

# The Intrinsic Activity of the Brain and Its Relation to Levels and Disorders of Consciousness

*Michele Farisco<sup>1</sup>, Steven Laureys<sup>2</sup>, and Katinka Evers<sup>1</sup>*

*1 – Centre for Research Ethics and Bioethics  
University of Uppsala, Sweden*

*2 – Coma Science Group, Cyclotron Research Centre  
University and University Hospital of Liège, Belgium*

## Abstract

Science and philosophy still lack an overarching theory of consciousness. We suggest that a further step toward it requires going beyond the view of the brain as input-output machine and focusing on its intrinsic activity, which may express itself in two distinct modalities, i.e. aware and unaware. We specifically investigate the predisposition of the brain to evaluate and to model the world. These intrinsic activities of the brain retain a deep relation with consciousness. In fact the ability of the brain to evaluate and model the world can develop in two modalities, implicit or explicit, that correspond to what we usually refer to as the unconscious and consciousness, and both are multilevel configurations of the brain along a continuous and dynamic line. Starting from an empirical understanding of the brain as intrinsically active and plastic, we here distinguish between higher cognitive functions and basic phenomenal consciousness, suggesting that the latter might characterize the brain's intrinsic activity as such, even if at a very basic level. We proceed to explore possible impacts of the notion of intrinsic cerebral phenomenality on our understanding of consciousness and its disorders, particularly on the diagnosis and management of patients with disorders of consciousness.

## 1. Introduction

According to widely shared neuroscientific and philosophical views, consciousness is a system-level feature or configuration<sup>1</sup> of the brain shaped

---

<sup>1</sup>The distinction between feature and configuration is suggested by the recent proposal of Georg Northoff (2016) to apply the conceptual framework of “structural realism” in the definition of brain and related mental phenomena, like consciousness. These are consequently defined according to a process-based ontology, which states the existence and reality of structure and relation instead of discrete features of fixed objects (like the brain), as affirmed in an object-based ontology. Consequently, brain and related mental phenomena cannot be defined in themselves, but only within the constitutive relationship with the world they are involved in.

by its structural and functional organization. Even if recently questioned by Bayne *et al.* (2016), scientific and public perceptions of consciousness share the idea that we can be conscious at different levels: intrapersonally (we have different levels of consciousness depending on the state or activity we are involved in), or interpersonally, when distinct individuals do not share the same level of consciousness, especially if healthy subjects are compared with people suffering from disorders of consciousness (DOCs).

DOCs generally mean a relatively acute impairment of consciousness resulting from severe brain damage. This can first lead to a clinical condition of non-responsiveness, called coma, in which the patients cannot be awakened even if intensively stimulated. Coma can be followed by fast recovery, brain death, locked-in syndrome, where the patient is fully awake and aware but unable to interact with the external, or vegetative state / unresponsive wakefulness syndrome (VS/UWS), where the patient retains wakefulness (i.e. levels of consciousness), but not awareness (i.e. content of consciousness). VS/UWS can then evolve into minimally conscious state (MCS, subdivided in MCS+ and MCS-), where the patient recovers some aware abilities, or into persistent vegetative state, if VS/UWS lasts more than one month. MCS can then end in recovery of consciousness or in a supposed permanent MCS (Gosseries 2011).

The empirical progress in the classification and diagnosis of DOCs has been impressive in the last years. Nevertheless, an overarching conceptual assessment of the different possible levels of consciousness that patients with DOCs may retain is still lacking (Hohwy and Fox 2012).

In this assessment, we suggest, it is useful focusing on the intrinsic brain activity, specifically on the intrinsic predisposition of the brain to evaluate and model the world.<sup>2</sup> This is a bi-modal (either implicit, i.e. unaware, or explicit, i.e. aware) and multilevel dynamic brain characteristic that is not limited to our cognitive and reflective abilities. Starting from a model of the brain as intrinsically and spontaneously active, in this article we investigate the possibility that the brain in itself maintains a basic level of consciousness, an “unaware consciousness”, corresponding to unreflective consciousness (e.g. we can feel things without being focally, reflectively aware that this is taking place). We call this “organic” consciousness insofar as it characterizes an organ, the brain, which is part of a biological organism, the body.

The definition of consciousness as a fundamental characteristic of the living brain related to its intrinsic propensity to evaluate and model the world is conceptually clear and epistemically parsimonious: specifically, given the models available today (Metzinger 2000, Pereira and Lehmann

---

<sup>2</sup>We may note that the “world” that the brain evaluates and models includes the body and eventually the brain itself as potential targets, otherwise self-conscious experiences and experiences depending on particular brain malfunctions (e.g. chronic pain) would be impossible.

2015), it seems the simplest way to approach consciousness. In fact, if consciousness, as it seems, exists along a continuum, it is reasonable to think that it might be ontologically co-extensive with the living and intrinsically active brain: consciousness could be implicitly present, while not explicitly expressed. We aim to show that while this understanding of consciousness may initially seem counterintuitive and thus potentially controversial, it is scientifically plausible, and clinically and ethically relevant.

At the conceptual level, connecting the concept of consciousness to the brain's propensity to evaluate and model the world avoids the risk of a categorical fallacy, specifically the objection that not brains but "persons" are conscious. Since the concept of consciousness we suggest is wider than the cognitive consciousness we usually refer to when defining a subject as conscious (Cerullo 2015), we argue that it can be referred to the brain as such rather than being exclusively applicable to the "person". Moreover, within our naturalistic framework we prefer to refer to the brain rather than to the "person" also because, while the definition of the former, notwithstanding ongoing debates and controversies, is empirically well grounded, the definition of the latter seems to us too ambiguous, vague and controversial to serve well in this context (and it will not be part of the present analysis because it is not relevant for our argumentation).

A comprehensive conceptual assessment of consciousness and related topics is beyond the aim of this paper. Numerous issues arise in the conceptual framework we suggest that would deserve further analysis, e.g. the concept of life, of minimal conditions for conscious life, of brain death, the possibility of fetal, animal and artificial consciousness, the connection of our model with monism and panpsychism, the specific identification of neuronal signatures of different modalities of consciousness, to name just a few. Our aim is to offer a general conceptual framework for further analyses of these and other issues.

## **2. Consciousness:**

### **An Intrinsic Characteristic of the Brain**

Neuroscience has moved away from depicting the brain as a simple mechanistic input-output device, and towards a view that describes it as a complex, dynamic, and plastic organ that is spontaneously active and projective (Changeux 1986, Edelman 1987, LeDoux 2002, Evers 2009, Laureys 2015). From the embryonic to the adult stage, an ongoing spontaneous activity is present throughout the nervous system, particularly but not exclusively at the level of cortical workspace neurons, which send and receive projections to many distant areas (Dehaene and Changeux 2005). Moreover, a wide distributed network of areas has been detected

to be more active at rest, i.e. in absence of actual stimulation, than during active task, constituting the so-called resting state (RS) brain activity. This network includes dorsal and ventral medial prefrontal, lateral parietotemporal and posterior cingulate cortices (Gusnard *et al.* 2001, Vanhaudenhuyse *et al.* 2011).

The spontaneous activity of the brain and its RS activity are the foundation of the brain's relative autonomy from external stimuli: the brain develops spontaneous representations in what has been described as its "projective style", even in absence of actual external signals (Changeux 2004, Sanders *et al.* 2012). Projective here means that the brain is pre-disposed to build a model of the world that is useful for the satisfaction of its needs and for survival. Model here means not directly a mental representation, but a particular neuronal configuration corresponding to a specific prediction about the world. As a consequence, even if feedback and feedforward activity in the brain, particularly in cortical layers, is continuous and on-going, our perception results from comparing an internal representation of the world, resulting from both previous feedback loops stored in memory and the spontaneous projective style of the brain (Frith 2007, Friston 2010).

The focus on the intrinsic and RS activities of the brain does not imply a closed or "monadic" view: brains do not live in isolation, but they are complex adaptive systems nested in larger complex adaptive systems (Dudai and Evers 2014). They reside in bodies, which are in constant interaction with their environments. A sharp distinction between intrinsic and extrinsic (i.e. reactive to external stimuli) activity, or between feedback and feedforward activity of the brain is difficult to draw: the first is a necessary condition for the latter, which in turn modulates the former (Changeux 2004).

The brain's relationship with its external environment is essential for its development (Changeux *et al.* 1973). A continuous process of "pruning" and selection of synapses gives rise to a mechanism of neuroselection, which constantly produces new combinatorial models in a plastic way allowing the same afferent message to stabilize different arrangements of connections. The brain is thus shaped by mechanisms resulting from a complex interplay between genetics and environment.

These mechanisms are epigenetic. The epigenetic model of neuronal development stands on the premise that the synaptic architecture of the brain is not pre-specified in the genetic code, but learning and experience (i.e. the interaction with the external environment) heavily affect the brain's development within the boundaries of a "genetic envelope" (Changeux *et al.* 1973). The synaptogenesis and the development of the human brain take place both prenatally and postnatally, lasting much longer than in any other mammalian species. These processes result from epigenetic selection.

The epigenetic shaping of the brain takes place through cerebral activities that are largely unaware; our brain is able to correlate information, associate meanings, reason in a very fast way, develop complex computations, perform sophisticated mathematical operations, selectively focus on information, develop complex inferences (Dehaene 2014), and even perceive the affective value of stimuli and influence motivation, value judgment and goal-directed behavior without awareness (Berlin 2011). According to the so-called predictive coding model, the anticipation of external information that the brain is able to develop affects the way we are conscious of that information (Northoff 2013a).

Our aware conscious experience is delayed and reconstructed: it depends on preceding processes taking place without awareness. The brain's relation with the external environment is not limited to conscious awareness and is even, in part, independent of it. This activity gives rise to awareness when a change from RS occurs. What is usually called "unconscious" exhibits the ability to evaluate the external world, i.e. to assign it values. A "value" here means a direct relevance to the brain's needs as expressed in its configuration resulting from epigenetic development. Particularly, the unaware evaluation of stimuli is not free from emotional dimensions: the affective value of the information is largely processed outside our awareness (Berlin 2011). Furthermore, recent empirical investigations showed that even activities traditionally associated with aware consciousness, such as reading or doing arithmetic, can take place without awareness at the level traditionally defined as unconscious (Sklar *et al.* 2012).

Using a technique called "continuous flash suppression", which consists of the presentation of a target stimulus to one eye and the simultaneous presentation of rapidly changing masks to the other eye, allowing subliminal presentations that last seconds, Sklar and colleagues have shown that even quite sophisticated human cultural products, such as semantically processing a number of words and solving arithmetic equations, can take place outside explicit awareness. Namely, participants were presented with semantically coherent and semantically non-coherent expressions. The latter became aware before the former, showing the ability of the brain to semantically process them outside explicit awareness.

Summarizing empirical evidence, Hassin (2013) concludes that the unconscious is able to perform every fundamental high-level cognitive functions usually performed by consciousness (e.g. cognitive control, pursuit of goals, information broadcasting, reasoning). Hassin's conclusions are in line with other studies and related interpretations (Dijksterhuis 2006, Kastrup 2017), within a new scientific approach that has been called "the new unconscious" (Hassin *et al.* 2005).

In particular, even if not universally accepted (Hatzimoysis 2007), the concept of unconscious emotion has gained increasing scientific legitimacy,

both in the sense of unawareness of the stimuli eliciting emotion and of unawareness of the emotion itself (Ohman *et al.* 2000, Winkielman and Berridge 2004, Smith and Lane 2016). In conclusion, notwithstanding on-going controversies regarding the specific characterization of the unconscious and its abilities (Hesselmann and Moors 2015), including the very concept of unconscious perception (Prinz 2015), there is increasing scientific agreement on the fact that the unconscious is far more complex and similar to consciousness than we hitherto thought.

Neuroscience thus increasingly reveals the complexity of the unconscious, suggesting that even the deep neuronal distinction between conscious and unconscious levels may need to be revised: stimuli processed without awareness can activate high-level cortical regions (Berlin 2011) – albeit without being connected to the global neuronal workspace – while aware consciousness might be difficult to segregate from them (Merker 2007).

Conceptually, the issue arises how to describe the unconscious and consciousness as well as their mutual relationship. The traditional approach keeps the two terms separated as two distinct conceptual categories. In such a framework, unconscious experiences are not conscious by definition. In the framework that we here develop, their relationship is differently described: consciousness is the overarching conceptual category that may express itself in two modalities, implicit/unaware or explicit/aware, which are not binary but exist on a continuum with different levels.

From neuroanatomical and neurophysiological points of view, there are major debates concerning the identification of specific “neural correlates of consciousness” (NCC), i.e. a set of neuronal structures and functions correlated with conscious phenomena. Since their formal introduction in the scientific debate at the beginning of the 1990s (Crick and Koch 1990), NCC have been widely scrutinized from both conceptual and empirical points of view (Metzinger 2000, Koch *et al.* 2016). Conceptually, NCC are defined by Chalmers (2000) as minimal neuronal activations necessary for consciousness. Such general definition has been widely accepted in both philosophical and empirical contexts.

More specifically, NCC can be depicted in two basic ways: referring to general, global state of consciousness, i.e. as neural correlates that mark the difference between being and not being conscious, or referring to particular contents of consciousness, i.e. as neural correlates that are sufficient for a specific object to enter consciousness (Chalmers 2000, Overgaard 2017).

It is worth noting that NCC are qualified as sufficient but not necessary because otherwise the definition would be too strong (in fact there might be more than one NCC of a given conscious experience). Moreover, NCC are qualified as “minimally sufficient” – in fact Chalmers distinguishes between total NCC (comprising the totality of physical processes

absolutely required for a conscious state) and core NCC (comprising only the core processes correlated with the target conscious state). Importantly, Chalmers specifies that being a *correlate* of consciousness does not imply that NCC are only dedicated to consciousness, or that NCC are the most responsible for the generation of consciousness, or that NCC are an explanation of consciousness.

Notwithstanding this legitimate caution, the above-summarized description of NCC has been widely used in scientific research. Regarding content-specific NCC, there has been a debate among neuroscientists (see Overgaard 2017) whether to identify them with systems in the prefrontal cortex (late activations) or with systems in occipital/parietal cortices (early activations). The increasingly accepted view is that the latter hypothesis is more likely, while late activation in prefrontal cortex would be a correlate of metacognition, attention, task execution, monitoring and reporting rather than of consciousness (Aru *et al.* 2012, Koch *et al.* 2016). According to the most recent research in the field, the same is true for NCC of state consciousness. Even in this case the best current anatomical candidates are localized in a temporo-parietal-occipital zone of the posterior cerebral cortex (Koch *et al.* 2016).

In addition to NCC, background conditions for consciousness are recognized as important. Particularly, neuronal populations within subcortical regions, like the brainstem, hypothalamus and basal forebrain, provide an important background condition for consciousness facilitating effective interactions among cortical areas (Parvizi and Damasio 2001). Yet these background conditions might be unnecessary for consciousness if an appropriate subset of cortical regions has sufficient intrinsic activation (Nir *et al.* 2011, Koch *et al.* 2016). Accordingly, the role of basal ganglia, claustrum and thalamus in enabling consciousness is still debated.

Notwithstanding the impressive advancement in the localization of NCC for specific conscious experiences, their explanatory power with regard to consciousness remains limited: being minimally sufficient but not necessary, NCC do not explain why there is consciousness rather than not. Trying to explain consciousness requires taking into account also other necessary factors, e.g. intrinsic and RS brain activities, or cortical-subcortical structural and functional connections.

Despite the different specific scientific models that have been suggested, it is generally agreed that distributed activity of the brain is necessary for consciousness, which can be seen as the result of trans-regional networking in the brain (Dehaene and Changeux 2005, Dehaene and Changeux 2011). The functional organization of the brain is relevant for conscious experience, which is system-level rather than limited to the activation of specific brain areas. Awareness in particular is not related to activity in a single brain region only but to thalamo-cortical connectivity in the frontoparietal network. Conscious awareness critically depends on

the functional integrity of thalamo-cortical and cortico-cortical frontoparietal connectivity within and between the midline default mode network (DMN) (“intrinsic” system) and the lateral frontoparietal cortices or “extrinsic system” (Noirhomme *et al.* 2010).

The specific function of DMN, which anatomically encompasses the cingulate cortex, medial pre-frontal cortex, medial temporal lobe, and angular gyrus (Andrews-Hanna *et al.* 2014), is still debated in scientific literature (Raichle *et al.* 2001, Raichle and Snyder 2007), even if increasing data indicate its implication in several activities, e.g. introspection, day-dreaming, and memory recall (Andrews-Hanna 2012). Particularly, studies on sleeping, anesthetized and DOC subjects reveal a positive correlation between functional connectivity of DMN and consciousness (Greicius *et al.* 2008, Horovitz *et al.* 2009, Vanhaudenhuyse *et al.* 2010, Heine *et al.* 2012), especially self-referential consciousness (Whitfield-Gabrieli *et al.* 2011).

Recent findings (Noirhomme *et al.* 2010, Huang *et al.* 2016) also suggest that the conscious perception of a stimulus is associated with whole-brain dynamic alterations in functional connectivity (i.e. in the connectivity between brain regions sharing functional properties). The point is that consciousness is not dependent on the activation of particular, independent cerebral areas, but on a brain network as a *system*: we could say that consciousness is a trans-regional dynamic configuration of the brain involving different areas constituting a functional and structural systemic unity. The brain’s intrinsic activity, the RS activity and the relative involved areas (Boly *et al.* 2008, 2009) play a critical role in this systemic configuration of the brain.

The relevance of the brain’s intrinsic activity and of RS activity for consciousness is illustrated by DOCs. Recent empirical investigations suggest that DOCs could be defined as an impairment of the intrinsic and RS activities of the brain. Specifically, the impairment affects the residual ability of the RS activity to change in a nonlinear way: it results in decreased functional and effective connectivity as well as decreased or even absent higher-frequency oscillations in the RS (Boly *et al.* 2008, Vanhaudenhuyse *et al.* 2010). Furthermore there is a decreased neuronal reactivity or propensity of the RS to changes in its neural activity (Northoff 2014b). Functionally, this impairment of the RS results in a limitation of its encoding of neural activity in terms of spatial and temporal differences. Since aware consciousness emerges from the RS’s ability to change in these terms, there could be a residual cognitive or sensory or emotional processing without corresponding aware conscious activity: RS as such is not enough for aware consciousness, because different steps occur between the two (Northoff 2014b).

In short, consciousness is a graded characteristic of the brain, which could be more specifically described as an intrinsic ability of the brain



to configure itself independently and/or in relation to the world. This dynamic configuration shows a positive correlation with the functional connectivity of RS, particularly of the DMN and the thalamus (Vanhaudenhuyse *et al.* 2010, Huang *et al.* 2014). In addition to the impairment of functional connectivity, the effective (i.e. causal) connectivity appears impaired in DOCs (Rosanova *et al.* 2012). So, in DOCs there is a collapse of global and trans-regional functional and effective connectivities, especially in midline regions as the core of the DMN. Neural activity is more local, simple and short in DOCs compared to healthy conditions that show global, complex and longer activity (Boly *et al.* 2007a, Northoff 2013b, 2014b). Less RS's predisposition to changes, less rest-rest interaction and absence or decrease of high-frequency oscillations cause the absence of aware consciousness.

As a consequence, from a clinical point of view, it is reasonable to assume that the degree of electrophysiological activity, including high-frequency oscillations, can be used to distinguish between different levels of consciousness. The connectivity strength of DMN is, in fact, proportionally related to the level of consciousness (Boly *et al.* 2009).

### 3. Consciousness: A Multilevel Characteristic of the Brain

Starting from the aforementioned empirical data, our conceptual hypothesis is that consciousness should be defined in connection to the intrinsic predisposition of the brain to model and simulate the world in order to assign it values, i.e. to check the world's salience to the brain's needs. This propensity is inherent to the architecture of the brain, and raises a complex flow of feedforward and feedback loops. Intrinsic and RS brain activities play a critical role in this process. So long as the brain is alive and retains residual intrinsic and RS activities there will be some residual ability to experience and evaluate the world in the sense outlined above, even in cases of non-REM sleep, faint, epileptic seizure, sleepwalking, anesthesia or coma (Laureys 2015). The brain can be completely silenced during deep isoelectric anesthesia or in rare cases of very severe acquired brain damage (Laureys *et al.* 2004), but we can only turn it completely off by dying.

An intrinsic "aboutness" characterizes the brain. Gerald Edelman (1992) suggests that the conscious brain is essentially an intentional organ, in the sense that it is constantly engaged in producing mental images and models *of* and *about* its internal or external environment. Analogously, Jean-Pierre Changeux (2004) talks about the projective style of brain functions describing the brain as a motivated and self-organizing system engaged in the exploration of its environment or in abstract stimulus-

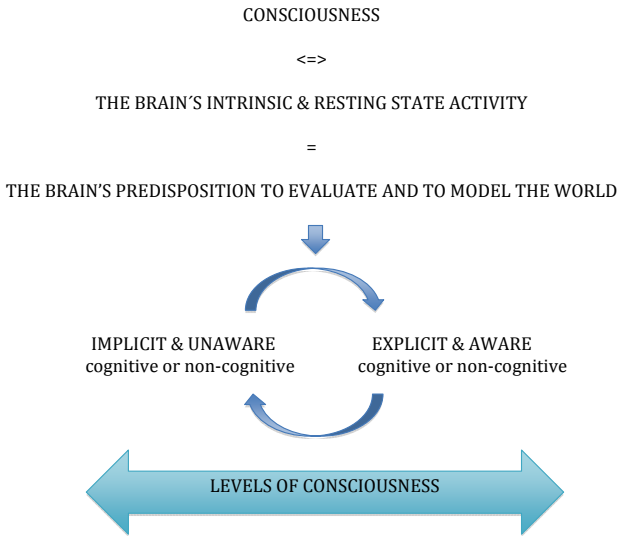


Figure 1: Consciousness has a deep relation with the brain's intrinsic and resting state activities, specifically with the brain's predisposition to model and evaluate the world. This predisposition may express itself in two modalities, implicit/unaware or explicit/aware, which are not binary but exist on a continuum. Both of them can be cognitive or non-cognitive. Consciousness is an overarching brain characteristic with different levels.

independent thinking (Laureys 2015). Drawing from their views, we suggest that consciousness is an intrinsic characteristic of the brain, that the brain is intrinsically conscious, as long as it retains the ability to evaluate and model the world by appropriate intrinsic and RS activities. In this perspective, consciousness in its broadest sense corresponds to the phenomenal, evaluative and modeling abilities of the brain. Thus consciousness is an overarching brain characteristic. More specifically, consciousness thus conceived can express itself in two distinct modalities: explicit (i.e. aware or reflective) consciousness, and implicit (i.e. unaware or unreflective) consciousness. The point is that consciousness exists on a continuum and is not reducible to higher cognitive abilities (see Fig. 1).

Additional empirical support of such a view emerges from the study of the *Bereitschaftspotential*, also known as pre-motor potential or readiness potential. From Kornhuber and Deecke's (1965) research and onwards, several studies have revealed that aware, volitional action is preceded by an unaware, spontaneous activity in the motor cortex and supplementary motor area.

On the basis of these scientific premises, we suggest that conscious-

ness is an intrinsic cerebral characteristic, which has two multilevel and dynamic modalities: explicit (aware) and implicit (unaware). These two modalities can have different levels of complexity and content, and they are dynamical because they exist along a continuum and merge with each other. Moreover, they are asymmetrically interconnected, for whilst it is impossible to have aware consciousness without an underlying unaware consciousness, unaware consciousness can exist without awareness, e.g. in non-responsive DOCs (Dehaene and Changeux 2005).

These two modalities can be defined according to different levels of complexity and content. It follows that consciousness (both aware and unaware) is a multilevel nonlinear dynamic configuration of the brain (Laureys 2015). According to our framework, the intrinsic and RS activities of the brain are both necessary and sufficient for one modality of consciousness (i.e. unaware consciousness), while they are necessary but not sufficient for the other modality (i.e. aware consciousness).

Even if not universally accepted (Baars and Laureys 2005, Dehaene *et al.* 2006, Lamme 2006, Schier 2009, Kouider *et al.* 2010b), it is common to distinguish between “access” and “phenomenal” consciousness (Block 1995). Access consciousness can be defined as the interaction between different states, particularly the availability of one state’s content for use in reasoning and rationally guiding speech and action. Phenomenal consciousness can be defined as the subjective feeling of a particular experience, “what it is like to be” in a particular state (Nagel 1974, Block 1995). In our account, the unaware modalities of both types of consciousness are intrinsic to the brain.

A distinction between phenomenal and access consciousness seems to us useful to draw, both from a conceptual and from an empirical point of view, at least by an inference to the best explanation: we do not experience the content of the information without a subjective quality associated to it. The same content is more or less significant (i.e. emotionally qualified) depending on previous personal experience. Moreover, as suggested by the abovementioned recent findings about cognitive and emotional unconscious, both access and phenomenal processing seem to be deeper and wider than aware consciousness.

This is exemplified by the fact that attention and consciousness are not co-extensive (Koch and Tsuchiya 2012): we can be conscious without previous top-down attentional processing, and selective attention on information can take place outside aware consciousness. This means that attention might be neither necessary nor sufficient for aware consciousness (van Boxtel *et al.* 2010). Kouider *et al.* (2010a) have rightly specified that instead of a total absence of attention we could have a residual attention at lower levels of processing, for instance as sensory and non-conceptual selection. So the relevant differentiation is between reflective and unreflective selection of information.

In our view, this unreflective selection of information can give rise to both aware and unaware consciousness. Such unaware consciousness can be a basic level of access consciousness but also a basic level of phenomenal consciousness. More specifically, this basic level of consciousness can be qualified as non-cognitive rather than cognitive, i.e. not related to the high cognitive functions consciousness is usually identified with (Cerullo 2015) but rather with a basic capacity of meaningfully interacting with the environment, i.e. of evaluating it by an interaction in which a central role is played by emotions.

If it is true that subliminal priming, i.e. the semantic processing of information at the level of what is traditionally defined as unconscious, occurs at visual, semantic, and even motor levels (Dehaene and Changeux 2011), and if what is traditionally described as unconscious is also emotionally qualified (Ohman *et al.* 2000, Winkielman and Berridge 2004, Smith and Lane 2016), then it is reasonable to think that the unaware selection of information could bias not only our cognitive access to information but also our subjective feeling of information (i.e. the subjective likeness of the experiences we live as cognitive subjects). This might be interpreted in the sense that unaware consciousness is a sort of pre-phenomenal consciousness, i.e. it precedes the proper beginning of phenomenal consciousness and it affects the aware cognitive phenomenal consciousness. In this interpretation both access and phenomenal consciousness are defined as cognitive dimensions, i.e. they are both associated with a cognitive structure like the self or the mind. In contrast, we suggest that the basic level of unaware consciousness might be a non-cognitive modality of consciousness associated with the intrinsically active brain itself. This basic level of unaware consciousness is phenomenal in itself, a non-cognitive and non-reflective modality of phenomenal consciousness.

As described above, consciousness appears to be the result of a complex distributed activity within the brain, a multilevel reality. Notwithstanding the recognized central role of the identified NCC, even chemical reactions at the subcortical levels, as well as spinal cord, cerebellum and visceral ganglia are highly complex and relevant for consciousness, which could suggest that consciousness, both aware and unaware, depends on subcortical and cortical processes (Merker 2007). This is in line with our conceptual model, according to which it is reasonable that phenomenal consciousness in particular involves different levels of the brain, not only the cortical one.

According to what has been defined as “neurophenomenal” approach, no specific function – whether affective, sensorimotor or cognitive – is a necessary and enabling condition for consciousness, which results from neuronal processes and mechanisms preceding any specific function (Northoff 2013b, 2014a). These processes and mechanisms preceding consciousness are intrinsic characteristics of the brain, i.e. RS and neural code. An

alternative to our account is to define them as “prephenomenal” rather than non-phenomenal or phenomenal.

According to this view, a brain-based explanation of consciousness should focus on the necessary rather than on the sufficient conditions for consciousness, i.e. on the neuronal states that can become phenomenal consciousness rather than on neuronal mechanisms of specific consciousness contents. Such neuronal predispositions of consciousness are intrinsic characteristics of the brain. The brain’s intrinsic activity, as a pre-stimulus neural activity, gives rise to a spatiotemporal continuity that organizes the incoming stimuli in space and time (Northoff 2013b, 2014b). In this way, the intrinsic activity of the brain is like a template for processing external stimuli, and provides the form of our consciousness.

This differs from our approach, which does not only relate consciousness to the intrinsic activity of the brain, but defines such activity as itself conscious, i.e. non-cognitively unaware conscious. We would like to note that the idea that the living intrinsically active brain is inherently conscious does not entail panpsychism: life as such is not co-extensive with consciousness because consciousness requires some conditions to be satisfied, e.g. a central nervous system. A related issue, which will not be addressed here, is what level of complexity is required for the central nervous system to be described as conscious, or even to be described as a central nervous system (Laureys 2005).

#### **4. Impacts on Diagnoses and Management of Patients with DOCs**

The semantic enlargement of consciousness and the identification of (very basic levels of) consciousness with the brain’s intrinsic and RS activities implies that patients with DOCs are still conscious if their brains are still alive and retain appropriate residual intrinsic and RS activities, specifically a residual ability to model and evaluate the world. This might have important implications for the diagnosis of DOCs. For one thing, the question will not be “whether” the patient has any level of consciousness (since this would necessarily be the case), but on what level it is present: assessing a DOC means assessing the residual intrinsic and RS activities of the brain (Giacino *et al.* 2014, Northoff 2014b). We are aware that clinicians, in the case they use a neurotechnological assessment like neuroimaging, already focus on residual brain activity in assessing consciousness, but our model suggests to focus not only or primarily on the activity of the brain in reaction to actual external stimuli, but on the residual intrinsic and RS brain activities checking the integrity of the relevant cerebral areas.

A related question is how the consciousness retained by patients with DOCs is characterized: since the functional organization of their brain

is deeply affected, it is reasonable to conclude that the residual attitude to evaluate and model the world, both implicitly (unaware) and explicitly (aware), can be significantly different from that of healthy subjects – a challenging issue for mind-reading and neuro-semantic (Evers and Sigman 2013).

According to our model, which is supported by empirical evidence (Kouider *et al.* 2010b, Mudrik *et al.* 2014, Barttfeld *et al.* 2015, Huang *et al.* 2015, Raichle 2015), consciousness is heterogeneous but continuous. Empirical studies also suggest that DOCs are heterogeneous but continuous (Noirhomme *et al.* 2010, Bruno *et al.* 2012): the differentiation between different forms of DOCs might be not so sharp as traditionally thought (Fisher and Truog 2017). Residual consciousness in DOCs can be assessed in terms of both aware consciousness (i.e. explicit evaluation and modeling of the world) and unaware consciousness (i.e. implicit evaluation and modeling of the world), as defined above. It is important to take into account this bi-modal and multilevel characterization of consciousness in assessing patients with DOCs. Otherwise we risk looking for only the highest levels of consciousness underestimating the possibility that the patient retains other, lower levels of consciousness, particularly the non-cognitive consciousness related to the intrinsic and RS brain activities.

At the clinical level, our approach highlights the importance of analyzing the brain on different levels in order to determine adequate diagnostic and health care procedures. Namely, instrumental diagnostic approaches focusing on structural and functional brain organization, particularly of intrinsic and RS brain activities, should complement traditional behavioral approaches, allowing clinicians to detect residual intrinsic brain activity that is relevant for assessing residual consciousness as well (Rosazza *et al.* 2016).

The dynamics of RS and its connection with consciousness have been recently explored (Barttfeld *et al.* 2015). Long-range RS functional connectivity has been explained in two complementary ways: as arising from a spontaneous, endogenous activation of cognitive processes or as the result of a semi-random circulation of spontaneous neural activity. The point at stake is the following: Is RS activity only a manifestation of the organized structural connectivity matrix, preserved even in absence of (aware) consciousness? What are, then, the aspects of RS brain activity specifically related to (aware) consciousness? A possibility suggested by Barttfeld and colleagues is that signatures of the aware conscious state lie in the dynamics of spontaneous brain activity. Given the centrality of RS brain activity in the conscious activity of the brain we suggest that a proper assessment of residual consciousness in DOCs should focus on the intrinsic residual brain activity, which is not reducible to aware consciousness and even independent from it.

To date we are lacking a specific investigation of how RS changes in loss

of (aware) consciousness. Particularly, temporal dynamics of brain networks should be very different during wakefulness and after loss of aware consciousness. According to Barttfeld and colleagues, a high diversity of network states characterizes the aware condition, while in the unaware condition the spontaneous activity is reduced to a random pattern of neural activity shaped and constrained by the anatomical connectivity.

In this way, focusing on the RS brain activity, it is possible to disentangle aware from unaware brain activity. We suggest the adoption of a brain-centered perspective, so that consciousness becomes an overarching concept corresponding to the spontaneous and intrinsic brain attitude to evaluate and model the world. In this perspective DOCs become disorders of intrinsic brain activity and of RS, and they can be quantified by clinicians assessing, e.g., the RS' predisposition to changes, rest-rest interaction, presence and rate of high-frequency oscillations and the diversity of network states.

At the clinical level, our model suggests to focus more on the brain's intrinsic predisposition to evaluate and model the world, which is multilevel and bi-modal (aware/unaware), and its intrinsic phenomenality. These intrinsic cerebral characteristics call for specific clinical and ethical attention: the edge between consciousness and the unconscious with the resulting clinical and ethical primacy usually attributed to the former seems to be too simplistic and not in line with recent neuroscientific findings and theories. The exclusive primacy of awareness seems to be a biased perspective, and we suggest expanding the focus to include assessment of the brain's residual intrinsic and RS activities and looking for retained unaware as well as aware abilities.

In particular, organic consciousness may be related to a multilevel capacity for sensitivity and sentience, e.g. capacity for experiencing suffering and pleasure at a non-cognitive level. In our approach even the lowest levels of consciousness are important to assess: the organic consciousness we describe can be relevant in order to determine the most appropriate clinical care because it allows for pleasure and/or suffering to occur even at the lowest levels. The brain of patients with DOCs, although damaged, is still able to feel in some way, and has implicit tendencies that may be qualified in terms of needs and preferences.

A growing number of clinical studies aim to show retained responsiveness to external stimulation in patients with DOCs (Boly *et al.* 2007b, Monti *et al.* 2010). The interpretation of the emerging results is controversial because attention and aware consciousness are not co-extensive: the mere ability to attend or react to external stimulation is not enough to conclude that a patient retains aware consciousness (Kouider *et al.* 2010b). In our perspective, checking whether a patient retains aware consciousness is not a discriminative point for deciding the most appropriate clinical procedure. In our model what is usually defined as unconscious is not an

amorphous, apathetic and impersonal dimension, but it has a particular subjectivity, which may be important to take into account in ethical and clinical assessments. The unaware modality of consciousness is subjective because it results from a peculiar epigenetic process that is “inscribed” in the neuronal configuration of the brain, so that it interacts with the external environment in a peculiar and specific way. This subjectivity has different dimensions, aware and unaware, cognitive and non-cognitive. All these dimensions should be properly acknowledged and assessed.

If we regard the intrinsic and RS activities of the brain as pre-phenomenal (i.e. necessary but not sufficient for phenomenal consciousness) or (as we here suggest) as phenomenal (i.e. necessary and sufficient for phenomenal consciousness, even if at a basic and unaware level), this will potentially result in different diagnostic categories and in different positions regarding the treatment options. If the brain is phenomenal in itself, it can feel somehow. From this fact, within our framework a possible ethical consequence arises, which needs to be investigated further: we should treat the damaged brain so as to respect its ability to retain a certain degree of phenomenality. This does not in itself imply that aware and unaware consciousness and related needs have the same ethical value, but the question can be raised: Why are people inclined to attribute a greater ethical importance to aware consciousness than to unaware consciousness?

We do not tackle these issues directly here, but we stress the urgency to discuss the possible ethical relevance of the unaware abilities retained by the brain, their impact on the aware abilities and their importance for a proper ethical judgment (Farisco and Evers 2017). We consider it necessary to pursue a deeper evaluation of the ethical importance of emotions, both positive (like pleasure) or negative (like pain). In particular, we find it unjustified to limit the moral importance of emotions only to those that are felt by an aware cognitive consciousness excluding those felt by unaware non-cognitive consciousness. In our framework, phenomenology goes beyond aware cognitive consciousness. Our brain can feel something even though we are not aware of it. This, we suggest, seems in accordance with both empirical evidence and ordinary experience.

In the long-term perspective, holding that the brain, as long as it is intrinsically active, is *ipso facto* intrinsically phenomenal (even if at different levels) might support the view that we should care about living brains and make efforts in approaching patients with DOCs not only on the basis of the retained aware abilities, but also on the basis of the retained unaware abilities, which are currently not well investigated and maybe underestimated.



## 5. Conclusion

If consciousness exists on a continuum, i.e. the distinction between consciousness and the unconscious is not discrete, and it is understood as the intrinsic brain predisposition to evaluate and model the world, the living brain with residual intrinsic and RS activities is inherently conscious (even if at different, eventually very basic and non-reflective levels). The idea of inherent consciousness recognizes two important features of what traditionally is called unconscious. It is an active and subjectively characterized (i.e. phenomenally shaped) dimension of cerebral life, and it makes a huge contribution to our conscious life (actually being part of it).

This view may seem counterintuitive, but it seems philosophically and scientifically more advanced than defining a too sharp distinction between consciousness and the unconscious within the brain. In our view, the active and reactive brain is only one reality with several modalities characterized by different levels. This philosophically monistic approach is scientifically and epistemologically parsimonious: the object to investigate is one (the brain as an evaluative organ), and we do not have any gap within it between different dimensions, but only relative and blurring differentiation between modalities of the same (empirical and metaphysical) reality.

This view is not less complex than the traditional way of defining consciousness as clearly distinguished from and even opposed to the unconscious. But it offers a different theoretical framework that is simpler and clearer because it conceives the brain as a unified reality with different levels of the same conscious activity. This framework is potentially useful in clinical contexts, e.g. for providing more refined diagnoses and better management of patients with DOCs.

## Acknowledgements

This research is supported by funding from the European Union's Horizon 2020 research and innovation program under grant agreement 720270 (HBP SGA1). Special thanks to Jean-Pierre Changeux, Arleen Salles, Mariano Sigman, the participants at the CRB seminars and to two reviewers for important comments on previous drafts of this paper.

## References

- Andrews-Hanna J.R. (2012): The brain's default network and its adaptive role in internal mentation. *Neuroscientist* **18**(3), 251–270.
- Andrews-Hanna J.R., Smallwood J., and Spreng R.N. (2014): The default network and self-generated thought: component process, dynamic control and clinical relevance. *Annals of the New York Academy of Science* **1316**, 29–52.

- Aru J., Bachmann T., Singer W., and Melloni M. (2012): Distilling the neural correlates of consciousness. *Neuroscience Biobehavioral Review* **36**(2), 737–746.
- Baars B.J. and Laureys S. (2005): One, not two, neural correlates of consciousness. *Trends in Cognitive Science* **9**(6), 269; author reply 270.
- Barttfeld P., Uhrig L., Sitt J. D., Sigman M., Jarraya B., and Dehaene S. (2015): Signature of consciousness in the dynamics of resting-state brain activity. *Proceedings of the National Academy of Sciences of the USA* **112**, 887–892.
- Bayne T., Hohwy J., and Owen A.M. (2016): Are there levels of consciousness? *Trends in Cognitive Science* **20**(6), 405–413.
- Berlin H.A. (2011): The neural basis of the dynamic unconscious. *Neuropsychanalysis* **13**(1), 5–31.
- Block N. (1995): On a confusion about a function of consciousness. *Behavioral and Brain Sciences* **18**(2), 227–287.
- Boly M., Balteau E., Schnakers C., Degueldre C., Moonen G., Luxen A., Phillips C., Peigneux P., Maquet P., and Laureys S. (2007a): Baseline brain activity fluctuations predict somatosensory perception in humans. *Proceedings of the National Academy of Sciences of the USA* **104**, 12187–12192.
- Boly M., Coleman M.R., Davis M.H., Hampshire A., Bor D., Moonen G., Maquet P.A., Pickard J.D., Laureys S., and Owen A.M. (2007b): When thoughts become action: An fMRI paradigm to study volitional brain activity in non-communicative brain injured patients. *Neuroimage* **36**(3), 979–992.
- Boly M., Phillips C., Tshibanda L., Vanhaudenhuyse A., Schabus M., Dang-Vu T.T., Moonen G., Hustinx R., Maquet P., and Laureys S. (2008): Intrinsic brain activity in altered states of consciousness: how conscious is the default mode of brain function? *Annals of the New York Academy of Science* **1129**, 119–129.
- Boly M., Tshibanda L., Vanhaudenhuyse A., Noirhomme Q., Schnakers C., Ledoux D., Boveroux P., Garweg C., Lambermont B., Phillips C., Luxen A., Moonen G., Bassetti C., Maquet P., and Laureys S. (2009): Functional connectivity in the default network during resting state is preserved in a vegetative but not in a brain dead patient. *Human Brain Mapping* **30**(8), 2393–2400.
- Bruno M.A., Majerus S., Boly M., Vanhaudenhuyse A., Schnakers C., Gosseries O., Boveroux P., Kirsch M., Demertzi A., Bernard C., Hustinx R., Moonen G., and Laureys S. (2012): Functional neuroanatomy underlying the clinical subcategorization of minimally conscious state patients. *Journal of Neurology* **259**(6), 1087–1098.
- Cerullo M.A. (2015): The problem with phi: a critic of integrated information theory. *Plos Computational Biology* **11**(9), e1004286.
- Chalmers D. (2000): What is a neural correlate of consciousness? In *Neural Correlates of Consciousness: Empirical and Conceptual Questions*, ed. by T. Metzinger, MIT Press, Cambridge, MA, pp. 17–39.
- Changeux J.-P. (1986): *Neuronal Man: the Biology of Mind*, Oxford University Press, New York.
- Changeux J.-P. (2004): *The Physiology of Truth: Neuroscience and Human Knowledge*, Harvard University Press, Cambridge.

- Changeux J.P., Courrège, P., and Danchin A. (1973): A theory of the epigenesis of neuronal networks by selective stabilization of synapses. *Proceedings of the National Academy of Sciences of the USA* **70**, 2974–2978.
- Crick F. and Koch K. (1990): Towards a neurobiological theory of consciousness. *Seminars in Neuroscience* **2**, 263–275.
- Dehaene S. (2014): *Consciousness and the Brain: Deciphering How the Brain Codes Our Thoughts*, Viking Adult, New York.
- Dehaene S. and Changeux J.P. (2005): Ongoing spontaneous activity controls access to consciousness: A neuronal model for inattentive blindness. *PLoS Biology* **3**(5), e 141.
- Dehaene S. and Changeux J.P. (2011): Experimental and theoretical approaches to conscious processing. *Neuron* **70**(2), 200–227.
- Dehaene S., Changeux J.P., Naccache L., Sackur J., and Sergent C. (2006): Conscious, preconscious, and subliminal processing: a testable taxonomy. *Trends in Cognitive Science* **10**(5), 204–211.
- Dijksterhuis A. and Nordgren L.F. (2006): A theory of unconscious thought. *Perspectives on Psychological Science* **1**(2), 95–109.
- Dudai Y. and Evers K. (2014): To simulate or not to simulate: What are the questions? *Neuron* **84**(2), 254–261.
- Edelman G.M. (1987): *Neural Darwinism : The Theory of Neuronal Group Selection*, Basic Books, New York.
- Edelman G.M. (1992): *Bright Air, Brilliant Fire: On the Matter of the Mind*, Basic Books, New York.
- Evers K. (2009): *Neuroetique. Quand la matière s'éveille*, Odile Jacob, Paris.
- Evers K. and Sigman M. (2013): Possibilities and limits of mind-reading: A neurophilosophical perspective. *Consciousness and Cognition* **22**, 887–897.
- Farisco M. and Evers K. (2017): The ethical relevance of the unconscious. Submitted to *Philosophy, Ethics and Humanities in Medicine*.
- Fisher D.B. and Truog R.D. (2017): The problems with fixating on consciousness in disorders of consciousness. *AJOB Neuroscience* **8**(3), 135–140.
- Friston K. (2010): The free-energy principle: A unified brain theory? *Nature Reviews Neuroscience* **11**(2), 127–138.
- Frith C. (2007): *Making up the Mind: How the Brain Creates Our Mental World*, Wiley-Blackwell, London.
- Giacino J.T., Fins J.J., Laureys S. and Schiff N.D. (2014): Disorders of consciousness after acquired brain injury: The state of the science. *Nature Reviews Neurology* **10**(2), 99–114.
- Gosseries O., Vanhaudenhuyse A, Bruno MA, Demertzi A, Schnakers C, Boly M.M., Maudoux A, Moonen G., and Laureys S. (2011): Disorders of consciousness: Coma, vegetative and minimally conscious states. In *Experimental Insights into Meditation, Waking, Sleep and Dreams*, ed. by D. Cvetkovic and I. Cosic, Springer, Heidelberg, pp. 29–55.

Greicius M.D., Kiviniemi V., Tervonen O., Vainionpaa V., Alahuhta S., Reiss A. L., and Menon V. (2008): Persistent default-mode network connectivity during light sedation. *Human Brain Mapping* **29**(7), 839–847.

Gusnard D.A. and Raichle M.E. (2001): Searching for a baseline: Functional imaging and the resting human brain. *Nature Reviews Neuroscience* **2**(10), 685–694.

Hassin R.R. (2013): Yes it can: On the functional abilities of the human unconscious. *Perspectives on Psychological Science* **8**(2), 195–207.

Hassin R.R., Uleman J.S., and Bargh J.A. (2005): *The New Unconscious*, Oxford University Press, Oxford.

Hatzimoysis A. (2007): The case against unconscious emotions. *Analysis* **67**(4), 292–299.

Heine L., Soddu A., Gomez F., Vanhaudenhuyse A., Tshibanda L., Thonnard M., Charland-Verville V., Kirsch M., Laureys S., and Demertzi A. (2012): Resting state networks and consciousness: Alterations of multiple resting state network connectivity in physiological, pharmacological, and pathological consciousness states. *Frontiers of Psychology* **3**, 295.

Hesselmann G. and Moors P. (2015): Definitely maybe: Can unconscious processes perform the same functions as conscious processes? *Frontiers of Psychology* **6**, 584.

Hohwy J. and Fox E. (2012): Preserved aspects of consciousness in disorders of consciousness: A review and conceptual analysis. *Journal of Consciousness Studies* **19**(3–4), 87–120.

Horowitz S.G., Braun A.R., Carr W.S., Picchioni D., Balkin T.J., Fukunaga M., and Dwyer J.H. (2009): Decoupling of the brain’s default mode network during deep sleep. *Proceedings of the National Academy of Sciences of the USA* **106**, 11376–11381.

Huang Z., Dai X., Wu X., Yang Z., Liu D., Hu J., Gao L., Tang W., Mao Y., Jin Y., Wu X., Liu B., Zhang Y., Lu L., Laureys S., Weng X., and Northoff G. (2014): The self and its resting state in consciousness: An investigation of the vegetative state. *Human Brain Mapping* **35**(5), 1997–2008.

Huang Z., Zhang J., Longtin A., Dumont G., Duncan N. W., Pokorny J., Qin P., Dai R., Ferri F., Weng X., and Northoff G. (2015): Is there a nonadditive interaction between spontaneous and evoked activity? Phase-dependence and its relation to the temporal structure of scale-free brain activity. *Cerebral Cortex* **27**(2), 1037–1059.

Huang Z., Zhang J., Wu J., Qin P., Wu X., Wang Z., Dai R., Li Y., Liang W., Mao Y., Yang Z., Zhang J., Wolff A., and Northoff G. (2016): Decoupled temporal variability and signal synchronization of spontaneous brain activity in loss of consciousness: An fMRI study in anesthesia. *Neuroimage A* **124**, 693–703.

Kastrup B. (2017): There is an “unconscious”, but it may well be conscious. *Europe’s Journal of Psychology* **13**(3), 559–572.

- Koch C., Massimini M., Boly M., and Tononi G. (2016): Neural correlates of consciousness: Progress and problems. *Nature Reviews Neuroscience* **17**(5), 307–321.
- Koch C. and Tsuchiya N. (2012): Attention and consciousness: Related yet different. *Trends in Cognitive Science* **16**(2), 103–105.
- Kornhuber H.H. and Deecke L. (1965): Hirnpotentialänderungen bei Willkürbewegungen und passiven Bewegungen des Menschen: Bereitschaftspotential und reafferente Potentiale. *Pflügers Archiv für die gesamte Physiologie des Menschen und der Tiere* **284**(1), 1–17.
- Kouider S., de Gardelle V., Dehaene S., Dupoux E., and Pallier C. (2010a): Cerebral bases of subliminal speech priming. *Neuroimage* **49**(1), 922–929.
- Kouider S., de Gardelle V., Sackur J., and Dupoux E. (2010b): How rich is consciousness? The partial awareness hypothesis. *Trends in Cognitive Science* **14**(7), 301–307.
- Lamme V.A. (2006): Towards a true neural stance on consciousness. *Trends in Cognitive Science* **10**(11), 494–501.
- Laureys S. (2005): The neural correlate of (un)awareness: Lessons from the vegetative state. *Trends in Cognitive Science* (12), 556–559.
- Laureys S. (2015): *Un Si Brillant Cerveau. Les états limites de consciences*, Odile Jacob, Paris.
- Laureys S., Owen A.M., and Schiff N. D. (2004): Brain function in coma, vegetative state, and related disorders. *The Lancet Neurology* **3**(9), 537–546.
- LeDoux J.E. (2002): *Synaptic Self: How Our Brains Become Who We Are*, Viking, New York.
- Merker B. (2007): Consciousness without a cerebral cortex: A challenge for neuroscience and medicine. *Behavioral and Brain Science* **30**(1), 63–81; discussion pp. 81–134.
- Metzinger T., ed. (2000): *Neural Correlates of Consciousness. Empirical and Conceptual Questions*, MIT Press, Cambridge.
- Monti M.M., Vanhaudenhuyse A., Coleman M.R., Boly M., Pickard J.D., Tshibanda L., Owen A.M., and Laureys S. (2010): Willful modulation of brain activity in disorders of consciousness. *New England Journal of Medicine* **362**(7), 579–589.
- Mudrik L., Faivre N., and Koch C. (2014): Information integration without awareness. *Trends in Cognitive Science* **18**(9), 488–496.
- Nagel T. (1974): What is it like to be a bat? *Philosophical Review* **8**(4), 435–450.
- Nir Y., Staba R.J., Andrillon T., Vyazovskiy V.V., Cirelli C., Fried I., and Tononi G. (2011): Regional slow waves and spindles in human sleep. *Neuron* **70**(1), 153–169.
- Noirhomme Q., Soddu A., Lehembre R., Vanhaudenhuyse A., Boveroux, P., Boly M., and Laureys S. (2010): Brain connectivity in pathological and pharmacological coma. *Frontiers in Systems Neuroscience* **4**, 160.
- Northoff G. (2013a): *Unlocking the Brain Volume 1, Coding*, Oxford University Press, Oxford.

- Northoff G. (2013b): What the brain's intrinsic activity can tell us about consciousness? A tri-dimensional view. *Neuroscience and Biobehavioral Reviews* **37**(4), 726–738.
- Northoff G. (2014a): *Minding the Brain: A Guide to Philosophy and Neuroscience*, Palgrave Macmillan, Basingstoke.
- Northoff G. (2014b): *Unlocking the Brain Volume 2, Consciousness*, Oxford University Press, Oxford.
- Northoff G. (2016): Neuroscience and Whitehead I: Neuro-Ecological Model of Brain. *Axiomathes* **26**(3), 219–252.
- Ohman A., Flykt A., and Lundqvist D. (2000): Unconscious emotion: Evolutionary perspectives, psychophysiological data and neuropsychological mechanisms. In *Cognitive Neuroscience of Emotion*, ed. by L. Nadel, G. Ahern and R.D. Lane, Oxford University Press, New York, pp. 296–327.
- Overgaard M. (2017): The status and future of consciousness research. *Frontiers in Psychology* **8**, 1719.
- Parvizi J. and Damasio A. (2001): Consciousness and the brainstem. *Cognition* **79**(1-2), 135–160.
- Pereira A. and Lehmann D., eds. (2015): *The Unity of Mind, Brain and World. Current Perspectives on a Science of Consciousness*, Cambridge University Press, Cambridge.
- Prinz J. (2015): Unconscious perception. In *Oxford Handbook of Philosophy of Perception*, ed. by M. Matthen, Oxford University Press, Oxford, pp. 371–392.
- Raichle M.E. (2015): The restless brain: How intrinsic activity organizes brain function. *Philosophical Transaction of the Royal Society of London Series B* **370**(1668).
- Raichle M.E., MacLeod A.M., Snyder A.Z., Powers W.J., Gusnard D.A. and Shulman G.L. (2001): A default mode of brain function. *Proceedings of the National Academy of Sciences of the USA* **98**, 676–682.
- Raichle M.E. and Snyder A.Z. (2007): A default mode of brain function: A brief history of an evolving idea. *Neuroimage* **37**(4), 1083–1090; discussion pp. 1097–1089.
- Rosanov M., Gosseries O., Casarotto S., Boly M., Casali A.G., Bruno M.A., Mariotti M., Boveroux P., Tononi G., Laureys S., and Massimini M. (2012): Recovery of cortical effective connectivity and recovery of consciousness in vegetative patients. *Brain* **135**(4), 1308–1320.
- Rosazza C., Andronache A., Sattin D., Bruzzone M.G., Marotta G., Nigri A., Ferraro S., Sebastiano D.R., Porcu L., Bersano A., Benti R., Leonardi M., D'Incerti L., Minati L., and Coma I. (2016): Multimodal study of default-mode network integrity in disorders of consciousness. *Annals of Neurology* **79**, 841–853.
- Sanders R.D., Tononi G., Laureys S., and Sleigh J.W. (2012): Unresponsiveness not equal unconsciousness. *Anesthesiology* **116**, 946–959.
- Schier E. (2009): Identifying phenomenal consciousness. *Consciousness and Cognition* **18**(1), 216–222.

Sklar A.Y., Levy N., Goldstein A., Mand R., Maril A., and Hassin R.R. (2012): Reading and doing arithmetic nonconsciously. *Proceedings of the National Academy of Sciences of the USA* **109**, 19614-19619.

Smith R. and Lane R.D. (2016): Unconscious emotion: A cognitive neuroscientific perspective. *Neuroscience and Biobehavioral Reviews* **69**, 216-238.

van Boxtel J.J., Tsuchiya N., and Koch C. (2010): Consciousness and attention: On sufficiency and necessity. *Frontiers in Psychology* **1**, 217.

Vanhaudenhuyse A., Demertzi A., Schabus M., Noirhomme Q., Bredart S., Boly M., Phillips C., Soddu A., Luxen A., Moonen G. and Laureys S. (2011): Two distinct neuronal networks mediate the awareness of environment and of self. *Journal of Cognitive Neuroscience* **23**(3), 570-578.

Vanhaudenhuyse A., Noirhomme Q., Tshibanda J., Bruno M.A., Boveroux P., Schnakers C., Soddu A., perlbag V., Ledoux D., Bricchant J.F., Moonen G., Maquet P., Greicius M.D., Laureys S., and Boly M. (2010): Default network connectivity reflects the level of consciousness in non-communicative brain-damaged patients. *Brain* **133**(1), 161-171.

Whitfield-Gabrieli S., Moran J.M., Nieto-Castanon A., Triantafyllou C., Saxe R. and Gabrieli J.D. (2011): Associations and dissociations between default and self-reference networks in the human brain. *Neuroimage* **55**(1), 225-232.

Winkielman P. and Berridge K.C. (2004): Unconscious emotion. *Current Directions in Psychological Science* **13**(3), 120-123.

*Received: 23 June 2017*

*Revised: 31 October 2017*

*Accepted: 09 November 2017*

*Reviewed by Alfredo Pereira and another, anonymous, referee.*