Do consciousness and attention have shared neural correlates?

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Abstract

Over the last few years our understanding of the brain processes underlying consciousness and attention has considerably improved, mainly thanks to the advances in functional neuroimaging techniques. However, caution is needed for the correct interpretation of empirical findings, since both research and reflection are hampered by a number of conceptual difficulties. This paper reviews some of the most relevant theoretical issues surrounding the concepts of consciousness and attention in the neuroscientific literature, and presents the implications of these reflections for a coherent model of the neural correlates of these cognitive functions. Although orthogonally defined as essentially separate neural processes, consciousness and attention show a consistent and overlapping pattern of brain activity, specifically recurrent processing within fronto-parietal association areas. Future research will shed more light on the possible relationship of processes that relate to common brain activity across functions.

Introduction

Only in recent years the development of new scientific techniques have allowed scholars capable to investigate the activity of the living brain. Sophisticated neuroimaging methods, such as the functional magnetic resonance imaging (fMRI) and the positron emission tomography (PET), have been widely used in order to determine the activation of cerebral areas in connection with specific cognitive functions. Although these methods of inquiry have limitations in terms of both spatial and temporal resolution (Logothetis & Wandell, 2004; Raichle, 1998), the hope is that in the future their improvement make us able to identify with an acceptable degree of accuracy the neural correlates of any aspect of mental activity. However, the outcome of this project relies not only on the novel insights of technological instruments, but also on our correct interpretation of the empirical data. A precise analysis of experimental results is of crucial importance, especially in the study of human cognitive functions. In principle, all brain activities might be mapped in order to find a neural correlate for any mental aspect. In fact, it is highly controversial whether distinct neural correlates can be matched with precision to each of the copious details of human cognition.

We can see how empirical and theoretical issues are strongly interrelated in the quest for explaining consciousness and attention (Koch, 2004). Notably, 'consciousness' and 'attention' refer to different concepts with regard to our theoretical framework. For instance, we can roughly single out three different concepts of consciousness (Zeman, 2001) - that is to say, consciousness as waking state, consciousness as experience and consciousness as mind. But other distinctions are possible. We can, for example, distinguish inside of consciousness a phenomenal and an access consciousness according to its different functions (Block, 1995).

The concept of attention is no less questionable. One of the points at issue here is whether or not attention entails the presence of consciousness, and vice versa. What is the relationship between these two functions? Can attention be elicited by subjects having unconscious perception? And, conversely, are there cases in which consciousness can occur without attention? Over the last few years several lines of research have been trying to answer these questions but we are still far from having a complete neuroscientific account for these phenomena. Needless to say, the answers will necessarily depend on what we mean by 'consciousness' and 'attention'. If we accept that consciousness and attention are closely connected, yet ultimately separate activities of the brain, we must also admit that they do have distinct neural correlates. On the other hand, if we are prone to consider these functions intimately united and indistinguishable, we have to be sceptical about the putative differences in the brain processes subduing them. This paper reviews some of the most relevant theoretical issues surrounding the concepts of consciousness and attention in the neuroscientific literature. The final section introduces the implications of these reflections for a coherent model of the neural correlates of consciousness and attention.

The many facets of consciousness

Without consciousness we would not be the persons we are. Undoubtedly consciousness is one of the most fundamental (and also dazzling) properties of our brain. On the one hand, it seems that we can cope with the world without the help of consciousness - the blind vision (Weiskrantz, 1997) and the zombie behaviours (Koch & Crick, 2001) are examples that show how this faculty is not essential for performing simple actions that are based on innate or apprehended automatisms. It has been argued that the early stage of Homo sapiens' history was characterised by a brain-mind bicameral model which allowed unconscious social interactions (Jaynes, 1976; for criticism see Cavanna et al., 2007). On the other hand, it seems reasonable to assume that without consciousness we cannot behave and make things the way we do. For instance, we cannot learn to speak a new language or to play a musical instrument without being conscious of what we are doing. This is probably so because sophisticated emotional experiences can not be appropriately evaluated by unconscious subjects. Moreover, we definitely need consciousness for moving the body in response to complex external stimuli, for taking decisions, for making projects for the future and for recalling memories from the past. In general, it is agreed that all our major mental processes, such as thought, emotion, memory, imagination, language and action planning have more or less to do with consciousness (Zeman, 2001).

The pervasiveness of this concept in human life has certainly contributed to its several meanings. Nevertheless, from the standpoint of neuroscientific research, probably only few of them are of real interest. The most relevant concepts of consciousness within the biological framework of its neural correlates are 'consciousness as waking state' and 'consciousness as awareness (of something)' or phenomenal consciousness. The waking state is fundamental for any cognitive function. In this sense, consciousness appears to be a matter of degree that can be measured quite objectively. Thus, a waking subject can more or less be vigilant, alert or aroused. But wakefulness itself is not enough to account for consciousness, because when we are conscious in this first sense we are, at the same time, always conscious *of something*. In logical terms, it sounds nonsensical to argue that a subject might be conscious without being conscious of anything. Consequently, these two meanings of consciousness are so intertwined that it can be hard to discriminate at the level of neural processes what is essential for one and what for the other. In fact, we know from experimental research that different brain areas are involved in those processes, but still the causal connections among the components of these neural networks remain unclear.

Other problems arise when we examine further meanings of consciousness. For instance, consciousness as mind is too general as a concept, and has literary and metaphoric implications which are beyond the scientific study of brain function at the level of the neural correlates. This sense involves, if any, the profound relationship between self-consciousness and language. Furthermore, some concepts are so technical that it is arguable whether they can be of any use in the account of what happens in the brain when we are in a conscious state. Two examples are Chalmers's distinction between awareness and consciousness, and Block's distinction between phenomenal and access consciousness. According to Chalmers, awareness can be defined as 'the state wherein information is accessible for verbal report and deliberate control of behaviour' (Chalmers, 1996). This account has deep similarities with Block's definition of access consciousness, according to which a representation is access-conscious 'if it is poised for direct control of reasoning, reporting and action' (Block, 1996). Although theoretically sound, this distinction has failed so far to find a sound correlate at the level of neural activity.

In summary, the debate on the nature of consciousness is therefore not only empirical, but quintessentially conceptual. Roughly speaking, we will not be able to find anything if we do not know exactly what we are looking for. Moreover, this issue is tightly interwoven with the problems that arise in the study of attentional processes.

Distinct functional roles for attention and consciousness

Like consciousness, attention can have different and plausible nuances with regard to our tenets. A classic description of attention was put forth by William James in his widely quoted classic *The Principles of Psychology*. According to James 'Every one knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others' (James, 1890).

Since James's times, much experimental work addressing attention has been conducted. However, agreement on a possible theory of attention is far to come. According to many authors, including James, attention as a cognitive faculty is essential for consciousness. For instance, Zeman writes that 'attention is the sentry at the gate of consciousness' (Zeman, 2001). Others hold that 'there is no conscious perception without attention' (Mack and Rock, 1998). Another claim following this line of thought is that 'what is at the focus of our attention enters our consciousness, what is outside the focus of attention remains preconscious or unconscious' (Velmans, 2000). However a number of other scholars point out that consciousness and attention, though closely connected, are nonetheless separate processes of the brain (Baars, 1997; Koch and Tsuchiya, 2006).

In a sense, claims such as 'awareness is a product of attention mechanism' (Lycan, 1996) and 'attention is not sufficient for consciousness and is not the same as consciousness' (Damasio, 1999) can provide support to the opinion that, *pace* William James, 'no one [really] knows what attention is, and … there may even not be an "it" there to be known about' (Pashler, 1998). However this conclusion is perhaps too pessimistic and the discrepancies among scholars will reveal apparent.

Broadly speaking, there is a degree of agreement on the idea that attention is a mechanism that selects relevant information from our sense data. In other words, 'the concept of attention refers to one of the basic characteristics of cognition, namely the capacity to voluntary and involuntary give priority to some parts of the information that is available at a given moment' (Naghavi and Nyberg, 2005). As a cognitive function, attention has the remarkable property of being either voluntary or involuntary. This is of crucial importance, because it allows to distinguish between a top-down attention and a bottom-up attention. The former stems from endogenous factors - that is, a degree of control by the conscious mind in order to point at a particular feature (feature-based attention), object (object-based attention) or region in space (focal attention). On the other hand, bottom-up attention is exerted by exogenous factors - that is, stimuli with a certain degree of intensity that fleetingly attract one person's focus.

Undoubtedly, consciousness is connected with both kinds of attention. In most cases it is true that bottom-up attention represents the gate for consciousness. Likewise, it is mainly true that top-down attention occurs in the presence of awareness status. Nevertheless a few recent experiments (summarized by Koch and Tsuchiya, 2006) have convincingly put forward that attention and consciousness can be related to distinct activities of the brain. Intuitively, most of the time we are conscious of the world that surrounds us but without paying specifically attention to its discrete elements. Top-down attention is excluded in perceiving the gist of a scene even if we are generally conscious of it. On the other hand, blindsight experiments with subject who have lesions in the visual areas occipital cortex support the idea that both top-down attention and bottom-up attention can occur without conscious perception. For instance, 'the blindsight patient GY has the usual reaction-time advantages for the detection of targets in his blind visual field when attentionally cued, even when the cues are located in his blind field' (Kentridge et al., 2004). Moreover, in other experiments with normal subjects, 'priming has been elicited for invisible words (suppressed by a combination of forward and backward masking), but only if the subject was attending to the invisible prime-target pair; without attention, the same word fails to elicit priming' (Koch and Tsuchiya, 2006).

These results suggest that the functional roles of consciousness and attention are different. Consciousness seems to be a global process capable to elaborate information in order to give a survey of what is going on inside and outside the body, whereas attention seems to be the capacity of mental states to shift and appreciate the sensory relevance or salience from one perception to another. This difference is expected to reflect into distinct neural correlates for consciousness and attention.

Brain mechanisms underlying consciousness and attention

Work on the neural correlates of consciousness has been not only theoretical. In the last few years the results of a number of highly sophisticated experiments have been published, made possible, at least in part, by the rapid development of neuroimaging techniques. With the above neurophilosophical arguments in mind, we will now turn to what neuroscience can tell us about the neural correlates of consciousness and attention.

Insight into the neural structures that are important for the level of consciousness (wakefulness) has come from classic and modern lesion studies as well as functional imaging studies, which show that consciousness is supported by a complex network that includes the ascending reticular activating system (ARAS) in the brainstem, the nonspecific nuclei of the thalamus, and the widespread thalamocortical projections to anterior cingulate, posteromedial cortex and fronto-parietal association cortices (Tsuchiya and Adolphs, 2007). According to the 'default mode' paradigm of brain function, a network of extensively interconnected cortical areas located mainly on the medial aspect of the hemispheres is activated more during wakeful rest than during perceptual and attentional engagement with the environment and likely to be crucial to the maintenance of consciousness (Raichle et al., 2001). The posteromedial parietal region (precuneus, posterior cingulate, and retrosplenial cortex), along with the anterior cingulate cortex, the medial frontal cortex and the lateral parietal cortex are activated when processing information related to self, emotion and internal monitoring (Cavanna and Trimble, 2006; Cavanna, 2007). Notably, this network shows strong connections not only among its components, but also with fronto-parietal association areas and nonspecific thalamic nuclei (Parvizi et al., 2006).

On the other hand, the scientific literature on the specific contents of consciousness (phenomenal consciousness) emphasizes structures that are believed to be involved in processing conscious percepts and emotions. One of the discoveries that motivated the search for the neural correlates of consciousness is that so much information processing goes on in the brain in the absence of phenomenal consciousness. These processes have been referred to as 'zombie agents'. This kind of unconscious processing has been first recognised in neurological patients experiencing neglect and extinction (Vallar, 1997), blindsight (Weiskrantz, 1997), and limbic status epilepticus (Monaco et al., 2005; Cavanna, 2008). Subsequently it has been observed in a number of neuroimaging studies on healthy subjects (Koch, 2004). Quite interestingly, the existence of zombie agents means that purposive behavior can happen in the absence of awareness of either the behavior or the stimulus that elicits it, as it has been postulated in the 'bicameral mind' model (Jaynes, 1976). A key comparison for studies on the neural correlates of consciousness is between conditions where the same information is processed with and without awareness. Such comparisons have led to the novel concept of essential nodes, i.e. circumscribed brain regions (or networks) that are necessary for consciousness of certain features or objects in the world. For example, it has been shown that an area called V4 within the fusiform gyrus is essential for subjective/phenomenal experience of color. If this region is selectively damaged (e.g. following a lacunar stroke), the patient will be unable to perceive color. Conversely, if the region is electrically stimulated (e.g. during brain surgery), then the subject will perceive color. However, neural activity in this region is essential but not sufficient for the conscious percept of color. According to a number of recent fMRI studies, interaction with other brain regions, in particular fronto-parietal activity, is also required for conscious visual perception (Naghavi and Nyberg, 2005). These findings have notoriously led to the hypothesis that the neural correlates of visual consciousness are not in the primary visual cortex; on the other hand, this kind of consciousness is an executive summary critically dependent on the prefrontal cortex (Rees et al., 2002; Koch, 2004). Likewise, Pins and Ffytche (2003) suggested that correlates of visual awareness are divided into primary and secondary network nodes, where early activity in the occipital lobe correlates with perceptual processes and later activity in fronto-parietal areas correlates with secondary processes contingent on the outcome of earlier perceptual processing.

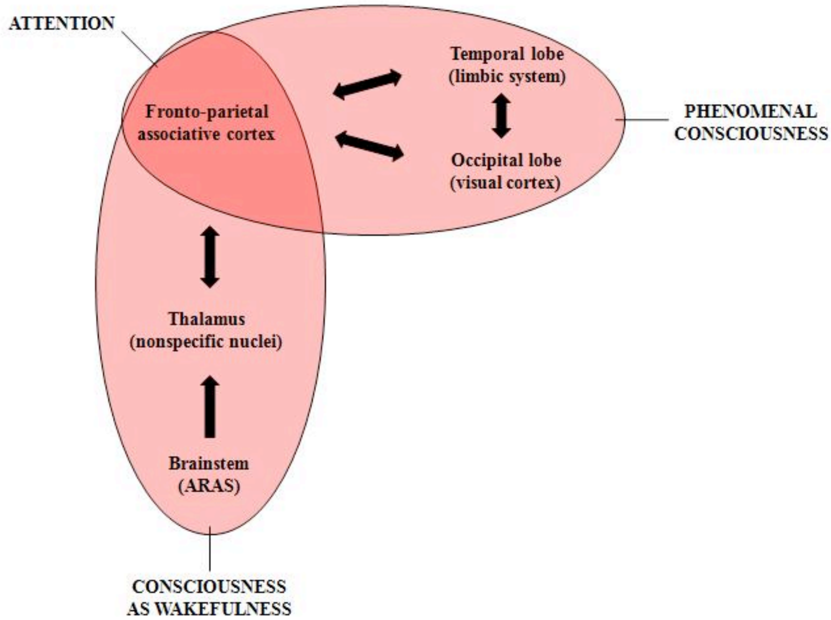
With regards to the emotional component of phenomenal consciousness, both experimental findings in healthy volunteers and clinical observations in patients suffering from mesial temporal lobe epilepsy (so called seizure-induced 'emotional qualia') provide support for the leading role of the amygdala in highly arousing emotions, especially fear, and the pivotal role of the insula in disgust (Monaco et al., 2005). However the picture is complicated by a number of factors including interindividual differences and interactions between the way in which the emotion is induced and the particular kind of emotion. Overall, what is the relationship between phenomenal experiences/emotion states and the level of consciousness? Tsuchiya and Adolphs (2007) have recently argued that in addition to arousal mechanisms in the brainstem and thalamus, emotional processing in cingulate cortex and other midline structures might be important for maintaining a sense of ownership, which in turn seems to be necessary for any conscious experience. However, other aspects of phenomenal consciousness have been shown to be subdued by brain processes which can be partially distinguished from conscious perception and attention processing.

Over the last decade, a wide variety of fMRI and PET studies have also tried to shed light on the nature of underlying neural mechanisms of attention, defined as the capacity to voluntarily or involuntarily give priority to some parts of the information that is available at a given moment. Most studies have revealed a distributed system of brain regions that control attention by enhancing the processing of attended aspects of information. These studies showed that the most consistent activation pattern for attention was in the bilateral parietal and dorsolateral prefrontal cortex (Pessoa et al., 2003).

In summary, the combined psychological and neural perspectives allow a clear distinction to be made between consciousness and attention. However, several studies have revealed that attention is essential for conscious visual perception. For example, a fMRI study by Rees et al. (1999) showed that visual recognition depends on attention even for highly familiar and meaningful materials. Rees and Lavie (2001) have proposed that distributed interactions between modality-specific posterior regions and fronto-parietal areas subserve both visual attention and visual awareness, and encouraged work that explores similarities in functional activation patterns related to various forms of attention and consciousness. Empirical evidence suggests attention and visual awareness engage overlapping patterns of activity in dorsolateral prefrontal and parietal cortex. These activation patterns have been linked to integration of distributed representations in multiple brain areas. The proposed central role of integration is consistent with general theories of the neural bases of consciousness which emphasize concepts such as global workspace (Baars, 1997; 2002). This latter can be viewed as a mental capacity which represents the dominant information that is widely distributed in the brain at each moment. According to this theory, conscious perception is not restricted to sensory analysis; rather, it enables access to widespread brain sources, whereas unconscious input processing is limited to sensory regions. Within the global workspace, selective attention enables access to conscious contents, and *vice versa*. Another key concept for the understanding of the neural correlates of higher-order cognitive functions is recurrent processing. Particularly, it has been highlighted that what seems necessary for conscious experience is that neurons in visual areas engage in recurrent processing (Lamme 2003; 2004). This would enable the widespread exchange of information between brain regions processing different attributes of the visual scene, and thus support perceptual binding. In addition, when recurrent interactions involve the frontoparietal areas, potential motor responses could modify the visual responses, which would form the neural equivalent of attention.

Both the involvement of the frontoparietal network *per se*, as suggested by the global workspace theory, and the recurrency, as suggested by the observation that reportable conscious percepts are associated with recurrent processing in visual as well as frontoparietal areas, could represent the essential neural ingredient of the overlap between consciousness and attention. Figure 1 graphically summarises these notions. It shows that, from the neural perspective, the two main aspects of consciousness (wakefulness and phenomenal awareness) and attention can be orthogonally defined as essentially separate neural processes, with partial overlapping within fronto-parietal association networks. Moreover, although it is logically possible to pay attention to something without any accompanying emotional experience, emotional states and phenomenal consciousness are known to influence the focus of attention and to modulate the degree of responsiveness to external stimuli.

Figure 1. Schematic representation of the intersection (and partial overlapping) of the neural correlates of consciousness and attention.



Abbreviations. ARAS, ascending reticular activating system.

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Conclusions

We all have an intuitive understanding of what 'attention' and 'consciousness' mean, but making this usage sufficiently precise for scientific investigation requires further distinction. This article has focused on the conceptual dissection of consciousness and attention, and on the theoretical domains where they overlap and interact. Converging lines of evidence suggest that these composite concepts indicate different, albeit interrelated, cognitive processes. Specifically, it appears that top-down attention and conscious perception are distinct phenomena that need not occur together, and are characterised by different brain correlates, which nevertheless show a degree of overlap in recurrent processing within fronto-parietal association areas. What is the functional significance of overlapping fronto-parietal activation patterns? Further research on brain mechanisms is needed to clarify processes related to integration of distributed representations. Specifically, relevant issues to be addressed concern the mechanisms whereby the integration of the neurobiological substrates of attention and consciousness draws a coherent representation of reality from a set of sundry perceptions. Moreover, we need to discriminate at a neural level the functional processes leading to conscious states on which there is no attentional focus and to attentional states in the absence of consciousness, respectively. Advances in neuroimaging techniques and experimental designs will help to give a better account for these phenomena. However, future work requires not only more empirical data, but also further theoretical development of the concepts that are under investigation. When grounded on solid theoretical background, the intersection of attention and consciousness is ripe for future experimental investigation and collaborations among neuroscientists, psychologists and philosophers.

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