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Imaging neural signatures of consciousness: 'What', 'When', 'Where' and 'How' does it work?

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ABSTRACT

'What' do we call consciousness? 'When' and 'Where' in the brain do conscious states occur, and 'How' conscious processing and conscious access to a given content work? In the present paper, we present a non-exhaustive overview of each of these 4 major issues, we provide the reader with a brief description of the major difficulties related to these issues, we highlight the current theoretical points of debate, and we advocate for the explanatory power of the "global workspace" model of consciousness (Baars, 1989; Dehaene and Naccache, 2001; Dehaene et al., 2006) which can accommodate for a fairly large proportion of current experimental findings, and which can be used to reinterpret apparent contradictory findings within a single theoretical framework. Most notably, we emphasize the crucial importance to distinguish genuine neural signatures of conscious access from neural events correlated with consciousness but occurring either before ('upstream') or after ('downstream').

Key words

Neural correlates versus neural signature of consciousness • Upstream processes • Downstream processes • Global neuronal workspace • fMRI • Electroencephalography

Introduction

Since the last two decades a significant set of functional brain-imaging studies explored the "neural correlates of consciousness", in part inspired by the seminal and stimulating research program launched by Crick and Koch (1990). In parallel to this progressive accumulation of empirical material, several major theoretical issues have been explicitly addressed such as: 'What' do we call consciousness? 'When' and 'Where' in the brain do conscious states occur, and 'How' do conscious processing and conscious access to a given content work?

In the present paper: 1) we will present a non-exhaustive overview of each of these 4 major issues, and of the relevant experimental evidence; 2) we will try to provide the reader with a brief description of the major difficulties related to these issues; 3) we will also highlight the current theoretical points of debate; and 4) we will advocate for the explanatory power of the "global workspace" model of consciousness (Baars, 1989; Dehaene and Naccache, 2001; Dehaene et al., 2006) which can accommodate for a fairly large proportion of current experimental findings, and which can be used to reinterpret apparent contradictory findings within a single framework.

Given the relatively large scope of this paper, we will not explore here the neural necessary conditions requested for a subject to be conscious, irrespective of conscious content (e.g.: difference between comatose or vegetative states and conscious state), but we will rather focus on the 'transitive' or 'intentional' nature of consciousness: what happens when a conscious subject becomes conscious of a given mental representation. The

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former issue is abundantly discussed in this volume and in previous reviews (Laureys et al., 2004; 2005). More precisely, we will focus on the special case of visual perception, but with the hypothesis that the proposed scenario of neural events implicated causally in conscious access should be grossly similar across sensory modalities and conscious contents.

What do we call consciousness to make it an empirically tractable question?

When looking for the neural signatures of conscious processing, one has first to define univocally the polysemic term of 'consciousness': what will we call a 'conscious representation'? One possible answer consists in using the 'subjective reportability' property of consciousness: when one is accessing consciously a given mental representation he/she can report its content to oneself: 'I perceive X, I want Y, I feel Z, I remember W, …'. Once internally formulated, such reports can then be communicated to an observer. According to this approach, it is possible to use subjective reports to probe the content of consciousness, and therefore to define as non-conscious any representation which is not reported by the subject even when questioned about it, but the existence of which can be demonstrated through behavioural and/or functional brain-imaging measure (e.g.: priming effects). The place of subjective reports has a long and moving history in psychology (Sackur in press), illustrated in particular by two key periods: first, the fancy for subjective reports contemporary to the introspectionist school of Wundt (end of XIXth century & beginning of the XXth century), and second, the radical denigration of the use of subjective data during the reign of bevaviorism (first half of the XXth century). These pendulum oscillations of the scientific interest for subjective data are not only of historical interest; it is possible to make sense of them: on the one hand anyone interested in consciousness has to deal with subjective reports, otherwise he/she will "throw the baby out with the bath water". But immediately one has to face a second problem: if one takes at face value subjective reports, he/she will fall in all the illusory and erroneous caveats associated with subjective reports. One possible solution to this apparent dilemma – a solution developed in particular by Dennett in his concept of heterophenomenology (Dennett, 1992) –, consists in considering subjective reports as the object of our research, without accepting them as alleged truths on the way our conscious minds proceed. One can collect subjective reports, and confront them with other sources of information (e.g.: behavioural and functional brain-imaging data) to understand the scientific conditions of conscious subjectivity.

Once considered as a valid method to study consciousness, the subjective report approach calls for various commentaries and raises many questions which we list here, so to provide the reader with a fair view of the complexity of this concept:

1) Reportability is not a behaviour, but an internal cognitive process which can (or cannot, for instance in some patients) be communicated to an external observer through speech or through another motor response (Naccache and Dehaene, 2007). It is a frequent error to identify subjective reports with the behaviours used to transmit them to an observer.
2) Is a conscious representation an internally reported representation, or an internally non-reported but reportable one? We consider that only internally reported representations should be labelled as conscious, suggesting that consciousness always proceed under a mode of reflexivity or as a metacognitive process, but this issue remains largely open (see below).
3) It is noteworthy that reportability is not limited to verbal reports, but can also be probed and communicated through non-verbal acts, as in non-human primates (Cowey and Stoerig, 1995), in infants, in disconnected right hemispheres split-brain patients (Gazzaniga et al., 1977), and in human patients with poor communication abilities such as conscious but locked-in patients (Laureys et al., 2005). However, in many cases, it is far from easy to disentangle such non verbal reports from non conscious behaviours.
4) One of the intrinsic limits of this approach lies in a form of 'observer interference effect': to know the conscious content of an individual at a given time, one has to ask the subject to communicate her/his internal report through a behavioural

response. Thus, as soon as a subjective report is collected, the spontaneous ongoing stream of consciousness is interrupted.

5) In direct link with the last comment on reportability, it is important to mention that if reliable neural signatures of this subjective report process can be identified, then we could get rid of the 'observer interference effect' by being able to determine, for instance, that a given stimulus has been consciously perceived without asking the subject. If such a major objective was reached, it could also be possible to detect consciousness in patients with impaired behaviours.

At this stage, we propose to use subjective reports as clear markers of consciousness. However, if anyone would agree that subjective reports are indexing conscious contents, the question remains open whether subjective reports are exhaustive estimates of conscious content: are we conscious of much more information than what we report? This is a strong and difficult question to address empirically. For instance, Ned Block developed the concept of 'phenomenal consciousness', as a much larger domain of conscious contents than the one accessible through reports (Block, 1995; 2007). A lucid view of this debate has to consider at least 3 remarks. First, if one keeps in mind that a subjective report is an inner mental state not to be assimilated to the behaviour used to communicate it to an observer, there is a possible loss (or alteration) between the internal report and the behavioural report. This gap is not easy to address empirically. Second and most important, it seems that the very notion of 'phenomenal consciousness' is grounded… on subjective reports, as illustrated by this sentence from Ned Block (2007): "When one has a phenomenally conscious experience, one is in some way aware of having it." Therefore, it seems difficult to advocate the existence of such a mental space, if it remains intractably entangled with the need to obtain subjective reports about it. Last, one has to keep in mind the fact that many experimental paradigms suggest that the intuitive notion of a rich but non-reportable phenomenal world is, to a large extent illusory. Otherwise, we may commit the same errors which were fatal to Wundt and introspectionists theories (Naccache and Dehaene, 2007; Sergent and Rees, 2007).

"When" and "Where" does consciousness happen?

A reader's guide to the "When and Where" of consciousness

Can we establish a spatio-temporal map of conscious processing in the brain? The quest for the neural correlates of consciousness has been very prolific so far, but going through this large and complex literature can be highly confusing without adopting some guiding rules for interpreting these results. Indeed scientific studies of consciousness have yielded apparently contradictory results and led to conflicting and sometimes opposite theoretical conclusions, spanning from "micro-consciousness" theories proposing that consciousness resides locally in the neural processors that are tuned to the various aspects of a conscious content, to "global workspace" theories proposing that conscious processing arises from the collaborative work of multiple distributed areas, notably connecting the extraction of sensory information with higher cognitive functions. Keeping in mind a very important distinction can help clearing most of the confusion: a neural event that correlates with consciousness does not necessarily constitute a *signature* of consciousness, i.e. a neural event that is both necessary and sufficient for consciousness. This distinction has very pragmatic consequences: a mere "correlate" of consciousness cannot be a definitive criterion for diagnosing consciousness in general and in particular in non-communicating patients. A striking illustration of the importance of this distinction can be found when considering the debates on the role of early sensory activity in conscious perception. It is now an empirical fact that conscious perception is almost systematically associated with enhanced sensory activity in the areas tuned to the perceived stimulus (Rees, Kreiman et al., 2002; Dehaene et al., 2006). Hence, sensory activity is indeed a neural correlate of conscious perception: for example increased activity in the fusiform face area correlates with conscious perception of a face (Tong et al., 1998). Some studies have shown that, in some instances, the strength of the early stages of sensory processing (typically within 100 ms post stimulus) correlates with conscious perception (Pins and Ffytche, 2003), leading some authors to suggest that conscious perception could arise early and reside locally in the strength of sensory activity evoked by an external stimulus (Zeki and Bartels, 1999; Zeki, 2003). However, it has been demonstrated recently that such correlation between sensory activity and conscious visibility of a stimulus can be found even *before* the presentation of the stimulus (Boly et al., 2007; Hesselmann et al., 2008; Wyart and Tallon-Baudry, 2009). Obviously these neural correlates, preceding the actual stimulus, cannot be considered as a signature of conscious processing of that stimulus: they constitute early predictors, biasing the processing of the subsequent stimulus towards conscious or non-conscious processing. These correlates are thus "upstream" of conscious processing per se (Fig. 1). In turn, this observation invites us also to interrogate the status of very early correlates of consciousness that can be found after stimulus presentation: do they constitute a signature of conscious processing or are they still "upstream" of the consciousness episode to come? In order to disentangle "upstream" events from the actual neural signature of conscious processing, we suggest that a few pragmatical rules could be followed: 1) contrasting conscious and unconscious processing with no or minimal difference in the external stimulation; 2) collecting report of consciousness on every trial; 3) analyzing the dynamics of sensory activity in time.

A large number of studies have also found that conscious perception is associated with activity in a more widespread network of areas than unconscious processing of the same stimulus, and that this network crucially involves higher-level areas in the parietal and frontal lobes (Lumer and Rees, 1999; Dehaene et al., 2001). It is thus tempting to conclude that activity in parieto-frontal areas constitutes a signature of consciousness (Rees et al., 2002). However, again, two important arguments invite us to caution when interpreting these results: first, unconscious processing can actually reach parietal and frontal areas in some specific instances, although such unconsciously driven frontal or parietal activity seem much more focal and evanescent than during conscious processing (van Gaal et al., 2008; van Gaal and Lamme, 2012). Secondly, although many neuroscientists nowadays would agree that observing maintained activity within a broad network of areas encompassing frontal and parietal regions would be *sufficient* to diagnose conscious processing (Owen et al., 2006; Monti et al., 2010), whether such extended and maintained activity is actually *necessary* for conscious experience to arise is still an intensely debated issue (Lamme, 2003; Block, 2005; Dehaene et al., 2006; Block, 2007). Indeed, since conscious perception allows a wider and more flexible range of cognitive computations than unconscious perception (Dehaene and Naccache, 2001), it is possible that most of this widespread activity is actually associated with more than the "core" conscious experience of the stimulus. It could be associated with activity "downstream" of conscious access (Fig. 1), i.e. further computations reflecting the control and use of the conscious information to fulfill current goals, notably to perform a specific task, set by the experimenter. In other words, the activities observed could be task-specific instead of consciousness specific (Goldberg et al., 2006). We suggest that this difficult question could be addressed by looking for the neural events that are common to conscious processing of a stimulus across different task requirements and by assessing the causal role of different brain areas on consciousness through inactivation studies or studies of brain-lesioned patients. Finally, the psychological refractory period paradigm allows distinguishing three stages in the processing of external information: a central processing stage which is capacity limited, and peripheral sensory and motor stages that can operate in parallel (Smith, 1967; Pashler, 1984; Sigman and Dehaene, 2005). This could constitute an interesting framework to analyze upstream, central and downstream processes during conscious perception.

In conclusion, we have now come to a point where we can sharpen our understanding of conscious processing by distinguishing three categories of neural correlates of consciousness, as illustrated in Figure 1: 1) neural events upstream of consciousness which contribute to biasing subsequent processing towards a conscious or an unconscious mode; 2) the actual neural signature of conscious access; and 3) neural events downstream of consciousness. We propose that a sharp transition distinguishes "upstream" events from the actual neural signature of consciousness (Dehaene et al., 2003; Sergent and Dehaene, 2004; Sergent et al., 2005; Del Cul et al., 2007; Gaillard et al., 2009). In the following section, we will provide empirical arguments in support of that view. In contrast, we propose that the fron-

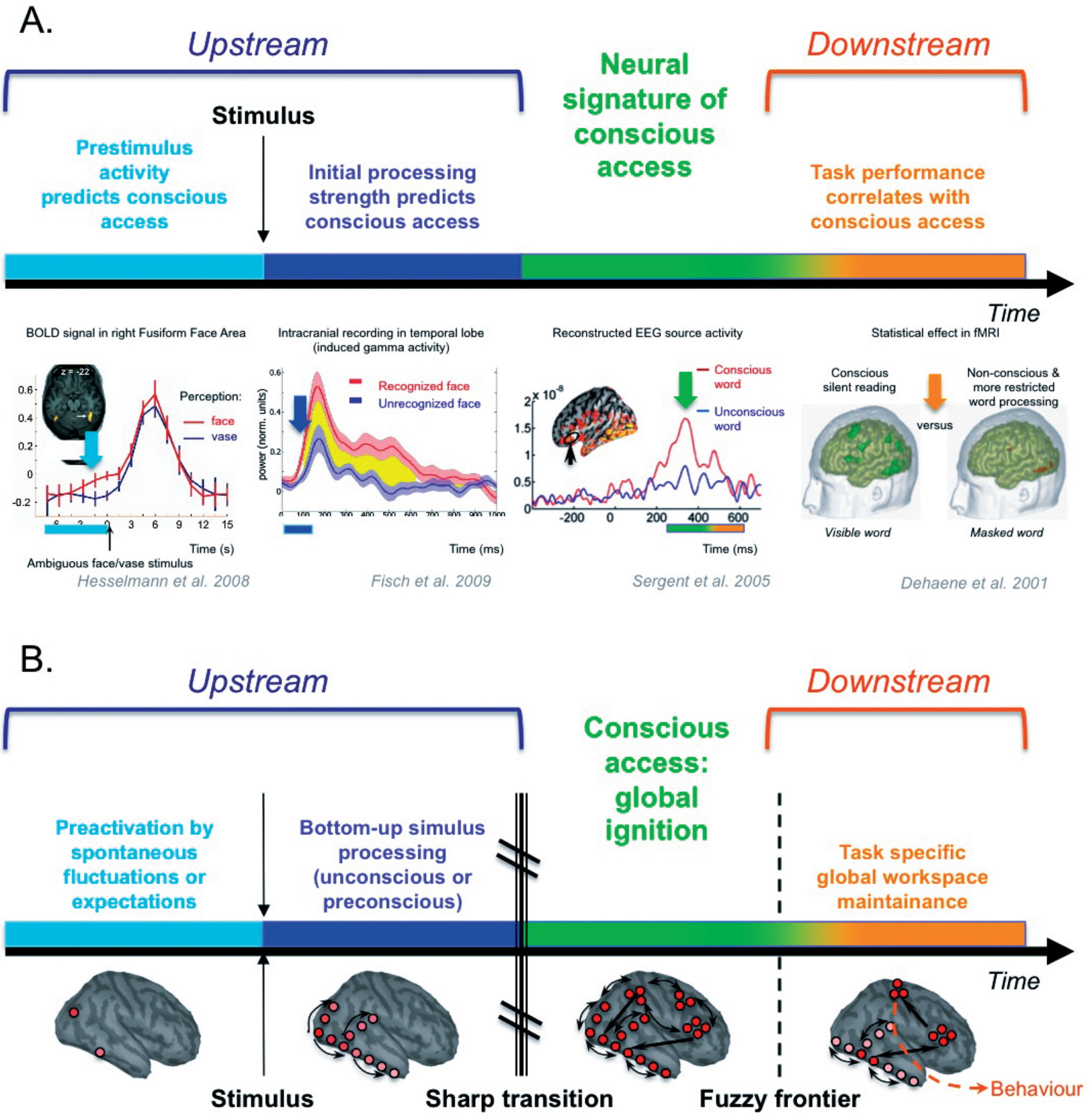

Fig. 1. - Distinguishing different categories of neural correlates of consciousness in time: "upstream", "neural signature" and "downstream". A shows how this classification applies to various classes of empirical data on the neural correlates of consciousness. B shows the proposed underlying neuronal mechanisms with each stage within the Global Neuronal Workspace theoretical framework.

tier between conscious access and "downstream" processes is, by nature, less sharp, since once consciously accessed, information is available for a large set of flexible processes. However, despite the fact that the network of areas involved in a particular episode of conscious perception and the duration of this episode itself is probably greatly dependent both on the particular sensory content and on the particular cognitive computations performed during this episode, we believe that it should still be possible to derive a "central minimal core" common to any type of conscious content and independent from task. In a following section ("Distinguishing "downstream" events…"), we will develop on some empirical strategies that can be used to achieve this goal.

This distinction between three types of neural correlates of consciousness also map onto pragmatical questions pertaining to the evaluation of consciousness in general, and in non-communicating patients in particular. Since activity in early sensory areas tuned to a specific stimulus is a necessary condition to perceive this stimulus consciously, evaluation of these upstream events thus constitute a sensitive but non specific test of conscious perception (Laureys et al., 2000; Perrin et al., 2006). Conversely, the observation of neural events associated with downstream processing can constitute a specific test of conscious processing, but potentially not a sensitive one (Owen et al., 2006; Bekinschtein et al., 2009; Monti et al., 2010; Faugeras et al., 2012).

In the following sections, we first briefly review current empirical evidence on the potential extent of unconscious processing (see below), and we apply the aforementioned categorization to make sense of the rich and complex literature on the neural correlates of conscious processing (see below).

Spatial and temporal extent of unconscious processing

What are the extent and limits of unconscious processing? How deep can be the processing of an external stimulus outside the scope of conscious processing? Are there "forbidden zones" in the brain for unconscious processing? From a temporal perspective, is unconscious processing intrinsically evanescent? Answering these important questions could help delineate the borders of conscious processing. This approach has yielded surprising results, which actually reveal the richness and complexity of the computations occurring non-consciously. For example, a number of experiments now allow us to follow the neurophysiological route of an unconsciously perceived written word. Converging evidence show that visual words that are rendered invisible either by masking or by using attentional manipulations such as the attentional blink, are nonetheless processed through early visual areas of the cortex, then higher level area in the temporal cortex that extract the visual form of the word (Dehaene et al., 1998; 2001; Naccache et al., 2005; Gaillard et al., 2009). Even more surprisingly, information about the meaning of a word can also be extracted unconsciously. Indeed, several experiments have shown that unconscious words can nevertheless evoke a N400 waveform, which is an ERP marker of semantic processing (Luck et al., 1996; Sergent et al., 2005). Such unconscious semantic information can even influence subsequent decisions, a phenomenon referred to as "unconscious priming" (Marcel, 1983; Dehaene et al., 1998). A combined fMRI and EEG study (Dehaene et al., 1998) showed that this influence takes place at the level of motor preparation, suggesting that unconscious priming is not, or not only, a pre-activation of certain semantic fields: the appropriate decision criterion that is set consciously is applied to the unconscious information, up to the motor response stage. Other studies have demonstrated that unconscious number processing can trigger activations in parietal areas (Naccache and Dehaene, 2001). Yet another line of research has revealed that emotional stimuli can trigger activity in the amygdala (Naccache et al., 2005). Finally, very fine properties of the stimulus can be encoded in visual cortex in the absence of conscious perception (Haynes and Rees, 2005; Kamitani and Tong, 2005). Several recent experiments have also unsettled a long-standing *a priori* by showing that unconscious information can trigger processes associated to cognitive control (Lau and Passingham, 2007; van Gaal et al., 2008; 2009; van Gaal and Lamme, 2012). Such high-level unconscious effects notably involve activations within the prefrontal cortex. Other studies have shown that unconscious stimuli can also bias spatial attention (Woodman and Luck, 2003).

In conclusion, unconscious processing does not appear to be confined to any specific regions of the brain (e.g. low-level sensory areas). Furthermore, although unconscious activations are usually found to be much more limited in time than conscious activations, in some specific instances unconscious stimuli have been found to affect neural activity at very long latencies: up to 400 ms or even 800 ms following stimulus presentation (Luck et al., 1996; Vogel et al., 1998; Naccache et al., 2005; Sergent et al., 2005). At this point it thus already becomes apparent that we will not be able to summarize the neural signature of consciousness by the activation of a specific set of areas or by the occurrence of neural activity at a specific latency. Conscious processing rather seems to correspond to a specific mode of processing associated with more complex neural signatures. Imaging studies contrasting conscious and unconscious processing do indeed reveal this complexity.

Where does perceptual consciousness occur?

Importance of sensory processing strength

Several studies have shown conscious perception to be associated with increased activations in stimulus specific sensory areas. Ress and Heeger showed that activity in early visual areas (V1, V2 and V3) increased when participants succeeded in detecting a faint contrast increment in a visual stimulus as compared to when participant failed to detect the same contrast increment (Ress and Heeger, 2003). Interestingly, such increased activation in V1, V2 and V3 was found both for veridical detection (hits) and for "false" detection in the absence of the external stimulus (false alarms), suggesting that the level of activation in V1 follows conscious experience rather than the external stimulation. Similarly, activations in areas of the temporal cortex responsible for extracting more complex features of the stimulus have been shown to closely follow fluctuations in subjective conscious experience in the absence of an objective change in external stimulation (Tong et al., 1998). This was observed using a binocular rivalry procedure in which one eye of the participant received the image of a face while the other eye was presented with the image of a house. Since these conflicting images could not be fused, the conscious experience of the subjects spontaneously alternated between the perception of the face and the perception of the house in the absence of actual external change. In fMRI, the periods during which participants reported the conscious experience of a face were associated with increased activity in the fusiform face area (an area of the temporal lobe specialized in face processing) and decreased activity in the parahippocampal place area (an area of the temporal lobe specialized in the processing of visual scenes). This pattern reversed when conscious perception switched to the "house" percept. For other complex stimuli such as words, conscious perception has been found to be associated with increased activation in the visual word form area as well as visual cortex (Dehaene et al., 2001). Such findings have been replicated at a very fine spatial scale using intracranial electrodes (Gaillard et al., 2009).

These numerous examples of a close match between sensory activations and conscious experience suggest that activity levels in sensory areas play an important role in conscious perception. Are we to conclude that consciousness actually resides locally in the different brain areas tuned to the various features of a stimulus? Following this logic, Semir Zeki has proposed that consciousness is essentially a local phenomenon, each sensory area responsible for coding one particular feature of the stimulus producing a "microconsciousness" of that feature (Zeki and Bartels, 1999; Zeki, 2003). In apparent support of this interpretation, in a recent fMRI study, the only areas that showed a reduced response when a simple visual pattern was rendered invisible by dichoptic masking were found to lie beyond V1 and V2 but still confined within the occipital cortex (Tse et al., 2005). Again, this observation led the authors to suggest that conscious perception might lie in this "intermediate" territory of the visual cortex.

The limits of the sensory processing strength hypothesis

However, such conclusions are contradicted by other studies showing that similar levels of activity in sensory cortices can be associated with very different outcomes in conscious perception. Such dissociations have been found in patients with unilateral neglect following damage to parietal cortex, where response in right V1 to a face presented in the left visual field was found to remain as strong when this face stimulus was extinguished than when it was seen (Rees et al., 2000; Vuilleumier et al., 2001). Another striking illustration of the fact that visual activation can be uncorrelated to the conscious experience of the visual stimulus was found in an fMRI study in healthy volunteers using metacontrast masking (Haynes et al., 2005). While conscious visibility of the masked target followed a clear U shaped function with varying target-mask SOAs from 0 to 100 ms, activity levels in the target-specific parts of V1, V2, V3, V3A and V4 remained unchanged across SOAs. Rather than localized fluctuations in stimulus specific areas, conscious perception of the target was revealed to correlate closely with the strength of effective connectivity between V1 and higher-level areas such as the fusiform cortex. In other words in some experimental protocol conscious perception relies on the strength of the dialogue across different parts of the visual cortex (and possibly beyond) rather than local fluctuations in any particular sensory area.

Furthermore, in the vast majority of studies contrasting conscious and unconscious processing of the same stimulus, conscious processing is found to be associated with much more distributed activations than unconscious processing. This wider "conscious network" almost systematically involves fronto-parietal areas (Dehaene et al., 2001; Rees et al., 2002; Gaillard et al., 2009). Interestingly, fronto-parietal regions seem to play a pivotal role in the selection of a unique conscious interpretation when facing external stimulations that can have several alternative interpretations, as for example during binocular rivalry (Lumer et al., 1998; Lumer and Rees, 1999). These observations have led several authors to postulate that the level of activity within sensory areas alone cannot account for the difference between conscious and unconscious processing, but that the involvement of higher "control" areas of the brain is crucial for conscious access to occur (Dehaene and Naccache, 2001; Rees et al., 2002; Dehaene et al., 2003; Baars, 2005).

Towards a resolution of these discrepant results

How can we make sense of these highly contradictory data? Conscious perception is associated with increased sensory activity in most of the studies imaging conscious perception. However, sensory enhancement is usually not found as an isolated correlate of consciousness, with very few exceptions (Tse et al., 2005): it is usually accompanied by drastic changes in activity in a broad network of areas well beyond classical sensory cortices, notably in parts of the frontal and parietal lobe (Beck et al., 2001; Dehaene et al., 2001; Carmel et al., 2006; Gaillard et al., 2009). Moreover, it has been shown that drastic changes in conscious perception can occur in the absence of modulations in associated sensory areas (Haynes et al., 2005). In other words, while minimal activity levels in relevant parts of the sensory cortex encoding the stimulus at stake is obviously a necessary condition for conscious perception, this does not seem to be sufficient for conscious perception of that stimulus to arise.

We propose that the varying levels of correlations found between sensory activity and conscious perception in different experiments can best be understood and reconciled when distinguishing different sources of correlation that can easily be confounded with low temporal resolution techniques such as fMRI: in different studies, enhanced sensory activity can either be the cause or the consequence of conscious perception, or both. Analyzing the temporal dynamics of sensory contribution to conscious perception is key to establishing these important distinctions.

When does perceptual consciousness occur? Distinguishing upstream and downstream stages from conscious access

Pre-stimulus activity can predict conscious perception

Several experiments have revealed that ongoing activity in the brain *before* the presentation of a stimulus can predict subsequent conscious perception of that stimulus (Super et al., 2003; Boly et al., 2007; Hesselmann et al., 2008; Busch et al., 2009; Mathewson et al., 2009; Wyart and Sergent, 2009; Wyart and Tallon-Baudry, 2009). Variability in ongoing activity before stimulation explains the puzzling variability in evoked sensory activity across repetitions of the same external stimulation (Arieli et al., 1996), which in turn explains why identical stimuli can sometimes be consciously perceived and sometimes remain unconscious. In a recent fMRI study, Hesselmann and colleagues revealed that activity levels in the fusiform face area (FFA) predicted whether an ambiguous face-vase stimulus would be perceived as a face or a vase (Fig. 1A) (Hesselmann et al., 2008). At lower level in the visual hierarchy, several factors have been shown to predict the subsequent conscious detection of stimuli at threshold. In V1, overall activity levels as well as the level of correlation across neurons before stimulus presentation predict the subsequent detection of a figure embedded in a textured background (Super et al., 2003). Pre-stimulus attention decreases local synchrony in the alpha band (around 10 Hz) at posterior regions (Thut et al., 2006), which in turn influences subsequent stimulus detection (van Dijk et al., 2008). At an even finer temporal scale, whether a brief near threshold stimulus is subsequently seen or missed has been shown to depend on whether it is presented during a through or a peak of occipital alpha oscillations, respectively

(Busch et al., 2009; Mathewson et al., 2009; Wyart and Sergent, 2009). In the lateral occipital cortex, higher levels of local synchrony in the gamma band (40-60 Hz) 300 to 200 ms before stimulus presentation predicts subsequent conscious detection of faint Gabor patches (Wyart and Tallon-Baudry, 2009). This factor was found to be independent of to the otherwise observed influence of attention on alpha synchrony within the same region.

All these observations show that the context of ongoing brain activity even before stimulus presentation can have drastic consequences on conscious perception. These pre-stimulus factors seem particularly important when dealing with near-threshold stimuli. Furthermore, it should be noted that not only local sensory pre-stimulus activity biases subsequent processing: a recent study also suggests that activity within dorsolateral prefrontal cortex and lateral intraparietal cortex favored conscious detection of a threshold somato-sensory stimulus while activity in another network of areas encompassing medial frontal cortex and precuneous predicts that the same stimulus will remain unconscious (Boly et al., 2007). All these pre-stimulus neural factors are clearly upstream of the neural signature of consciousness. They play an important role especially for biasing subsequent perception of near-threshold or ambiguous stimuli. A more delicate issue is to decide which neural events, following stimulus presentation, still belong to this "upstream" phase and which are part of the actual neural mechanism of consciousness.

Distinguishing post-stimulus "upstream" events from the neural signature of consciousness

When an external stimulus is presented, sensory information is rapidly transmitted through ascending connections from lower level sensory areas to higher-level areas analyzing increasingly complex and "global" aspects of the stimulus. This first stage of information processing is often referred to as the "feed-forward sweep" of information processing, which is thought to be completed within 100 ms after stimulus onset (Lamme and Roelfsema, 2000). Beyond that stage, stimulus processing by the brain is further refined through horizontal connections within each specific sensory areas (probably associated with local increases in gamma synchronization), and through feed-back or "top-down" connections (probably associated with increased long-range synchronization in the beta frequency band, around 15-20 Hz). One of the most debated issues among the various theories of consciousness relates to how these different stages of sensory processing contribute to the actual neural signature of conscious perception. Empirically, both early neural events, before or around 100 ms post-stimulus (Pins and Ffytche, 2003; Fisch et al., 2009), and later neural events, around 200 ms and beyond (Sergent et al., 2005; Koivisto et al., 2009), have been shown to correlate with conscious report of the stimulus and have been proposed as neural signatures of conscious processing. Accordingly, some theories propose that conscious processing starts locally and as soon as lateral connections come into play to refine sensory processing (Lamme, 2003; Block, 2007). Later top-down influences would only reflect the additional influence of the attentional network. In contrast, other theories suggest that top-down influence could constitute the gateway to actual conscious processing (Dehaene et al., 2006).

This issue is not yet resolved, and at this point we can only tentatively propose arguments to support our own view. We propose, as a selection principle, that a neural event that can be found to correlate with conscious perception only on some instances but not on others should be considered as being "upstream" of conscious perception or "preconscious" (Dehaene et al., 2006) and not directly belonging to the neural signature of conscious perception *per se*. This seems to be typically the case for neural events within or around 100 ms post-stimulus: while some studies show very convincing correlations between sensory activity within 100 ms and subsequent conscious report of the corresponding stimulus, other studies have shown that the first 200 ms of sensory processing can take place identically for conscious and unconscious stimuli. Using an attentional blink paradigm in which a visual word was sometimes seen and sometimes not detected under identical stimulation conditions, Sergent et al. have shown that the initial sensory processing of the word was indistinguishable for seen and unseen words up to 200 ms after stimulus onset, as reflected by identical P1 and N1 event related potentials. In contrast, beyond 200 ms, conscious and unconscious processing showed drastic differences (Fig. 1A).

This appears to us as a strong argument in favor of the view that conscious processing starts at a stage of sensory processing where top-down influences come into play, i.e. typically beyond 200 ms. In further support of that view, another experiment showed that conscious processing during the attentional blink was associated with increased long-range synchronization within the beta frequency band, probably reflecting the establishment of functional connections across distant brain areas (Gross et al., 2004).

We further suggest that conscious access is associated with a sharp transition in brain activity, which marks the frontier between upstream events and the actual neural signature of conscious access (Fig. 1). Even in masking protocols where both early and late sensory processing are found to correlate with conscious perception, one can observe a clear-cut frontier between "upstream" events and events that actually take part in the mechanisms of conscious access itself (Del Cul et al., 2007; Gaillard et al., 2009). In pattern masking, conscious perception of the masked visual stimulus typically follows a non linear function: as stimulus-mask SOA progressively increases, one observes a sharp increase in conscious detection around a threshold value of SOA (usually at 50 ms SOAs) Using scalp EEG, Del Cul and colleagues showed that although early components of visual processing (P1 N1) were affected by the strength of visual masking, only later components (N2 P3), from 200 ms onwards, actually followed the same non-linear function as subjective awareness of the stimulus (Del Cul et al., 2007). In other words, again, neural events beyond 200 ms post-stimulus were more tightly matched to conscious perception than earlier events. Using intracranial EEG, Gaillard and colleagues showed that conscious processing of visual words was associated with a surge in brainscale changes in activity, including strong and sustained evoked activity across different brain areas from occipital recording sites to frontral recording sites, increased oscillatory activity in the gamma frequency band, and increased communication between distant areas of the brain through synchronization in the beta frequency band (Gaillard et al., 2009). Again, these drastic changes in brainscale activity typically arose at 200 ms post-stimulus.

Such a non-linear transition in neural activity thus appears as a promising marker of entering conscious processing. However, sharp transitions have also been found to arise early and "locally" : a recent study using intracranial recording in humans showed that successful recognition of a masked object correlated with sudden increases in gamma power around 150 ms in the areas tuned to that specific object (Fisch et al., 2009). However this study did not assess whether these local increase in gamma power were associated with more global changes in the dialogue between distant brain areas. Furthermore, since increase in local gamma power around 150 ms post-stimulus can also be observed for totally unconscious stimuli (Gaillard et al., 2009), we favor the interpretation that, although displaying some non-linear properties, these local modulations of activity still reflect modulations of early sensory processing, predicting but not directly participating in conscious access (Fig. 1).

This sharp transition in brainscale activity between early sensory processing upstream of conscious access and conscious access *per se* could nicely map onto the transition from a peripheral sensory phase of processing, that can operate in parallel for multiple stimuli, to a central, capacity limited phase of processing as postulated in theories of the psychological refractory period (Smith, 1967; Sigman and Dehaene, 2005; 2008).

Finally, we would like to emphasize that, beyond these empirical arguments, there is also a fundamental logical argument supporting the view that conscious access arises at the time where a dialogue between sensory areas and areas involved in higher-level cognitive functions is established through long-range connectivity : if conscious experience can be defined as a state where sensory information becomes available for "report", either covertly to oneself, or overtly to a third party, then it must imply long-range connections between areas of the brain encoding sensory information and areas of the brain allowing the "retrieval" of that information in one form or another.

Distinguishing "downstream" events from the neural signature of consciousness

When observing the network of areas that are activated during conscious *versus* unconscious processing of a stimulus, one faces a difficult question: what part of this network corresponds to the actual neural signature of conscious access and what part corresponds to "downstream" processes reflecting computations associated with the specific task that the participants are asked to perform? For example, Dehaene and colleagues compared fMRI activations associated with processing visible *versus* masked words while participants where asked to silently read these words (Fig. 1A) (Dehaene et al., 2001). The network of areas activated during conscious perception of the words thus included areas involved in conscious processing per se and also areas specifically involved in reading, such as the left angular gyrus and phonological areas. Indeed, participants were able to silently read the words only when they consciously saw them. More generally, as stated in section 1, in order to assess whether participants are conscious of a stimulus on a trial-by-trial basis, experimenters have to ask participants to overtly report their perception. This requirement can be minimal, such as simply reporting whether the stimulus was detected or not, usually via response buttons. Even such a simple task could in principle bring about additional activity that would not have been observed had the participants viewed the stimuli passively, while presumably still gaining conscious access of the stimuli.

However, we would like to make a strong point that this empirical problem could not be solved by assessing the neural correlates of consciousness during "inattentive viewing" of the stimuli (Tse et al., 2005), or at least not without taking further precautions in order to ascertain the actual conscious/non conscious status of the studied stimuli. Indeed, in these situations the experimenter has much lesser control on the actual conscious or unconscious experience of the participant. It is an empirical fact that stimuli that are easily detected consciously when participants are asked to report their presence, can become unconscious under inattentive viewing (Mack and Rock, 1998). Furthermore, passive viewing would not completely rule out any task-related activity under conscious processing: even if the experimenter did not specify any particular task to be performed on the stimulus, the participants could, by definition – and actually *would* – freely manipulate any consciously accessed information to pursue personal, internally generated goals. For example, when passively seeing words, a participant could decide to covertly count the letters.

In our view, distinguishing "downstream" events from the actual neural signature of conscious access is particularly difficult because the frontier between the two is, by nature, less sharp than the transition that marks the beginning of an episode of conscious access. Despite these intricate links, we believe that it should be possible to identify a "central minimal core" of neural processes that are common to any type of conscious content and independent from task. Empirically, such a neural signature of conscious processing should be replicated across paradigms and sensory modalities. In that sense, meta-analysis of studies of consciousness involving various types of paradigms could be particularly useful. Additionally, one could compare brain activations between conscious and non-conscious processing of the same stimuli when equating behavioral performances (Lau and Passingham, 2006). Finally, psychological refractory period paradigms could be powerful tools to explore the temporal extent of conscious access. These paradigms which study how the brain deals with the processing of two stimuli presented in short succession, have revealed that three stages of processing can be distinguished: an initial "peripheral perception stage" that can occur in parallel for both stimuli, a central stage that can only process one stimulus at a time (this is the stage where an interference occurs between the concurrent processes), and a peripheral "task execution" stage which again seems to proceed in parallel with concurrent processes. If one assumes that this central interference stage corresponds to conscious access per se, psychological refractory period paradigms could be crucial in our efforts to identify a "minimal neural signature of conscious access".

This postulated "minimal neural signature of conscious access" could be a minimal set of areas, at the intersection of the various networks found in different modalities and tasks (Rees et al., 2002), or, more probably, it could correspond to a specific mode of brain-scale neuronal processing (Tononi and Edelman, 1998), connecting sensory processing and higher level cognitive functions, as developed in section 3. Note that this common macro-signature of conscious access would share a general neurophysiological mechanism, while still allowing variations in its detailed functional anatomy according to the corresponding conscious contents.

How does conscious access occur in the brain? The global workspace hypothesis

It is time now to present a plausible scenario of the neurophysiology of conscious access in the light of the global workspace model. Again, we will illustrate this mechanism for the special case of visual perception, but with the hypothesis that the proposed cascade of neural events implicated causally in conscious access should be grossly similar across modalities and conscious contents.

The global workspace (GW) model of consciousness originates from Bernard Baars' (1989) theory, and has been developed both in terms of cognitive architecture, and of its plausible neural implementation (Dehaene and Naccache, 2001; Dehaene et al., 2006). The GW proposes that at any given time many modular cerebral networks are active in parallel and process information in an unconscious manner. Information becomes conscious, however, if the corresponding neural population is mobilized by top-down attentional amplification into a self-sustained brain-scale state of coherent activity that involves many neurons distributed throughout the brain. The long-distance connectivity of these 'workspace neurons' can, when they are active for a minimal duration, make the information available to a variety of processes including perceptual categorization, long-term memorization, evaluation, and intentional action. We postulate that this global availability of information through the workspace is what we subjectively experience as a conscious state. Neurophysiological, anatomical, and brain-imaging data strongly argue for a major role of prefrontal cortex, anterior cingulate, and the areas that connect to them, in creating the postulated brain-scale workspace.

Applied to the special case of conscious access to a visual representation, GW theory predicts that a first stage of non-conscious processing would occur, beginning in perceptual areas. More precisely, a first 'feed-forward sweep' – as nicely coined by Lamme (2000) – would correspond to a more and more abstract processing of the visual stimulus, originating from primary visual cortex, up to most anterior stages in the ventral visual pathway, in the frontal-eye-field and in even more anterior frontal regions. Interestingly, a large set of visual masking studies reported such early unconscious stages of processing in almost all throughout the brain, even in the frontal lobes (see Dehaene and Naccache, 2006, for a very short review). However, even the most anterior spots of activation would not correspond to conscious processing, because these activations would not yet be amplified and mobilized by a top-down attentional process, and therefore they would not be broadcasted through the GW. Then, in a second stage beginning around 250-300 ms in humans, fronto-parietal attentional networks would amplify the visual representation coded for instance in the ventral pathway. This top-down process would lead to an ignition of GW activity by the initially peripheral representation. In a recent work, we were able test the plausibility of this scenario using a time resolved and space resolved invasive electrophysiological technique (Gaillard et al., 2009). We compared conscious and nonconscious processing of briefly flashed words using a visual masking procedure while recording intracranial electroencephalogram (iEEG) in ten patients. Nonconscious processing of masked words was observed in multiple cortical areas, mostly within an early time window (< 300 ms), accompanied by induced gamma-band activity, but without coherent long-distance neural activity, suggesting a quickly dissipating feedforward wave. In contrast, conscious processing of unmasked words was characterized by the convergence of four distinct neurophysiological markers: sustained voltage changes, particularly in prefrontal cortex, large increases in spectral power in the gamma-band, increases in long-distance phase synchrony in the beta range, and increases in long-range Granger causality. In this study, we argued that all of those measures provide distinct windows into the same distributed state of conscious processing. These findings were supported by other works reporting similar long-rang synchrony effects in the beta band M/S/EEG signals supporting high-level cognitive processes (Tallon-Baudry et al., 2001; Tallon-Baudry et al., 2004; Lachaux et al., 2005; Buschman and Miller, 2007). In particular, Gross et al. (2004), using MEG in humans, observed that the main correlate of target visibility during the attentional blink paradigm was a massive change in beta-band synchrony across distant frontal and parietal sites.

Note however, that all these results may potentially be exposed to the 'downstream bias': once conscious of a visual stimulus (word, number, face, …), the subject may use this information for task-related processing, and therefore the observed late correlates of consciousness, could post-date the conscious access per se (see above for similar discussions and proposed solutions).

While non-conscious processing is often evanescent, some results indicate that late non-conscious semantic responses can be observed, such as the N400 semantic incongruity ERP effect (Luck et al., 1996; Sergent et al., 2005), or like the amygdala response to threatening words (Naccache et al., 2005). How is it possible to explain such late and localized non-conscious effects within the GW model? One possible explanation could make use of short-range recurrent processing: while long-range synchronies may well be causally associated with conscious access, it may well be the case that local reverberations across close regions may actively sustain information locally. Gaillard, rather than Lamme

Clearly, time resolved techniques seem to be the best suited tools to probe finely the neural dynamics causing conscious access. The use of Granger causality measures (Seth, 2005), or dynamic causal modelling tools (Kiebel et al., 2009) may help to make a step further toward causality. In the same direction, patients study may help to provide direct causal arguments. For instance, Del Cul and colleagues (Del Cul et al., 2009) recently measured visual conscious threshold using a visual masking paradigm in a population of patients with frontal lobe lesions. Interestingly, they found that both objective and subjective measures of stimulus visibility were significantly affected by prefrontal cortex lesions, in comparison with controls. This result strengthens the role of top-down amplification effects originating from GW regions distant from non-visual areas in conscious vision. In addition to patients studies, the possibility to actively interfere with brain activity also provides a powerful method to differentiate non-causal correlates of conscious access from genuine neural signatures necessary and sufficient to cause conscious access. Intracranial stimulations, TMS, TMS/EEG or tDCS stimulations, or neuropharmacological manipulations (e.g.: anesthesia) already provide important clues. For instance, a recent finding revealed that while a single TMS pulse delivered to conscious patients evoked both early local but also late, sustained and distant EEG responses implicating in particular frontal cortices, the very same stimulation delivered under midazolam anesthesia only evoked the early local response (Ferrarelli et al., 2010). Such studies may help to better test some GW predictions.

Conclusion

We conclude by proposing that substantial efforts should be put in closing down on the "core" neural signature of conscious access by clarifying its frontier with upstream and downstream events. In the present article we suggested some directions to achieve this empirical goal within the framework of the GW model of conscious access. This theoretical stance, grounded in the examination of empirical evidence, invites us to consider the objective of finding a neurophysiological biomarker of conscious access as reachable. Such a biomarker of conscious access should comply with the following constraints:

- it should be identified at the level of the individual trial;
- it should diagnose conscious access with perfect specificity and sensitivity;
- it should be observed every time conscious experience occurs, whatever the content and the associated task.

Obviously, such a biomarker would be very useful not only to explore conscious access in healthy volunteers, but also to probe consciousness in non-communicating patients.

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