

Neural processes underlying conscious perception: Experimental findings and a global neuronal workspace framework

Claire Sergent^{*}, Stanislas Dehaene

*Institut National de la Santé et de la Recherche Médicale Unité 562, Service Hospitalier Frédéric Joliot,
Commissariat à l'énergie Atomique, 4, place du Général Leclerc, 91401 Orsay Cedex, France*

Abstract

One striking property of perception is that it can be achieved in two seemingly different ways: either consciously or non-consciously. What distinguishes these two types of processing at the neural level? So far, empirical findings suggest that conscious perception is associated with an increase in activity at the sensory level, the specific involvement of a fronto-parietal network and an increase in long-distance functional connectivity and synchrony within a broad network of areas. We interpret these data in the framework of the global neuronal workspace model which proposes that the neural basis of conscious access is a sudden self-amplifying process leading to a global brain-scale pattern of activity. In contradiction with several theories which assume that there is a continuum of perception, associated with a gradual change in the intensity of brain activation, the model predicts a sharp non-linear transition between non-conscious and conscious processing.

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1. Introduction

Many studies have revealed that non-consciously perceived stimuli can reach high levels of processing [41]. In an imaging experiment, Dehaene et al. have demonstrated that the processing of non-consciously perceived words could reach the level of motor preparation [13]. Along with other studies [14,33,41,61], this experiment is a demonstration that non-conscious and conscious perception share many processing routes. This observation immediately brings to mind the question of what is the added role of consciousness. What distinguishes conscious and non-conscious processing? Are there neural operations and processes that only proceed consciously? Or can all cognitive processes unfold in the absence of consciousness, thus leaving to consciousness a mere epiphenomenal role? Such

are the problems that we attempt to address in the present chapter.

In order to contrast both types of processing, experimenters use protocols that give rise either to conscious or non-conscious perception with minimal or even no change in the external stimuli. This can be achieved, for example, with a masking paradigm, in which a brief stimulus, although perfectly visible when presented alone, is rendered invisible when presented in close temporal proximity to another stimulus (mask). Experimenters also use inattention, e.g. in Change Blindness [46] and Attentional Blink [6,44] protocols, to temporarily disrupt the perception of otherwise supra-threshold stimuli. Finally other perceptual phenomena such as multistable perception (e.g. binocular rivalry) are also currently studied to contrast conscious and non-conscious processing.

In this chapter, we focus on experimental findings in the domain of visual perception. We start with an overview of relevant empirical findings organized in five issues that we think capture the major potential differences between

^{*} Corresponding author. Tel.: +33 01 69 86 78 40; fax: +33 01 69 86 78 16.

E-mail address: sergent@shfj.cea.fr (C. Sergent).

conscious and non-conscious vision. In a second part, we present the global neuronal workspace model of consciousness [12,15]. We review how this model integrates these empirical findings and may account for the unique properties of conscious perception. We conclude that many computations can only be achieved consciously, thus conferring to the postulated global workspace an important functional role in human cognition.

2. Empirical findings

2.1. Enhanced stimulus-specific sensory processing during conscious vision

Although sensory processing can occur in the absence of consciousness, there is much evidence that conscious perception is accompanied by an enhancement of sensory processing. In an fMRI experiment, Grill-Spector et al. [21] showed increased activation in object-specific areas as a function of recognition performance. Participants were presented with brief images of objects followed by a masking pattern composed of scrambled images. For very brief presentation duration of the object image (below 40 ms), participants were unable to recognize the object. Recognition performance increased drastically from 40 to 120 ms presentation duration and then only slightly increased from 120 ms to 500 ms. The bold response in early visual areas (e.g. V1) was hardly affected by target duration. However, the amplitude of the bold response in several object-selective regions followed the same non-linear pattern as recognition performance: activation in the lateral occipital complex (occipito-temporal object areas) increased from approximately 30% of its maximal activation to almost 90% as target duration increased from 40 to 120 ms. Maximal reference was measured for unmasked targets presented for 500 ms. Moreover, for a same 40 ms target duration, activity in this area increased after training in accordance with increased recognition performance.

Similarly, Bar et al. [4] showed an increase in bold response in the occipito-temporal sulcus and in the anterior fusiform gyrus as a function of recognition rating on a four steps scale for masked object images presented for a fixed duration.

Dehaene et al. [14] made similar observations for word-related activations. Visual words were embedded in a rapid stream of masking geometric patterns. For minimal changes in the position of blanks and masks surrounding the word, the word was either visible (when it was immediately surrounded by blanks) or invisible (when it was immediately surrounded by masks). In fMRI, visible words activated a broad network of areas. A subset of these areas was also found to be activated for invisible words: left extrastriate, fusiform and precentral areas. However, activation in these regions was much reduced. In particular, in the left fusiform gyrus, including a region called the

“visual word form area” [8], activation to invisible words was 8.6% of the activation to visible words.

Rees et al. [45] showed an even more drastic change in sensory processing of visual words between attentive and inattentive viewing. Two concurrent letter and object streams were presented superimposed at the center of gaze. The fMRI activations evoked by words relative to consonant strings during attentive viewing of the letter stream, became undetectable when participants attended to the object stream instead. Concurrently, subjects became unable to report the words.

Thus, conscious processing seems to be accompanied by an important increase in sensory processing. As illustrated above, this increase seems to be specific of the stimulus that currently undergoes conscious perception [41,57]. A study by Tong et al. [57] gives a striking illustration of this idea. When the right and left eyes are presented with dissimilar images, both images cannot be fused in one percept and conscious perception alternates between the two images. Tong et al. used this binocular rivalry phenomenon in an fMRI experiment where the rivaling stimuli were a picture of a house and a picture of a face. Reported changes in conscious perception from “house” to “face” were reflected in an increase in the bold response in the fusiform face area and a decrease in the parahippocampal place area, and vice versa when conscious perception changed from “face” to “house”. Thus, although the retinal input was unchanged, activity in stimulus specific areas correlated with the subjective alternation of conscious perception [57].

So far, we have described increased activity during conscious vision in fMRI, which is an indirect measure of neural activity. How is the observed increase in bold manifested at the neural level? Leopold and Logothetis performed single-cell recordings in monkeys’ visual cortex while monkeys reported their percept during binocular rivalry [30]. They observed several cells whose spiking rate increased when their preferred stimulus was consciously perceived and decreased when conscious perception changed to the rivaling stimulus, although retinal input was unchanged. Thus, the observed enhancement in conscious sensory processing is probably subtended by a population of cells in sensory areas whose firing activity is increased in a stimulus specific manner under conscious processing. Similar observations of perceptual amplification of neural activity in striate and extrastriate cortices have been made during various paradigms including masking [24,27,36], stimuli at threshold [54] and inattention [53].

2.2. Conscious processing affects specifically late components of sensory processing

What is the timing of sensory enhancement in conscious processing? This question could not be addressed using the fMRI technique due to its limited temporal resolution. Pins and Ffytche performed the same experiment, using stimuli at threshold, in fMRI and in ERPs, which have a very good temporal resolution [43]. They could correlate a decrease in

bold in V1 for undetected versus detected grating patches at threshold with a decrease of the P1 wave in ERP, which is an early component peaking at 100 ms post-stimulus. Similarly, Dehaene et al. showed that the P1 and N1 waves evoked by masked words were reduced as compared to unmasked words [14]. Some authors consider these very early differences as the essential correlates of conscious perception [43].

However, although early differences in sensory processing appear to be sufficient to determine whether a stimulus will be processed consciously or not, there is strong evidence that they are not necessary. Indeed, using ERPs, Vogel et al. showed completely preserved early components evoked by non-conscious stimuli during the Attentional Blink [59]. The Attentional Blink (AB) refers to the fact that, when two “mildly” masked targets are presented in sequence, attention to the first target induces frequent failure to report the second target when presented 200–500 ms after the first target [6,44]. Moreover, several electrophysiological studies suggest that masking affects specifically a late component of the neural response [24,27]. Kovacs et al. recorded single-neuron firing responses to backward-masked shapes in monkey inferior temporal cortex [24]. Monkeys had to discriminate between two target shapes. Recorded neurons responded selectively to one of the two shapes. In the strongest masking condition, there was still a significant difference in the neurons’ response between preferred and not-preferred targets, although the monkeys were at chance in discriminating both targets. In comparison with an unmasked condition, the mask did not reduce the initial response to the target but suppressed later activity (above 40 ms post-stimulus). These results suggest that the initial shape-selective response was not sufficient to elicit conscious perception of the masked target. Conscious perception seemed to require a more sustained response.

Super et al. recorded neurons in V1 while monkeys had to detect the presence of a figure within a textured background [54]. The figure was defined by a 90° orientation difference between the line segments that composed it and those in the background. Orientation selective neurons in V1 exhibited a contextual modulation: when the line segment falling in their receptive field belonged to the figure, they showed a greater response than when it belonged to the ground. This modulation only appeared after 90 ms, following a first response transient that was independent of the context. Moreover, the first response transient was present even when monkeys failed to report the presence of the target, whereas the later contextual modulation was abolished in those “not-seen” trials.

Hence, although very early differences can be found in some paradigms when contrasting conscious and non-conscious processing, they are not always present. Only a late component of neural response in sensory areas seems to be systematically associated with conscious processing.

More generally, differences between conscious and non-conscious activations seem to get stronger as the region is more anterior in the ventral visual pathway. As already

mentioned, Grill-Spector et al. found that activation in V1 was hardly affected when subjective object recognition dropped, whereas activation in the lateral occipital complex dropped drastically in parallel with perception [21]. Similarly, Dehaene et al. observed a progressive decrease in non-conscious activation intensity from extrastriate (~19% of the conscious activation) to fusiform (~8%) and precentral cortex (~5%) [14]. Those results can also be seen as indicating a progressively greater amount of conscious amplification relative to the non-conscious processing ($\times 5$ in V1, $\times 12$ in fusiform and $\times 20$ in precentral cortex). Finally, a series of electrophysiological studies on monkeys showed that the proportion of neurons whose activity correlated with monkey’s reported perception increased from V1 (20%) to V4, MT and MST (40%) and to STS and IT (90%) [30–32,51]. Our interpretation of these results is that, during non-conscious processing, activation fades away as it reaches higher levels, whereas conscious processing is associated with the establishment and the maintenance of a high level of activation even in highly integrated stages of processing.

In summary, conscious perception of a stimulus seems to be accompanied by an enhancement of its processing at a sensory level. This enhancement is specifically reflected by a late sustained activity in sensory neurons. Moreover, non-conscious processing seems to get weaker as it reaches higher levels. We now turn to what may be the source of perceptual amplification: the consistent finding of specific fronto-parietal involvement during conscious perception.

2.3. Involvement of a fronto-parietal network in conscious vision

Apart from increased activation in sensory areas during conscious vision, many empirical studies point to a set of higher order areas that seem to be exclusively activated under conscious vision [5,14,19,23,38]. Indeed, in Dehaene et al.’s masking study [14], activations at parietal, prefrontal and cingulate sites were found for unmasked words, but were simply absent for masked words.

Similar observations were made in a recent imaging study of the Attentional Blink (AB) by Marois et al. [38]. Marois et al. designed an AB experiment where subjects had to attend to an image of a face and report the presence and identity of a subsequent scene image. During the AB period, the scene was reported on some trials and missed on other trials for similar visual presentations. The Parahippocampal Place Area was significantly more activated in the contrast scene-present versus scene-absent, even in “miss” trials where the scene, although present, was non-conscious. However, the bold response in the lateral frontal cortex bilaterally showed a higher amplitude and was more prolonged for trials in which the scene was reported than for miss or scene-absent trials, whereas no difference was observable between miss and scene-absent trials in this region. Activation in the anterior cingulate cortex showed a similar pattern.

So, there seems to be a dissociation between sensory areas which are still evoked, although more weakly, by non-conscious stimuli, and higher areas, in the parietal, frontal and cingulate cortex, that appear to be specifically involved in conscious perception.

Some studies also highlight the fact that, contrary to sensory areas, these fronto-parietal sites seem to be involved in conscious perception regardless of the nature of the stimulus that is consciously perceived. Indeed, Beck et al., made this observation in an fMRI study using Change Blindness [5]. When a change occurs within repeated presentations of an image that flickers, subjects frequently fail to notice the change, even when it is huge, if attention is not focused on the stimulus that changes [42,46]. This phenomenon is called Change Blindness (CB). Beck et al. asked subjects to detect changes in flickering peripheral stimuli while performing an attention-demanding letter detection task at the center of gaze. The peripheral stimuli could be either faces or places. This protocol yielded a CB, i.e. changes were detected only on some trials. Within the ventral visual pathway, contrasting detected versus undetected changes revealed different activation patterns according to the nature of the changing stimulus. Conscious detection of face changes resulted in increased activity in the fusiform face area, whereas conscious detection of place changes yielded increased activity in another region of the fusiform gyrus, closer to the parahippocampal place area. However, conscious-related activation patterns in the dorsal stream and frontal lobe seemed to be identical for face and place changes, involving the parietal lobe bilaterally and the right dorsolateral prefrontal cortex. An analysis of the overlap further confirmed that these fronto-parietal activations were the only conscious-related activations common to faces and places. Consistent with these findings, an ERP study of CB by Fernandez-Duque et al., revealed that awareness of change evoked a unique positive deflection 350–600 ms after the change, the topography of which matched the parietal activation found in Beck et al.'s fMRI study [19].

Perceptual transitions with no change in the external stimulus also seem to be mediated by a fronto-parietal network. Lumer et al. [34] conducted an fMRI experiment in which they asked subjects to report perceptual transitions during binocular rivalry. Then, the subjects were presented with a replay of their reported perceptual sequence using monocular presentations, that did not give rise to rivalry. In both conditions, the conscious percepts and motor responses were identical. However, selective activations during rivalrous perceptual transitions were found in the fronto-parietal cortices. The authors suggested that these areas were involved in the selection of neural events leading to visual awareness, given a conflicting external presentation.

It should be noted that fronto-parietal networks also play a crucial role in attentional selection, whether spatial or based on stimulus features [9,22,62]. In a review article, Corbetta and Shulman distinguish two partially indepen-

dent attentional systems [9]: a “dorsal system”, including parts of the intraparietal cortex and superior frontal cortex, seems to be involved in the selection of visual stimuli based on current goals (top-down selection), while a “ventral system”, including the temporoparietal cortex and inferior frontal cortex, seems to play a crucial role in the redirection of attention towards unexpected salient stimuli. In particular, parietal and frontal regions show sustained activation when subjects maintain attention prior to the presentation of the stimulus to be processed [10,11]. Thus, a fronto-parietal network is involved in preparing the selection of stimuli that will be consciously perceived.

Finally, a perceptual phenomenon, called perceptual hysteresis, gives further insights in the dynamics of conscious perception. When progressively increasing a physical parameter in a stimulus presentation (e.g. stimulus contrast), the initially hidden stimulus pops-out for a particular parameter value. If the parameter is then progressively decreased, the stimulus generally drops out of conscious perception for a lower value of the parameter. This perceptual hysteresis phenomenon seems to be an indication that conscious processing corresponds to a particular metastable dynamic state at the brain scale. Indeed, in an fMRI study of perceptual hysteresis, Kleinschmidt et al. have demonstrated that this peculiar dynamic is not manifested in one particular area of the brain but in a broad network involving medial temporal, lateral occipital, frontal and parietal regions [23].

In conclusion, activation of a fronto-parietal network appears to be critical for conscious vision. This fronto-parietal network might be involved in selecting the stimuli to be consciously perceived, and in causing enhanced sensory processing of this stimulus in a top-down manner. Moreover, some studies suggest that consciousness not only involves the activation of a fronto-parietal network but that it is also associated with increased functional connectivity through a broad network of areas.

2.4. Increased long-distance functional connectivity and synchrony during conscious perception

In fMRI or PET studies, it is possible to assess the functional connectivity linking various areas of the brain according to experimental conditions [20]. After removing the main signal changes caused by the stimulation protocol, there remain fast variations in the signal. Experimenters can analyze the covariation of this residual signal among brain areas. If two distant areas show strong covariation of their residual signal in a particular experimental condition, it suggests that synaptic connections between these areas are at work in this condition and that these two areas function in synergy. Using this method, Dehaene et al. showed that the distant parietal, prefrontal and cingulate sites, found to be specifically activated by conscious unmasked words, were permanently intercorrelated and that these correlations increased for unmasked words as opposed to masked invisible words [14].

Lumer and Rees addressed the question of functional correlation in an fMRI study of binocular rivalry [35]. To avoid motor activations, in this study, no report of the perceptual alternation was required. Lumer and Rees established coactivation maps of the entire brain both with an extrastriate area previously found to reflect reported visual transition (BA 18/19), and with V1, whose activity did not vary with perceptual changes [34]. Coactivation with the extrastriate area revealed a broad network of regions including stimulus-specific areas in the fusiform gyrus, and regions of the parietal and frontal lobes. In contrast, the authors found almost no coactivation with V1. These results suggest that conscious perception during rivalry implies functional cooperation amongst a broad network of areas, whereas regions responding to the stable external stimulus independently of the conscious percept are less correlated.

Finally, in a positron emission tomography (PET) imaging study, McIntosh et al. found that the left prefrontal cortex was activated by tones predicting a subsequent target presentation only when subjects became aware of the predictive character of the tone [39]. This was associated with increased correlation between temporal and frontal regions.

Because of its higher temporal resolution, the EEG technique allows to specify the temporal dynamics of this increased functional connectivity in the course of stimulus processing. EEG studies have revealed large-scale synchronization over certain frequency bands, mainly gamma (around 40 Hz) during conscious perception, arising around 250 ms after stimulus presentation [47,55].

Tallon-Baudry et al. recorded EEGs while subjects viewed a classical Dalmatian dog picture [55]. For naive subjects, the picture only appeared as a meaningless pattern of black blobs. However, when informed that a Dalmatian dog could be hidden in the picture, the image became obvious to the subjects, whether the dog was presented facing leftward or rightward. When subjects were naive to the presence of a dog, the unperceived dog induced a faint increase in gamma power around 250 ms after stimulus onset, which was not different from trials where a neutral random blobs pattern was presented. But, when subjects were informed, the perceived dog induced a much larger increase in gamma power around 250 ms, with a large spatial extent around two peaks at occipital and right parietal locations. This increase was much larger than in the neutral presentation.

Similarly, Rodriguez et al. showed a consistent pattern of synchrony in the gamma range between occipital, parietal and frontal areas, arising 230 ms after the presentation of high-contrast faces. This synchrony was absent when faces were presented upside-down and not easily recognized as faces [47].

The observed synchronization in the gamma band probably reflects dynamic synaptic links among distant brain areas [58]. This could underlie the increased functional connectivity revealed in fMRI during conscious perception.

One might further speculate that increased long-distance synaptic links between a fronto-parietal network and sensory areas supports the late sustained neural activity observed in sensory areas for consciously perceived stimulus. The sustained contextual modulation observed in monkeys' V1 neurons when a figure is perceived [54] is probably caused by recurrent connections from higher areas. However, it is not yet established whether this feed-back has a fronto-parietal origin. This could be determined by inactivating different areas and observing the ensuing effect on contextual modulation.

2.5. Evidence for all-or-none bifurcation between conscious and non-conscious processing

The findings presented so far suggest that conscious and non-conscious processing diverge at some point in the underlying processing mode. Indeed, conscious perception seems to be specifically associated with a late and sustained increase in sensory processing, the involvement of a fronto-parietal network, and an increase in long-distance connectivity. An interesting issue is whether those divergences between conscious and unconscious processing are progressive, or reflect an all-or-none sudden change. Some authors consider that conscious perception merely corresponds to a gradual activation increase in sensory areas and, consequently, a progressive involvement of higher order areas [4,43]. However, other models postulate that conscious processing relates to the selective entry of sensory information into a particular stage. Among these, the two-stage model [7] is one of the most favored theoretical accounts of the Attentional Blink (AB) at present. This model postulates that there are two different stages in the processing of a stimulus and that only stimuli that are processed through the second stage are consciously perceived. Contrary to the first stage, the second stage would be capacity-limited, giving rise to a bottleneck for access to conscious processing. The AB deficit would arise from the fact that, as long as the second stage is occupied by the first target (T1), access to this stage is denied to the second target (T2). This delay would increase the probability that T2 is replaced by a following mask before gaining access to the second stage, i.e. before gaining access to the stage of processing necessary for conscious report.

The two-stage model has received strong support from experimental findings. A recent study in our laboratory has shown an all-or-none bifurcation in subjective report during the AB [49]. We asked participants to evaluate the visibility of target words on a continuous scale during the AB. A model postulating a continuum of perception would predict that the AB deficit corresponds to a gradual degradation of the representation of the target words. This would result, on the continuous scale, in a gradual displacement of subjective ratings towards lower visibility degrees. On the contrary, we found that participants used the continuous scale in an all-or-none fashion: targets were either identified as well as targets presented outside the

blink period or not detected at all (Fig. 1). Variations in the strength of the AB deficit as a function of the temporal lag between the first and the second target were manifested by varied proportions of seen and not-seen responses at both ends of the continuous scale. Control experiments allowed us to confirm that these bimodal patterns of response were not due to a response bias. These results suggest that a stochastic non-linear bifurcation in neural activity underlies the all-or-none perception observed during the AB.

A series of event related potential studies by Vogel et al. [33,59] have shown that several levels of perceptual and semantic processing are unaffected by the AB. Indeed, the P1, N1 and N400 waves were found to be preserved during the AB. However, the P300 wave, which reflects the updating of information in working memory, was suppressed during the AB. This result was confirmed by a recent ERP study showing a P300 suppression for “blinked” targets as opposed to detected targets in the AB period [25]. These findings suggest a qualitative difference in the neural processing that takes place inside and outside the AB, with a preservation of a first stage of processing and a complete disappearance of a second stage of processing for “blinked” targets. Preserved or suppressed subcomponents of the P300 wave might well be one correlate of the all-or-none subjective report that we observed using a continuous visibility scale (see [52] for a description of distinct subcomponents of the P300 wave). We are at present investigating this hypothesis using EEG.

In conclusion, conscious and non-conscious processing, although following similar routes at first, appear to diverge

at some point, suddenly and in an all-or-none manner, leading to different dynamic states. We now turn to a short description of the “global neuronal workspace” model, which tries to give a theoretical account of these different states.

3. Theoretical framework: the global neuronal workspace model

3.1. Presentation of the model

During conscious processing, various pieces of information about the stimulus, computed automatically in various specialized and localized processors in the brain, become available for explicit report and flexible manipulation. For example, once conscious, various properties of a stimulus (color, shape, name, motion...) can be reported verbally, but also memorized, evaluated, compared with other past or present stimuli etc. . . Any theory of conscious processing has to explain how the modularity inherent to the distributed architecture of brain areas, can be “broken” to allow the globalization of information, and how information can be maintained over a period of time sufficient to allow conscious report and potentially complex manipulation of this information.

The global neuronal workspace theory [12,15] tries to account for these essential properties by emphasizing the role of long-distance reciprocal connections among brain areas. According to this theory, conscious processing

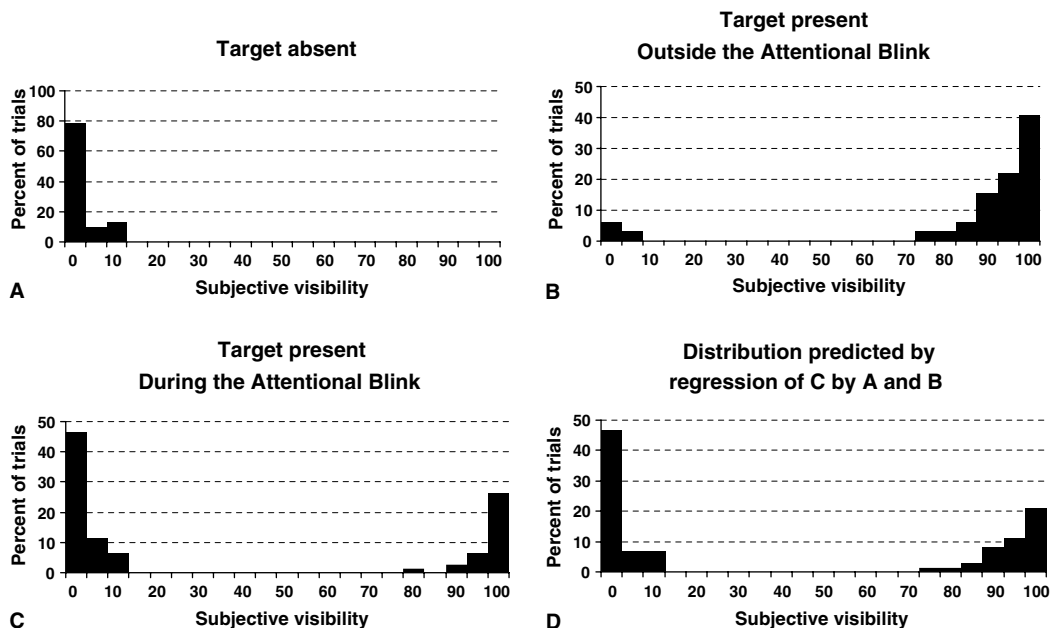


Fig. 1. Distribution of responses on a continuous subjective visibility scale in an Attentional Blink experiment. Data from one subject. When the target was absent, the subject used the left extremity of the scale (around 0% visibility) (A). When the target was present and outside the Attentional Blink period, the subject used almost exclusively the highest visibility ratings (B). During the Attentional Blink period, the response distribution was all or none (C). It seemed to be a combination of responses A (not seen at all) and B (perfectly visible). This was confirmed by performing a multiple linear regression on the distribution C, using distributions A and B as predictors (D): the model accounted for 98% of the variance with significant contributions of both predictors ($p < 0.001$).

crucially involves a set of neurons, the “workspace” neurons, which can work in synergy through long-distance reciprocal connections. Those neurons, which can access information, maintain it online, and make it available to virtually any other process, although particularly numerous in fronto-parietal areas, are distributed throughout the brain, thus constituting a “global workspace” [2,3]. This state of global availability is, according to the theory, just what it is to be conscious of a piece of information.

This theory provides a scenario of the neural events leading to conscious access. An external stimulus is first processed automatically by a series of sensory brain areas activated in a bottom-up manner. This first stage of processing would correspond to what has been called the “feed-forward sweep” of activity [26,28]. Then, processors receive feed-back from areas situated higher in the hierarchy through recurrent connections. This second phase in processing would allow for example contextual modulation in V1 as described by [54]. Importantly, this mechanism would give rise to a very rapid globalization of information concerning a particular stimulus. Workspace neurons in two processors can mutually reinforce their activity through reciprocal connections. This process of reciprocal amplification may be local at first. However, through long-distance connections, reciprocal amplifications can propagate quickly to many different levels in the cortical hierarchy, in a process that we term “cascading amplification”. Ultimately, this would lead to the global ignition of a broad set of workspace neurons, from sensory areas to parietal, frontal areas, and areas implicated in verbal report or motor action. This mechanism would allow broadcasting of information among distant brain areas, as well as amplification and maintenance of this information.

Naturally, not all workspace neurons would ignite at the same time. Powerful inhibition is postulated to maintain most workspace neurons in a silent state, while only a sub-

set of workspace neurons exhibits sustained activity. The particular set of workspace neurons involved in this mutual amplification process at a given time, would code for the current conscious content, and would delineate the possibilities of conscious manipulation, intentional actions and reports.

It should be noted that the theory does not postulate a “magic role” for reciprocal loops in creating conscious perception. It merely emphasizes that long-distance reciprocal connections in the brain may support the described mechanism of global amplification, which, in turn, may account for the central properties of conscious access. A detailed neuronal network simulation implementing part of the global neuronal workspace model has been published elsewhere [16] (Fig. 2).

3.2. Confrontation to empirical findings

In this section, we examine how the global neuronal workspace model may account for the aforementioned empirical findings on the differences between conscious and non-conscious processing.

3.2.1. Enhanced sensory processing

First, experimental studies have shown that conscious processing is associated with enhanced neural activity in sensory areas. Sensory enhancement could be achieved through cascading amplification in a global workspace, as described in the model. This process, engaging a wide range of processors at different levels in the hierarchy, would allow enhancement and stabilization of sensory information, which might reveal crucial for conscious report of this information, for potentially complex operations on this information, or for long-term memorization. Moreover, the contours of the global workspace engaged in amplification at a given time, are determined by the

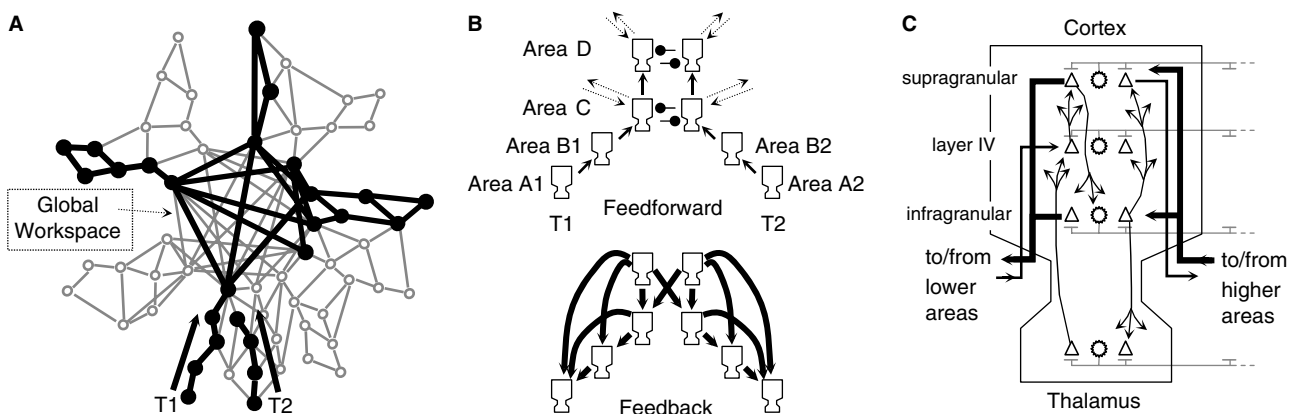


Fig. 2. Neuronal workspace model of conscious access. (A) Schematic architecture of brain areas (redrawn from Ref. [16]) comprising multiple specialized processors and a central network of high-level areas temporarily interconnecting them. During the Attentional Blink, the first target (T1) invades the workspace, where areas lock into a single assembly supporting conscious reportability. This invasion by T1 blocks the processing of the second target (T2) at a similar depth. (B) Subset of thalamo-cortical columns included in the present simulation. (C) Structure of a single simulated thalamo-cortical column, reproducing the laminar distribution of projections between excitatory neurons (triangles) and inhibitory neurons. Figure reproduced from Ref. [16], Copyright (2003) National Academy of Sciences, USA.

particular stimulus that is currently consciously perceived. This is in accordance with empirical data showing stimulus-specific enhancement during conscious processing.

Some empirical data also suggest that the neural activity evoked by non-consciously perceived stimuli fades away as it proceeds through more integrated processors [4,14,21]. Such fading is expected in the model when the first feed-forward wave of activity evoked by a stimulus fails to initiate cascading amplification, necessary for conscious perception. Global amplification might be a way to prevent this “fading of information”. This would require a progressive increase in the proportion of workspace neurons from low levels of sensory processing (e.g. V1) to higher levels (e.g. fusiform gyrus), as suggested by electrophysiological studies on monkeys [30–32,51].

3.2.2. General involvement of a fronto-parietal network

Fronto-parietal regions play a crucial role in the global workspace theory as they are supposed to hold a large concentration of workspace neurons, that send and receive connections to and from many distant areas through long-range axons. This hypothesis comes from the observation that associative fronto-parietal cortices are characterized by thickened layers II/III, which house pyramidal neurons that send and receive long-distance axons, throughout the cortex, and particularly through the corpus callosum [60]. Contrary to processors specialized for specific input parameters (e.g. elementary line segment detector in V1), the fronto-parietal network seems to be involved in supervisory executive functions, essential in working memory and planning [40,50]. From its potentially very rich long-distance connectivity, the fronto-parietal network naturally constitutes a central network in the global workspace in that it is likely to be necessarily involved in any global amplification episode. This view is in accordance with the very consistent finding that a fronto-parietal network is specifically activated during conscious processing, whatever the nature of the stimulus that is consciously perceived (see Section 2.3).

Placing the fronto-parietal network as an obligatory node in conscious processing has an important implication: in this view, conscious perception is not entirely determined by the strength of the first feed-forward wave of activity triggered by a stimulus, it also depends on its pertinence for more general executive functions and on the availability of the executive system at that moment. This idea seems to be supported by the observation that, in the Attentional Blink for example, a stimulus can fail to be reported consciously although the first ERP waves evoked by the stimulus are unaffected [33,59]. Marois et al. [37] have shown that such failure is all the more likely to occur if the frontal-parietal system is currently being engaged strongly by another task. Conversely, a stimulus evoking feeble sensory processing at first might be later reinforced through top-down workspace inputs depending on its pertinence for a current task. This might be the case in Beck et al.’s [5] change detection task where small stim-

ulus changes lead to detectable fMRI changes only when attended to.

Finally, perceptual transitions with no change in the external stimulus, during rivalry, also seem to be mediated by a fronto-parietal network [34]. This finding supports the view that the fronto-parietal network, from its central position, plays a key role in sculpting the contours of the global workspace and alternatively favor different interpretations of the same external presentation.

3.2.3. Long-distance connectivity, long-distance synchrony

Evidently, the workspace theory is in accordance with the finding of increased long-distance connectivity during conscious processing, as long-distance connectivity plays a central role in this theory in establishing and stabilizing a conscious content. The model further predicts that long-distance synchrony is established for a temporary period with a minimal duration of about 100 ms, sufficient for stable communication of multiple distributed areas. This order of magnitude corresponds to the time scale of phase synchrony episodes generally observed in empirical studies (see [58] for review). At longer time scales, a temporal series of successive metastable synchronous states is predicted. New tools of EEG and MEG analysis, such as microstate analysis [29] might be able to test this hypothesis.

3.2.4. Drastic bifurcation between conscious and non-conscious processing

Along with other theories on the neural correlates of conscious perception, the global workspace theory favors the hypothesis of a sharp difference between conscious and non-conscious processing.

This theory provides a possible neuronal account for the two-stage model of the Attentional Blink. A first stage of processing would correspond to automatic processing through the feed-forward sweep of activity, possibly with a small and local contribution of recurrent processing to refine this first wave of computation. The second, capacity-limited stage of processing described in the two-stage model, would correspond to the entry into the global workspace through cascading amplification. The model postulates that, according to the current configuration of the global workspace, only a single representation can be consciously processed at a time, thus leading to a perceptual bottleneck. During the Attentional Blink, the first target occupies the workspace while the second target triggers a first wave of activation. At some point, due to lateral inhibition from the representation of the first target currently being amplified, activation from the second target can fail to reach the dynamic threshold for self-amplification. In that case, activation is confined to the first stage of processing and the second target cannot be consciously perceived and reported. This would explain the observed sudden suppression of the P300 wave for “blinked” targets.

Furthermore, contrary to theories assuming a continuum of perception, the global workspace model predicts

an all-or-none bifurcation in perception: the information extracted from a stimulus is either available for conscious report through the global workspace or simply not reportable consciously. This strong prediction initiated the aforementioned behavioral studies of the Attentional Blink using a continuous measure of subjective visibility. Indeed, we observed an all-or-none bifurcation in conscious report during the “blink” period [49]. A neuronal network simulation of the global workspace model was shown to be able to reproduce the results from this experiment [16] (Fig. 2). What determines whether a stimulus reaches the threshold for conscious access given identical external stimulation? It might be small stochastic differences in the first wave of activation or even in the baseline activity preceding the stimulus. During the “blink” period, stochastic differences in the time and effort spent to process the first target might determine the all-or-none perception of the second target [37]. We suggest that, using a fine-grained subjective measure, bifurcation in subjective report should generalize to other experimental paradigms affecting conscious processing.

It should be noted, however, that the global workspace theory does not exclude the possibility of a gradual increase in the richness of the information available for conscious report, for instance as a progressively masked visual stimulus gains access to featural, shape and semantic levels of analysis [49]. Such a progressive increase has been observed in some studies on object recognition [4]. The global workspace amplifies the information that is available from sensory processing, allowing it to get access to explicit report, however detailed this information might be.

Finally, perceptual hysteresis could be accounted for by the dynamics of the global workspace. Indeed, recurrent amplification through a wide range of areas is supposed to give rise to a metastable activation pattern. Once established, this activation pattern is self-sustained and therefore is less easily destabilized. A lower value of the control parameter than necessary to stabilize this state would then be needed to destabilize it. Such non-linear dynamical phenomena can be described mathematically using catastrophe theory [48,56] and non-linear dynamics theory [1]. Indeed, one of the more exciting prospects of the workspace theory is to bring the physical concept of phase transition to bear on psychological theories of consciousness.

3.3. Summary and predictions of the model

In summary, the neuronal workspace model proposes that the neural basis of conscious access is a sudden self-amplifying bifurcation leading to a global brain-scale pattern of activity. We end by underlining several critical predictions of this view. First, when a stimulus is presented above threshold, we predict that, following an initial period of feed-forward sensory processing lasting ~100–200 ms, there is a sudden non-linear transition towards a temporarily metastable state of globally increased brain activity lasting ~200–300 ms. This sudden increase should be par-

ticularly evident in prefrontal, cingulate, and parietal cortices. It should be accompanied by a synchronous amplification of activation in sensory areas and by brain-scale synchrony in the gamma range (20–100 Hz). Finer scale electrophysiological or optical recordings should demonstrate that this state is selective to a subset of neurons coding for the stimulus, and is accompanied, in higher areas, by broad inhibition of neurons coding for other stimuli. Even higher resolution experiments may reveal a layer-specific distribution of activation, with intense top-down activity originating from a subpopulation of workspace neurons with long axons in supra- and infra-granular layers of prefrontal, cingulate and parietal cortices. The model also predicts that, when presented with a stimulus at threshold, workspace neurons respond in an all-or-none manner, either highly activated or totally inactivated. This all-or-none character should be detectable macroscopically as a bimodal distribution of parameters such as some subcomponents of the P300 wave in event-related potentials. Finally, pharmacological interventions or diseases that affect top-down connections or inhibitory interactions in higher cortical areas should alter the dynamics of workspace ignition, and should therefore modify subjective perception in a predictable manner, while possibly leaving subliminal feed-forward processing unaffected [17].

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