reported experiencing red.

Take higher-order theories now. These theories all have in common that they hypothesize that a mental state is conscious only if one is aware of oneself as being in that state. If a patient reports experiencing red, that means that she's aware that she's seeing red. The fact that she's aware that she's seeing red implies that the relevant metacognitive mechanisms are not relevantly impaired. Had the relevant metacognitive mechanisms been relevantly impaired, the patient would not have been aware that she was seeing red. And had the patient not been aware of that, she would not have reported experiencing red.

By their very nature, prefrontalist theories imply that the mechanisms relevant to consciousness are also necessary for providing reports about conscious experiences. It follows that any report of having a conscious experience is also evidence that the relevant mechanisms are preserved. Without those mechanisms being preserved, the patients could not have provided the relevant reports. While localist and prefrontalists disagree on whether cognitive access and metacognition are involved in consciousness or not, the fact that *reports* about occurrent experiences require these functions is not under debate. As a result, none of the lesion studies based on spontaneous reports from the patients provide any evidence against prefrontalist theories, or could provide such evidence even in principle—at least as far as global workspace theory and higher-order theories are concerned.

Still, you might ask: "why are reports of complete loss of consciousness following PFC lesions so rare?" I have three points in response.

The first is survivorship bias. PFC is a pretty big chunk of the brain. The kind of bilateral lesions required to completely destroy it would probably leave most people dead, and the few lucky survivors are unlikely to be in the type of conditions in which they can be tested in experiments. Patients who can't perform any task don't make for good case studies. And therefore, we should expect the literature on the effects of substantial PFC lesions to be biased. The few patients who can be tested are those with less extensive lesions, often tested long after the lesions have occurred. For reasons related to redundancy and degeneracy, already expressed by Odegaard et al. (2017), these patients are unlikely to provide decisive evidence.

Second, as we saw above, cases like visual neglect and anesthesia—in which interventions can be more carefully controlled and the effects more carefully evaluated, do provide some causal evidence. Other cases include, for instance, loss of consciousness in prefrontal seizures, where the loss of consciousness seems to depend on abnormal synchrony between PFC and parietal cortex (Bonini et al. 2016). More subtle impairments have also been reported. Barceló et al. (2000) report a higher miss rate in a detection task for patients with unilateral lesions to PFC. Del cul et al. (2009) showed that patients with PFC lesions have a higher backward masking threshold, with a greater impact on visibility ratings than objective performance. Similarly, Colas et al. (2019) report that the contrast required to perceive Gabor patches at threshold in patients with prefrontal lesions correlates with damage to dlPFC and the superior longitudinal fasciculus. Rounis et al. (2010) also showed that patients were less likely to report a target as visible following theta-burst transcranial magnetic stimulation to PFC, compared to a control condition. This effect was specific to visibility ratings and did not impact objective performance on a discrimination task—a result consistent with higher-order theories of consciousness.

Final point: spontaneous reports from patients with PFC lesions might be somewhat unreliable, given the possibility of 'phenomenal anosognosia'. Perhaps these patients literally don't know what they're missing.

Anosognosia—a condition in which patients remain unaware of their illnesses or deficits—is surprisingly common, even for deficits that seem like they should be obvious (McGlynn & Schacter, 1989). For instance, anosognosia for hemianopia—a condition in which half of the visual field is missing, often following a stroke, is quite prevalent (Chokron et al. 2020). Estimates vary a lot, but the prevalence of anosognosia for hemianopia ranges from 19% (Baier et al. 2015) to 62% (Celesia et al. 1997), and up to 88% (Bisiach et al. 1986) of hemianopic patients[14]. These patients do not spontaneously report anything different about their visual experiences after the stroke—even when explicitly asked, and do not complain about visual deficits when half the visual field is missing. Some achromatopsic and hemi-achromatopsic patients are also anosognosic. These patients do not realize that they do not perceive colors in part, or the totality, of their visual field (Siuda-Krzywicka & Bartolomeo, 2019). These are just two examples indicating that just because a deficit seems like it should be obvious does not mean that patients will spontaneously report it.

Prefrontalists should predict that phenomenal anosognosia is quite likely following PFC lesions. That's for two reasons. First, metacognition and cognitive access should both be involved in the detection of perceptual deficits, and we should expect PFC lesions to affect these capacities (Chiang et al. 2014; Fleming et al. 2010, 2014; Hoerold et al. 2013; Rounis et al. 2010; Turatto et al. 2004). Second, evidence indicates that anosognosia for other deficits is associated with PFC dysfunctions. That's the case for anosognosia in fronto-temporal dementia

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[14] The main reason for this difference in estimates is probably that Baier et al. (2015) tested patients a week after stroke-onset while Celesia et al. (1997) tested 24 hours after stroke-onset.

(Munoz-Neira et al. 2019), Alzheimer's Disease (Guerrier et al. 2018), hemiplegia (Pia et al. 2004), and schizophrenia (Pijnenborg et al. 2020). As in all these other cases, we should thus expect PFC lesions to raise the probability of anosognosia. So, if prefrontalism is correct, patients might sometimes fail to notice phenomenal deficits following PFC lesions.

A similar point might apply in the case of null results obtained following electrical stimulation of PFC, reviewed by Raccah et al. (2021a). There would be much to say about this important challenge to prefrontalism, but in the interest of space, I refer the readers to the response made by Naccache et al. (2021) (but see Raccah et al. 2021b). Here, I will just say that future progress in this debate will probably require combining electrical stimulation with a behavioral task, instead of simply collecting spontaneous reports. If stimulations cause some kind of neglect, for instance, it's plausible that patients won't report anything. By definition, that's not a change in experience subjects can attend to. In the stimulation studies by de Schotten et al. (2005) and Herbet et al. (2017), for example, neglect would likely have gone undetected had it not been for the fact that the experimenters combined stimulation with a line bisection task (see also Ng et al. (2021) for an effect of electrical stimulations to PFC on self-evaluation).

To be clear, my claim is not that impairments of consciousness following PFC lesions are undetectable in principle. Instead, I claim that one cannot confirm the null hypothesis that the patient's consciousness is not impaired based on a simple report from the patient. Uncontrolled, spontaneous reports should be replaced by controlled experimental settings involving tasks specifically designed to assess consciousness. The results reviewed above obtained in rigorous experimental conditions provide clear causal evidence for prefrontalism.

Conclusion

I reviewed the evidence for prefrontalism about consciousness. I do not believe that any specific piece of evidence on its own will be able to convince someone skeptical about this view. My goal was instead to show how multiple sources of evidence converge toward the view that PFC plays a significant role in consciousness. Relationalist prefrontalist theories, in particular, seem to have good explanatory power. A challenge will be to further distinguish between these theories and localist theories hypothesizing that late (> 250 milliseconds) local activity correlates with conscious perception. While there is strong evidence indicating that initial stimulus-related activity occurs unconsciously, feedback to sensory areas seems relevant for consciousness. Relationalist views and some localist accounts both predict this result. Investigating the role played by PFC structures in this feedback will be important[15]. In the interest of space, I focused on building a constructive case for prefrontalism instead of explaining why I believe that localism is less likely to be correct. I refer the readers to Michel & Doerig (2021) and Lau (2021) for discussions of some of the relevant evidence.

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[15] If the results reviewed above are further confirmed, and feedback from PFC does play a role for consciousness, the thorny issue of determining whether it is *causally* relevant for conscious experience, or *constitutively* involved in consciousness, will have to be addressed. I sure hope we're not in a world where feedback from PFC is *causally necessary* for consciousness while not being *constitutively* relevant for it. In that worst case scenario, distinguishing between some forms of localism and relationalist prefrontalism will be very hard.

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