The role of Prefrontal cortex in conscious perception: The localist perspective

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Abstract

In recent years the role of pre-frontal cortex (PFC) in conscious perception has acquired great interest since it became a pivotal issue distinguishing among prevailing neuronal theories of human consciousness. One can identify three major, and conflicting, views of this role. The Globalist view proposes that PFC is a major hub in a global work-space whose activation is a critical component for any conscious experience. The High order thought theory argues that the PFC has a more specialized role underlying higher-order reflection or evaluation proposed to be an essential element of consciousness. By contrast, the localist view argues that conscious content is linked to localized activations in content-specific cortical areas with no privileged role assigned to pre-frontal cortex in conscious experience in general. According to the localist view- Just as posterior cortical areas underlie the conscious experience of visual perceptions- so does the pre-frontal cortex underlie the conscious experience of specific categories of conscious contents such as reporting, thinking, speech and introspection. Here I will review experimental evidence derived from human imaging and recordings, cortical lesions and direct electrical stimulation in awake patients. Findings from these three methodologies converge in supporting the localist view and a common fundamental principle by which each cortical area specializes in a specific and unique category of conscious contents.

Scope of the review

The Prefrontal Cortex (PFC) is likely the most complex and poorly understood part of the human cerebral cortex. Numerous studies have contributed to mapping and defining its various functions and subdivisions. The aim of the present review is not to cover this rich and rapidly growing literature. Rather my aim here is to focus on one specific issue: the role of the PFC in human consciousness. The PFC has emerged in recent years as central in the hotly debated endeavor to come up with a theory that may link brain activity with conscious experience. Thus it is of great interest to examine how the experimental data derived from studying the human PFC and the cortex in general supports or refutes the claims of these theories. This will be the focus of my review- at the exclusion of providing detailed account of the growing list of findings relevant the specific functions and specializations of the human PFC.

Is the PFC a hub in a global work-space?

A central insight regarding the potential function and adaptive value of conscious experience is that it allows flexible behavior. For example, being conscious of a familiar face allows us to decide whether to ignore the person, start a conversation, memorize the scene where we met etc. etc. Such flexible and wide repertoire of subsequent behaviors appears to be lacking or greatly reduced when we are exposed subliminally to this individual. This insight has been greatly expanded and emphasized as a crucial functional advantage of conscious experience in the Global Workspace Theory e.g. (Mashour et al., 2020)). However, the proponents of this theory have extended this insight and implemented it within a large scale neuronal theory- proposing that brain activity does not cross the consciousness threshold unless it ignites a global network of areas- termed the “global workspace” associated anatomically with fronto-parietal

cortex. This global workspace network allows the flexible distribution of conscious contents to various executive networks and is, according to the theory, mandatory for any conscious experience to emerge.

While the psychological insight regarding the possible function of conscious experience is appealing- I will argue here that the cortical-based experimental evidence does not support GWT, and the essential role of PFC within it- rather it appears to largely contradict such a global role. For the sake of focus I will discuss mainly cortical activity associated with conscious visual perception- however, the same arguments can be extended to other contents of conscious experience as well.

Perceptual signals activate PFC

A major set of experimental findings cited in support for a PFC role in conscious perception stems from a number of cases in which perceptual signals appear to spread into pre-frontal regions. Figure 1 illustrates fMRI mapping of the cerebral cortex during passive viewing of a repeated movie. In addition to the expected activation in posterior visual cortex, consistent islands of PFC activity are apparent (marked by red arrows). Note that these PFC activations appear during passive, no-report, viewing conditions. Furthermore, perhaps not-surprising given the down-stream position of PFC- these frontal activations are enhanced when contrasting conscious vs. none consciously perceived stimuli under similar stimulus conditions. This is illustrated in figure 1B, comparing perceived to non-perceived visual stimuli during a continuous flash suppression paradigm (Hesselmann et al., 2011). Again, clear activation of PFC is evident. Importantly, in this experiment both target-perceived and not perceived conditions included identical motor responses- so the prefrontal activation could not be attributed merely to motor planning, decision or execution. Furthermore, frontal activations to visual stimuli have been consistently reported using more conventionally discrete and controlled visual stimuli - especially in lateral areas such as inferior-frontal gyrus. Interestingly, these areas appear to show visual category selectivity, in particular face-selectivity e.g. (Freiwald et al., 2016).

Based on these results and a number of other similar studies it appears that indeed neuronal signals associated with conscious perceptual contents spread into parts of specific cortical regions within pre-frontal cortex. Importantly, these activations may also occur under, passive conditions lacking an overt report (but see (Tsuchiya et al., 2015) for a different view).

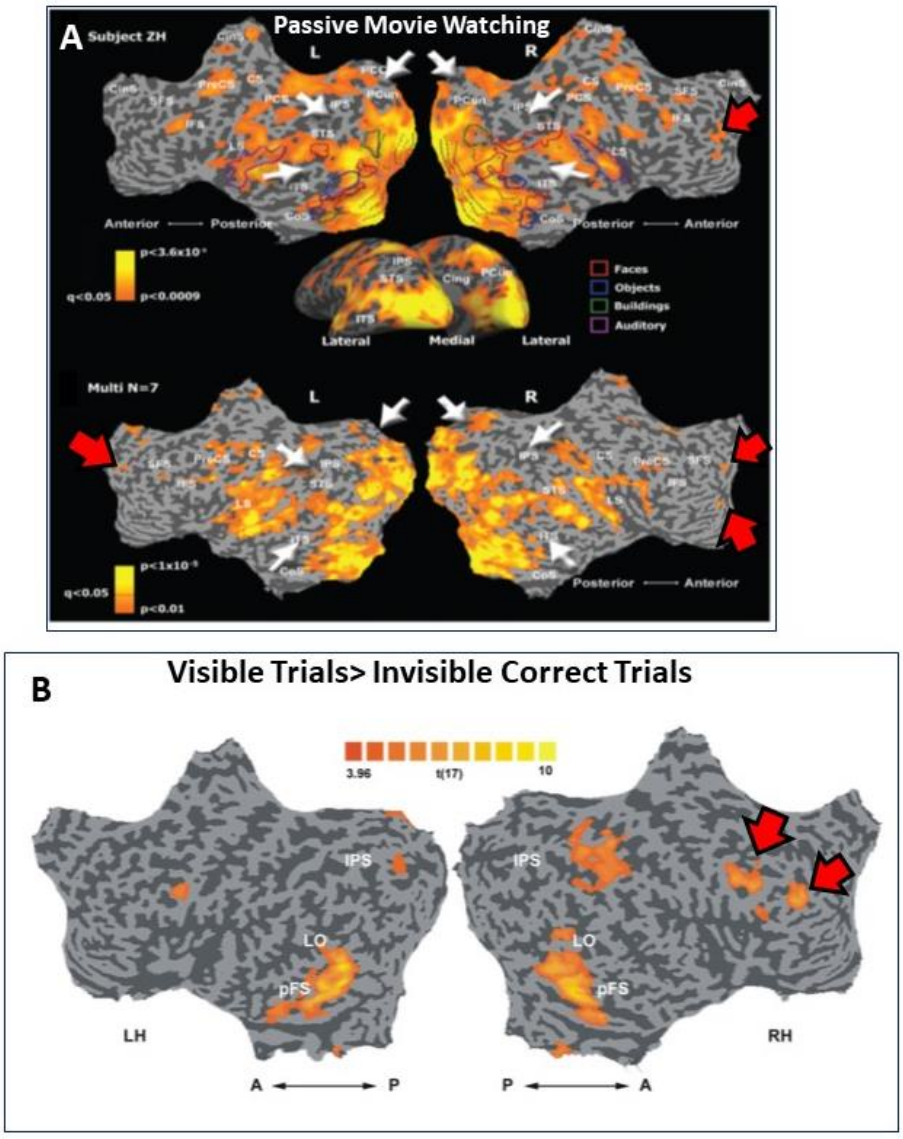

Figure 1. Visual activation spread to pre-frontal cortex revealed by fMRI. A. An example of cortical visual activation during passive movie watching. Activation of a representative and group participants are presented at top and bottom, respectively. Note PFC activation (red arrows) despite the passive viewing condition (For more details see (Golland et al., 2007). B. An example of preferential cortical activation to a consciously visible vs. invisible visual target in a continuous flash suppression paradigm. Note a clear pre-frontal activation (yellow-orange) in both examples (red arrows). Blue colors indicate inactivation. LO and PFS- Lateral Occipital and Posterior Fusiform visual areas. For more details see (Hesselmann et al., 2011)

Visual activation is global across the human cortex

While ample evidence reveals PFC activation to visual stimuli, it is important to note that "automatic" spread of visually-related activations to non-visual cortical areas is a common, ubiquitous phenomenon- and is certainly not restricted to fronto-parietal areas. For example, asking individuals to passively view short video clips results in robust activation not only in the expected visual areas but also in medial temporal structures including the hippocampus (Gelbard-Sagiv et al., 2008). Importantly- these hippocampal activations are significantly enhanced during conscious as opposed to non-conscious observations. This was demonstrated in an intra-cranial single neuron recording study during a back-ward masking paradigm (Quiroga, Mukamel, et al., 2008). Such "ignition" of hippocampal neurons related to conscious visual perception at threshold is depicted in figure 2 (top panel). Note the striking enhancement of hippocampal firing rates to the consciously perceived relative to the non-perceived targets under similar stimulus conditions.

In another clear illustration of the automatic spread of visual signals outside the visual system, activation in high order somato-sensory hand representations were found, surprisingly, when participants viewed, passively, an audio-visual movie (Hasson et al., 2004). Importantly, these somato-sensory activations were restricted to a specific visual category: they included only those scenes in which the actors manipulate objects with their hands (see figure 2, bottom panel).

Finally, a global, extremely rapid, spread of low amplitude activations was found across many cortical areas following passive viewing of visual stimuli in a large scale intra-cranial recording study (Noy et al., 2015). This global "glow" of activation further highlights the fast and global nature of visual signal spread outside the conventionally defined visual system and across the entire cortical mantle.

To summarize this point- automatic visual responses- even during passive viewing conditions outside of the "classic" visual areas is a common and wide-spread phenomena of the human brain. It is not restricted just to PFC specifically or fronto-parietal "workspace" networks generally.

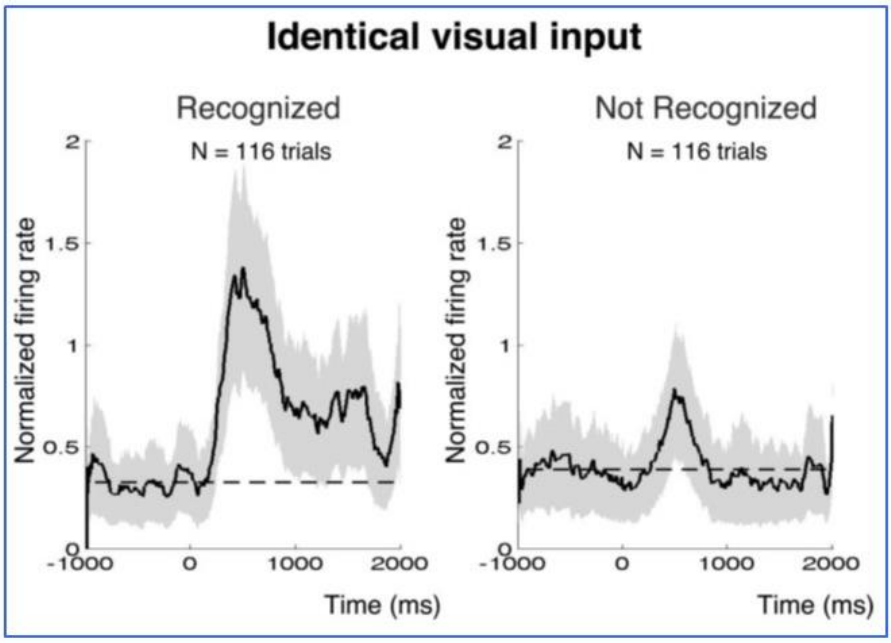

Figure 2. Spread of visual-perception signals into to non-visual targets. Top panel: An example of a visual "ignition" associated with consciously perceiving a visual target in human hippocampal neurons. Left and right panels depict single neuron activations during consciously recognized vs. unrecognized targets under identical threshold back-ward masking conditions. Note the typical signatures of local ignition: high amplitude of activation that is sustained for hundreds of ms. beyond stimulus termination. Bottom panel: an example of somato-sensory cortex activation during no-report audio-visual perception. Data obtained in an fMRI study of cortical activation during movie watching. BOLD-fMRI activation was recorded in the hand representation of secondary somato-sensory cortex (PCS). Shown are frames from the movie that were associated with peaks of BOLD activation to the visual content in this region. Note the selective activation to scenes that included images of hands manipulating objects (white arrows). Note that the

movies were watched passively by the participants and yet consistent activation was observed in specific non-visual (somato-sensory) cortical representations.

Functional specialization is highly localized in the human brain

The wide-spread, "globalist" picture of automatic activation across the entire cortex changes dramatically, however, when we take into account not only the mere activation of each cortical area to visual images but rather this area's functional specialization- i.e. the relative profile of activation of each cortical area across a wide range of stimuli and tasks. Here we find, consistently, and in a manner that seems not to be emphasized enough in the cortical literature, a landscape diametrically opposite to the globalist view. This landscape consistently manifests a highly localized functionality in which each cortical area expresses a distinct and unique profile of specialization. Critically, careful examination of cortical regions located outside the visual system and yet are evidently activated by visual stimuli- and in particular the PFC- reveals that their specialization is, in fact, of non-visual nature.

The hippocampus provides a striking illustration of this point. A careful examination of the tuning properties of the visual responses of human hippocampal neurons- uncovers that what they are truly specialized for is not visual images- but rather abstract concepts. Such concepts can, of course, be elicited by consciously perceived visual images- but can be equally invoked by auditory stimuli and even written names of these abstract concepts. Thus, careful mapping of their functional tuning reveals a clear and consistent picture: Human hippocampal neurons are actually not tuned to visual images at all- but rather to abstract, multi-modal, concepts- (Quiroga, Kreiman, et al., 2008).

Of particular relevance to the present review- careful examination of various PFC specializations reveals that they are largely non-visual in nature. This was illustrated, globally, in a massive survey of intra-cranial recordings contrasting passive and active viewing of similar images (Noy et al., 2015) in a 1-back recognition task. Specifically- in the 1-back task- the patients actively reported the occurrence of a repeated image by a button press (active condition) and refrained from action when images did not repeat (passive condition). The results of this study are demonstrated in figure 3. As can be seen fronto-parietal regions are largely specialized for the report and motor task conditions while posterior regions, by contrast, are specialized for the visual content of the images. It is important to note that in the Noy et al 1-back task- the passive condition was likely to engage also non visual processes associated with the decision to remain passive. Despite this likely confound, the vast majority of pre-frontal contacts still showed preferential tuning to the overt compared to the covert decision processes.

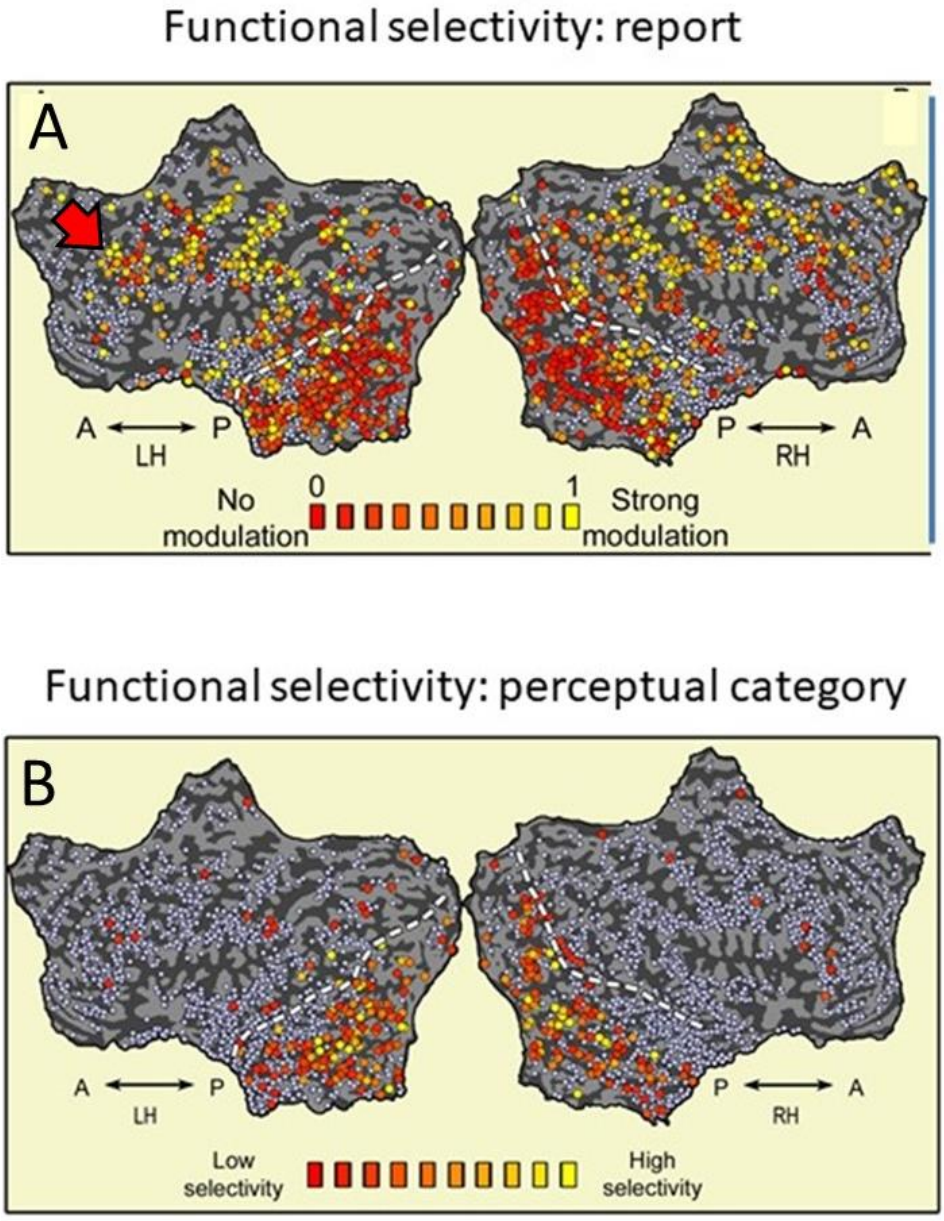

Figure 3. PFC is functionally specialized for report. Large scale intra-cranial recordings (4400 recording sites in 43 patients) during a 1-back recognition experiment. A. Functional specialization for report. Contacts are color coded according to their preferential activations during reporting the pictures vs passive viewing of the same pictures (yellow contacts). Note the prevalence of report-selective contacts in PFC (red arrow). B. Functional specialization for perceptual content. Contacts are color coded according to their preferential activation to visual categories (red and yellow). Note the concentration of content-selective contacts in posterior, visual sites with only minimal prevalence of content-selective contacts in lateral PFC. For more details see (Noy et al., 2015).

Examining specific PFC areas which show visual activations, such as the face-activated regions- reveals an extremely specialized tuning to images of the eyes rather than the entire face (Chan & Downing, 2011). Such precise tuning points to a specialized functional role of these PFC regions- likely associated with

controlling eye movements which has long been associated with frontal lobe function. This is in stark contrast with the proposed general perceptual role hypothesized for these areas under global theories of consciousness.

Generally speaking, one can view the truly huge and very successful project of human cortical mapping- with its remarkably massive and rapidly growing body of knowledge- as both an expansion and confirmation of the hypothesis that each cortical area is specialized for a different conscious content or mental function. As this research is rapidly expanding, and the mapping data keeps accumulating- it consistently, and unfailingly, uncovers finer and finer functional distinctions across each and every region of the human cortex. This is perhaps best illustrated with the recent, large scale, connectome project proposing a subdivision of the cortex into 360 cortical areas (Glasser et al., 2016). Extrapolating to the future –it is highly likely that this number is bound to grow.

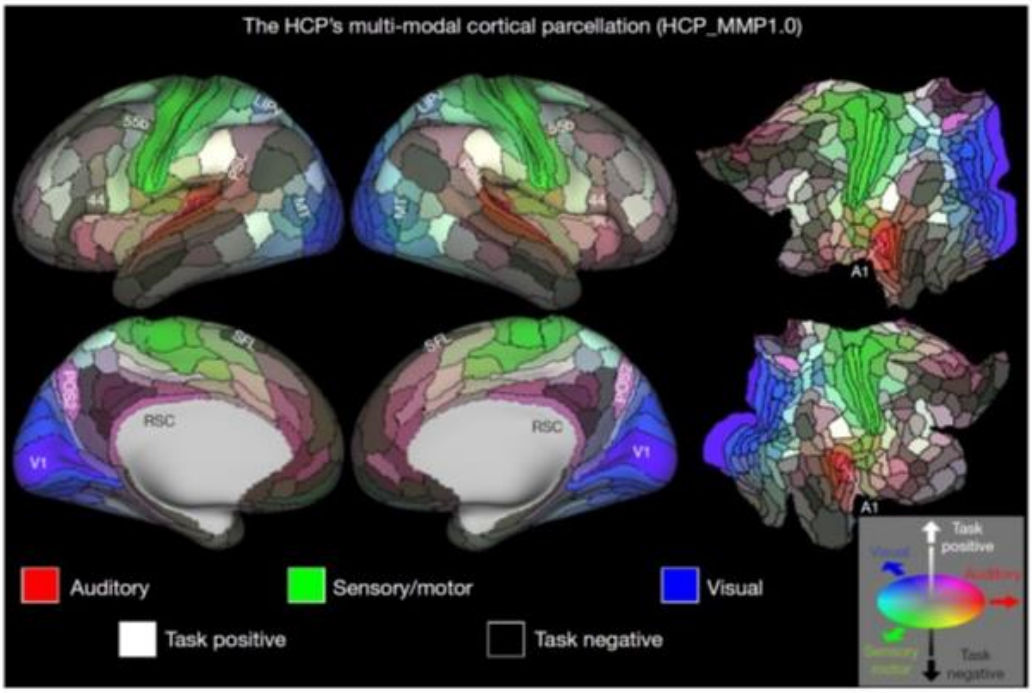

Figure 4. **Cortical parcellation into distinct functional areas**. The figure depicts inflated and unfolded maps delineating the borders of recently proposed subdivisions of the human cortex into functionally distinct cortical areas. Based on these distinctions the cortex is subdivided into 360 different cortical areas. Note the similarity in the size of cortical areas in the PFC compared to other cortical lobes. For more details see (Glasser et al., 2016).

Brain lesions and stimulation support the localist view

Considering our central question- what is the role of non-visual cortical areas, and specifically, PFC in conscious perception- the examination of activation patterns during visual perception thus reveals two contradictory pictures. On the one hand- when taking into account the mere activation to visual stimuli-

we see an extremely wide-spread collection of visually activated cortical areas- that goes far beyond posterior visual cortex and certainly includes the PFC within this range. However, when considering the functional specializing of these activations- i.e. the tuning profile of activation of each cortical site to different stimuli and sites- we see a diametrically opposing picture reflected in extremely localized specialization- in which each cortical region underlies a different, specialized function or categorical content of conscious experience.

Clearly just mapping the brain activations which are induced by conscious visual perception is not sufficient to resolve the question which of these types of activation profiles is obligatory for conscious content. To that end, such neural recording studies must be complemented with additional, causal, experimental observations. Here I would like to discuss two massive and detailed bodies of knowledge which are readily available but unfortunately not considered in enough rigor when trying to resolve this conundrum. These are, first, the vast clinical neuropsychological literature delineating in great detail the impact of lesions at different cortical sites on the contents of conscious experience. The second source of knowledge is the accumulated data derived from direct stimulation of various cortical sites- conducted as a routine clinical procedure in patients undergoing neurosurgery. I will note right from the start that the precision and reproducibility of these two data sets is highly problematic, and should be treated with great caution. It is of course far more limited in power compared to the level of accuracy and sophistication currently available in animal models. But taken with a proper level of care and particularly considering the inherent inaccuracies and confounds in such data- it can provide a decisive information with regards to the general question of the local vs global nature of conscious-related cortical activation in general, and the role of the PFC in particular. It is important to emphasize that, precisely because of their inherent inaccuracies, these two sources of information must be considered jointly and across repeated examples to be taken as valid (See also (Malach, 2021).

Considering clinical data detailing the various symptoms associated with localized cortical regions- the literature is vast, literally filling entire text-books, and more recently includes also detailed, whole brain atlases (e.g. (Pijnenburg et al., 2021) . It is far beyond the scope of this review to cover. However, a bird's eye view of this literature clearly highlights a remarkable convergence (again not stressed enough in theoretical discussions) between the functional specializations as revealed in brain imaging studies and the behavioral and phenomenal impact of localized cortical lesions. By contrast, the lesion data doesn't appear to support in any consistent manner a global, obligatory, role for PFC or any other fronto-parietal regions in consciousness in general. Specifically for the case of conscious visual perception-loss of face-perception following fusiform damage in posterior cortex is a particularly striking example of a localized lesion leading to the well- known phenomena of face-blindness (Sorger et al., 2007). Similarly, loss of object perception associated with damage to visual area LO (James et al., 2003), and the induction of motion-blindness associated with damage to the notion-selective visual area MT/V5 (Zihl et al., 1983) all reveal a consistent and striking match between localized functional specializations of the visual system as revealed by brain imaging and the corresponding loss of conscious content of specific visual categories associated with lesions of these specialized posterior visual cortical areas.

By contrast, no consistent evidence of similar visual blindness has been found following damage to PFC or even more extensive lesions of frontal cortex (Stuss & Benson, 1984). Surveying loss of visual functions resulting from non-visual cortical lesions, perhaps the most common and striking case is the phenomena of perceptual neglect, a unilateral behavioral failure of attention typically associated with right parietal lesions (e.g. (Corbetta et al., 2005). However, even this apparently global role of the parietal lobe in visual

perception appears, upon close examination, not to be obligatory. Thus, patients are still able to consciously perceive visual stimuli (albeit with severe loss of attentional control) , paradoxically, in those special cases when both parietal lobes are damaged, in what has been termed Balint patients (Moreaud, 2003).

Viewing this body of data broadly- the striking correspondence between the functional tuning of cortical areas and the selective effects of cortical lesions is one of the most outstanding demonstrations of the validity and functional importance of the localized specializations of cortical areas. In that respect the PFC is compatible with this overall view- it lacks specific tuning to perceptual content and, correspondingly, lesions of PFC fail to abolish perceptual content.

Critically, the association between localized functional tuning of cortical regions and conscious content is further supported by examination of the effects of direct electrical stimulation of different cortical areas. This clinical method is commonly used in diagnostic sessions and provides a wealth of causal data which, when carefully and rigorously examined, can be highly informative. Here, in a critical convergence with the lesion data, one finds a clear correspondence between the functional tuning of specific cortical areas and the conscious content elicited by electrical stimulation of these areas. Focusing on visual perception, again, the correspondence to the functional specialization revealed in fMRI is striking. A particularly dramatic example was provided by the finding of a selective face distortions experienced following precisely localized stimulation of specific face patches in the human visual fusiform gyrus (Parvizi et al., 2012). Similarly, stimulation of the motion-selective visual area MT has been shown to be related to experiencing visual motion (Rauschecker et al., 2011).

This picture changes dramatically when we examine the effects of electrical stimulation in pre-frontal cortex. In a recent study, a review of numerous stimulation sites in pre-frontal cortex failed to reveal consistent perceptual effects (Raccah et al., 2021). Although other studies have argued for the occurrence in a minority of patients of complex visual hallucinations (Blanke et al., 2000), these may be associated with spread of activation to fiber pathways (Andelman-Gur et al., 2020).

Acknowledging the subjective and poorly controlled nature of such clinical studies- it is important to avoid deriving general theoretical conclusions from anecdotal or rare cases- but rather to consider the carefully analyzed, most consistent and reproducible cases. Furthermore – as mentioned above- it is essential to adopt a conservative approach that is based on a convergence of all three central methodologies- brain recordings and imaging, electrical stimulation and lesion studies. For example- since most stimulation experiments lack detailed mapping of current spread to other networks and cortical sites- positive experiential effects may be due to activation spreading far beyond the stimulation site. The requirement that the stimulation effects will be corroborated by functional specializations revealed through brain imaging and the abolition of the observed experiential category through lesions of the candidate area- can substantially reduce such false interpretations.

Once such rigorous and convergent criteria are applied- the overall conclusion is inevitable: we find the vast literature of fMRI mapping, lesion and electrical stimulation data- all converging in pointing to the consistent association of specific categories of conscious contents with localized functional cortical areas. In particular this converging evidence pertains to the view of posterior high order visual areas

as a underlying a mosaic of localized categories of conscious visual content. By contrast- no such correspondence between lesion, electrical stimulation and visual activation results and conscious visual perception has been, so far, found in pre-frontal cortex.

Is pre-frontal cortex special?

When confronted with this evidence, proponents of a central role of pre-frontal cortex in conscious visual perception counter that pre-frontal cortex is architecturally different from posterior cortex. Specifically the argument is that PFC is more architecturally diffuse- which is in line with its global nature - and hence it is not realistic to expect localized lesions, as extensive as they may be, to abolish the functionality of such wide-spread and ill-defined functional regions (Odegaard et al., 2017). Similarly, due to its diffuse nature, it should not be expected that restricted stimulation sites should elicit changes in conscious content when applied to PFC. But is it really the case that PFC and frontal cortex in general contain a relatively more diffuse and poorly localized organization? Examining specific high order functions to which pre-frontal cortex appears to be specialized and how they map onto pre-frontal cortex- reveals a rather precise and localized organization that, when compared directly, appears quite similar in nature to posterior- high order visual areas.

In a few studies such a direct comparison was made between the precision and consistency of PFC activations and posterior visual cortical areas. In a study examining medial pre-frontal activations associated with introspection and self-evaluation, (Goldberg et al., 2006) have directly compared the inter- subject consistency and sharpness of activation boundaries of the pre-frontal activations with that of posterior, high order, visual cortex respectively. The results (see figure 4) revealed a remarkably consistent delineation of cortical activations which appeared of similar precision in both frontal and posterior cortices. In a recent study (Berkovich-Ohana et al., 2020) conducted inter-participant comparison of lateral pre-frontal activations during abstract-thoughts. This study again highlighted a remarkably consistent and precisely localized islands of PFC activations, which is intriguing considering the rather open and uncontrolled nature of the abstract-thinking task. Finally- it is interesting to note that the first and paradigmatic case of functional localization reported in the human cortex has actually been located to the PFC- namely in the language- related Broca's area. In this well studied cortical area- numerous reports highlighted a striking correspondence between fMRI specialization, lesion and stimulation effects, culminating in a recent successful implementation of brain-computer interface of speech production based on neuronal signals in this localized PFC region (Anumanchipalli et al., 2019).

To summarize- cortical areas located in the pre-frontal lobe appear as localized and sharply delineated as high order visual areas. Where they drastically differ is in their unique functional specializations- underlying contents such as introspection, language, thought and numerous other high level personality and decision making capabilities. Such categorical specializations may or may not require visual activations depending on their task requirements- but they are certainly not pivotal or obligatory for visual perception per se.

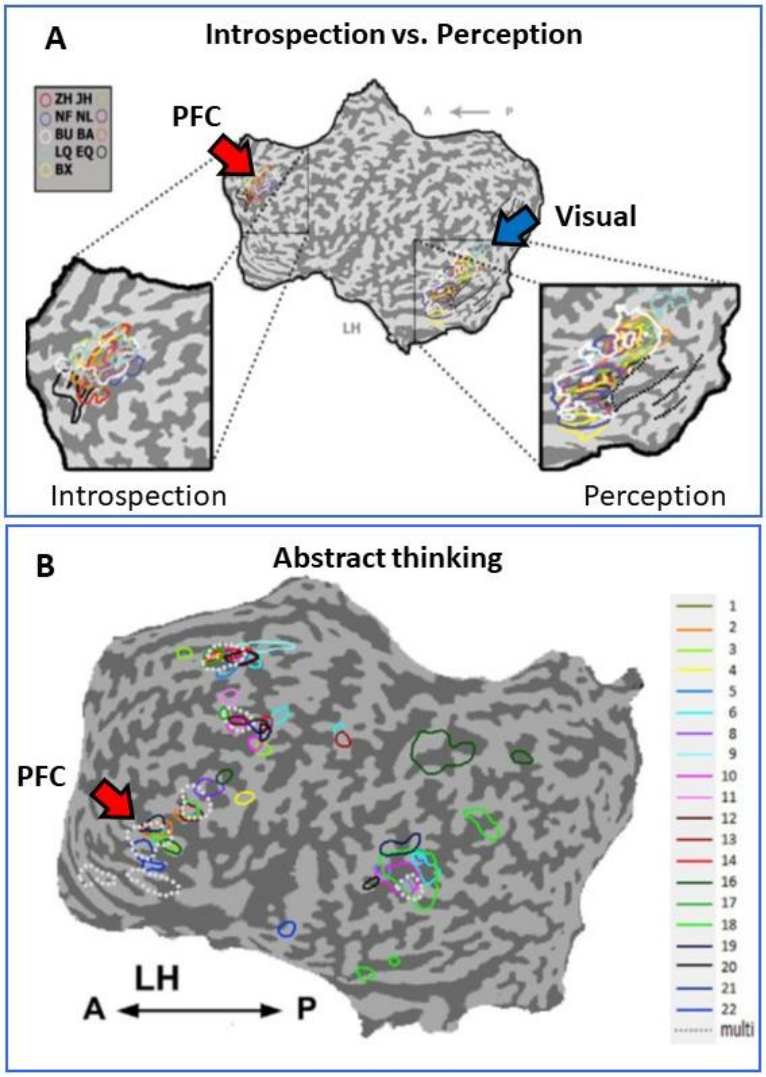

Figure 4. Localized activations in frontal cortex. A. Localized pre-frontal activations are comparable to posterior visual ones. Single participant, BOLD-fMRI maps of activations presented on unfolded cortical maps comparing introspection-related (red arrow) and visual (green arrow) activations in frontal and posterior cortex, respectively. Each individual activation is outlined with a different color. Note the well-localized and consistent medial-prefrontal introspection-related patterns of activations which are of comparable precision to the posterior visual activations ones. For details see (Goldberg et al., 2006). B. Consistent and localized islands of activations in pre-frontal cortex during abstract thinking. Single participant, BOLD-fMRI activations outlined in different colors during thinking focused on an abstract topic. Note the remarkable inter-participant consistency and precision of activation forming a series of sharply delineated islands in pre-frontal cortex. For more details, see (Berkovich-Ohana et al., 2020).

Are introspective and self-reflective processes, mediated by pre-frontal areas, an obligatory aspect of conscious visual experience?

An important alternative to the proposed role of PFC as part of a global work-space, could be a notion that accepts the view of PFC as a mosaic of different localized and specialized contents. However, under this theoretical formulation, often referred to as high order thought theories-some of these functional

specializations constitute an essential, obligatory, ingredient underlying all types of conscious experience. Specifically, it has been proposed (Lau & Rosenthal, 2011) , that consciousness is essentially a second-order, meta-cognitive and introspective process- and hence it depends on cortical areas mediating such second-order functions. Indeed, the data is compelling in showing that some PFC regions both medially and laterally appear to be, at least partially, specialized for introspective and meta-cognitive functions. However, is it truly the case that conscious experience in general, and conscious perception in particular depend on such introspective functions? While we clearly rely on introspection for reporting our conscious experiences- it is still debated, and far from being settled whether introspection is essential for conscious experience to emerge (Block, 2005).

A particularly relevant mental state to consider here is that of perceptual absorption. Imagine watching an extremely engaging action movie- so riveting that you are completely, both emotionally and intellectually, absorbed in the action that goes on the screen- to the extent that you completely "lose yourself" in the movie. No sense of self, no sense of time passing and certainly no introspection is available to you during such absorbing states- only a complete immersion in the unfolding movie experience. Remarkably, while these perceptual states are undoubtedly the most vivid and engaging we may experience- we are totally dependent on our memory system for introspection and reporting their content. In other words- absorbing moments appear to greatly suppress our ability to introspect or enter a reflective, meta-cognitive, stance – this is what the metaphors of absorption and losing ourselves so vividly portray.

It could be argued that it only seems that during absorbing moments we lose our meta-cognitive and introspective faculties. Perhaps they work subliminally, or in a sort of background, unnoticeable manner- creating the illusion of a complete absorption. Here is where brain imagine can be particularly effective in uncovering such sub-conscious introspective processes. Indeed, in an fMRI study designed specifically to address this question, (Goldberg et al., 2006) contrasted an absorbing picture categorization task with a self-reflective emotional introspection task of the same pictures. The results highlighted a well-defined, introspection-related cortical area located in medial pre-frontal cortex- which showed positive activation during the introspection condition (shown in Figure 4a and 5). Critically, when participants switched to the demanding rapid categorization task- the activity in this pre-frontal, introspection-related, region was *suppressed* below the baseline level (figure 5). A similar phenomena was observed when, instead of visual perception, participants had to introspect about and rapidly categorize auditory stimuli (Goldberg et al., 2006).

These findings indicate that introspection and visual perception are not yoked, mutually dependent functions - rather the opposite appears to be the case. As is consistently experienced during truly intense perceptual experience- sensory perception is vividly experienced at the expense of introspection and reflective meta cognitive functions which are suppressed.

In summary, these findings argue that the PFC indeed contains specialized regions underlying reflective and introspective functions- however sensory perception is mediated via specialized posterior cortical regions and can emerge independently of PFC activity and even when such frontal activity is suppressed.

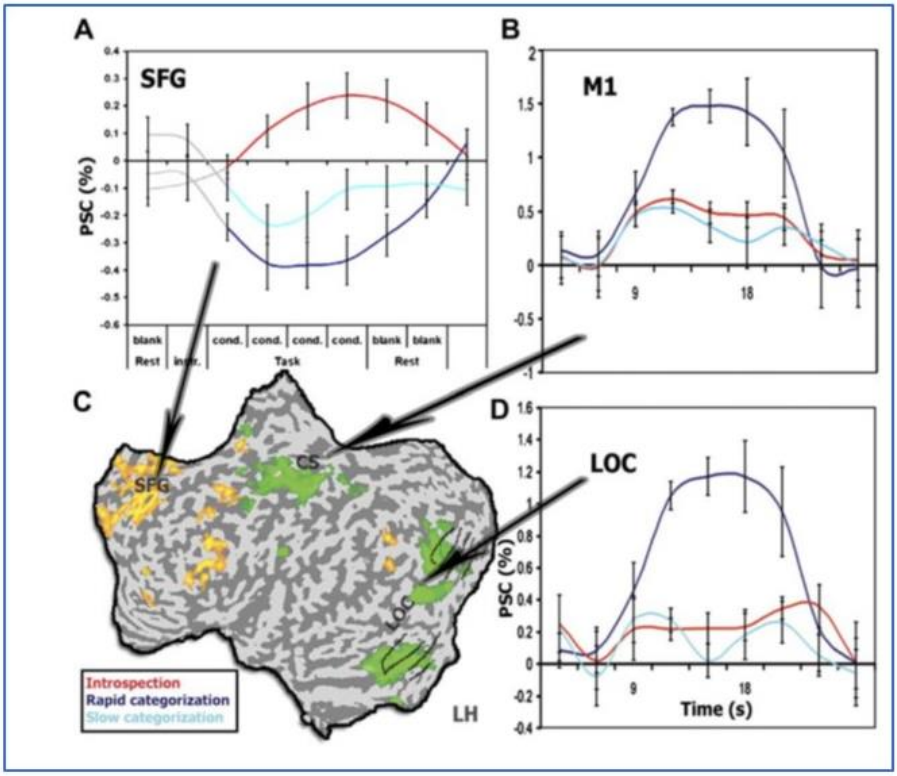

Figure 5. Suppressed pre-frontal introspection-related activity during absorbing vision. A. Activation time courses during an fMRI experiment contrasting an absorbing visual condition (rapid categorization of visual images) vs. introspection task (judging the emotional impact of these pictures).sampled from introspection-related medial PFC. Note the massive suppression of activity, below baseline, during the absorbing visual condition. B, and D. Activation time courses derived from motor (M1) and high order visual areas (LO) respectively, Note the high amplitude activation during the absorbing sensory-motor task – opposite to the response profile in medial PFC. C. BOLD-fMRI mapping presented on an unfolded cortical hemisphere during the experiment. Areas showing preferential activation to the perceptual task and the introspection task are marked in green and orange respectively. Note the sharp segregation of PFC and motor activations- arguing against a fuzzy organizational architecture of the PFC. These results demonstrate that absorbing conscious visual perception can emerge in the absence of introspection-related PFC function.

A local perspective of PFC function

How should we interpret this massive and complex body of experimental evidence obtained from human brain research, of which only a small sample was described here? Facing such diverse and multi-dimensional landscape- a crucial principle that is both powerful and fundamental is Occam's razor: our theoretical interpretations should always aim to be as simple and elegant as possible, while at the same time remain fully consistent with all rigorously demonstrated experimental findings.

With this principle in mind I would like to propose that the simplest picture that emerges from all the converging lines of evidence described in this review is rather straightforward: all cortical areas, from the PFC in front to the visual system at the back obey the same, common, principle: local functional specialization. According to this principle each and every cortical area, regardless if it in the front or back

of the cortex underlies a different conscious faculty- from introspection in the front to visual perception in the back. Neuronal activity in each of these cortical areas is associated with a separate category of mental content (See also (Malach, 2021). Under this localist hypothesis- the PFC does not hold any privileged, global, or essential position with regards to conscious experience. Rather, the PFC should be regarded as just another collection of specialized cortical areas- operating according to the same common principle of local functional specialization that underlies all other cortical areas. Just as posterior visual areas underlie visual motion, face and object perception so do localized frontal areas underlie language, thought, introspection and decision functions. Critically, there is no compelling experimental evidence supporting the view that PFC plays a global or obligatory, role in consciousness in general and conscious perception in particular.

It is important to clarify that the notion of localized, specialized cortical areas doesn't argue against complex interactions, mutual modulations and automatic spread of activations across various cortical areas and networks. However, critically, such network and inter-areal activity is modulatory in nature and is not mandatory for the emergence of conscious content per se.

Problems raised by the localist perspective.

While the local specialization hypothesis seems to account most elegantly with a large body of human brain studies- it leaves open a number of deep and unresolved questions that will necessitate further research.

A major unknown is what makes the different cortical areas functionally unique? To put it differently, how is the category-specific informational content of each specialized area coded and where does this code reside? It is not clear at this point, for example, what links neuronal activity in the motion area V5 with the experience of visual motion, while activity in the object area LOC should always be linked to object perception? An interesting proposal, inspired by structuralist ideas, is that the information is coded locally, in unique synaptic connectivity matrices in each cortical area. These area-specific and unique local connectivity patterns underlie specialized relational geometries in each cortical area. These relational geometries are reflected in the similarity matrices between activation patterns associated with different conscious contents and define the perceptual category and the specific conscious content coded by each cortical area. (See (Malach, 2021).

Another unknown is how the information across localized cortical regions is integrated in the cases of multi-modal, complex conscious experiences- which is in fact the rule during natural experiences rather than the exception. Again, future research, using more incisive experimental tools will be needed to uncover the mechanism that allows functional inter-areal and network binding. Based on experiments employing more naturalistic stimuli (e.g. (Hasson et al., 2004) it appears that multiplicity of cortical regions, each specialized for different experiential content, are activated simultaneously during such multi-dimensional experiences. Given the dense networks of cross-area communications that have been amply documented in the cortex (e.g. (Golland et al., 2007) these activations are likely to reverberate across areas and thus, presumably, lead to their functional integration.

Finally, one may wonder how activity originating from local foci of cortical activations can be so rapidly distributed across the cortical mantle – thus sub-serving the organism's needs for rapid and flexible behavioral responses, as, correctly, pointed out by global workspace theories (Mashour et al., 2020). The existence of fast and widespread network of cross areal fiber connectivity, likely employing small world

architecture (Bassett & Sporns, 2017) may mediate such fast and flexible behavioral responses. Indeed, essentially instantaneous, global communication of localized perceptual events have been demonstrated using wide-spread intracranial recordings (Noy et al., 2015).

In summary

The overall message of this review is rather straightforward: careful examination of three lines of experimental evidence derived from human brain research: neuronal activation, electrical stimulation and cortical lesions- converge in supporting the hypothesis that all cortical areas in fact obey one basic principle: local functional specialization- with each cortical area underlying a unique category of conscious experience. Within this framework, the PFC is not special – it is similar in principle to all other cortical areas- except that it subserves a cluster of unique, high order specialized functions- of which particularly relevant here are introspection and meta-cognition. By contrast, posterior visual areas underlie the various categories of conscious visual perception, and are not obligatory for, say, thinking or introspective functions. Stating this local specialization principle should not be taken as arguing against multi-area and network interactions- to the contrary- the complex, multi-dimensional, nature of conscious experiences under ecological conditions dictates such multiplicity of activations and cross-area integrations and is fully compatible with the principle of local functional specialization. Furthermore, as described above, reflexive spread of activation from localized regions to wide-spread cortical areas, functionally associated with these localized regions, is wide-spread. Critically however, such global spread is associated with but is not obligatory for the emergence of conscious content in the human mind

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