Consciousness and Cognition 49 (2017) 70–85

Contents lists available at ScienceDirect

Consciousness and Cognition

journal homepage: www.elsevier.com/locate/concog

Review article

Missing piece of the puzzle in the science of consciousness: Resting state and endogenous correlates of consciousness

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A R T I C L E   I N F O

Article history:
Received 3 February 2016
Revised 19 December 2016
Accepted 22 January 2017
Available online 1 February 2017

Keywords:
Consciousness
Correlate(s) (of consciousness)
Background state (of consciousness)
Stream(s) (of consciousness)
Specific states (of consciousness)
Default mode network (DMN)
Endogenous brain activity

A B S T R A C T

Consciousness still stands as one of the most interesting and the most elusive problems of neuroscience. Finding its correlates is the first step toward its satisfactory explanation. Several theories have proposed its correlates but none of them seem to be generally accepted even though most of them share some very similar elements. These elements are the activity of the thalamus, which is considered by some as the central region for consciousness, and gamma synchronization, which should be the general principal for the emergence of conscious experience. However, all of these proposed theories share one characteristic and that is that they do not take into consideration the recently discovered endogenous activity of the brain, which is generally associated with the default mode network. Although the activity of this large scale brain network is in correlation with various levels of consciousness it is still missing in discussions of consciousness. This review recognizes the importance of endogenous activity and points out the important discoveries of endogenous activity that could be an important step toward a satisfactory explanation of consciousness.

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http://dx.doi.org/10.1016/j.concog.2017.01.006
1053-8100/

1. Introduction

Consciousness represents the most enigmatic issue in current theories of the mind. There are at least three positions that can be taken regarding consciousness. The first is the position taken by radical reductionists, eliminativists and some orthodox neuroscientists. These claim that consciousness should not be even considered as an issue because it does not exist and therefore any move we make explaining it is automatically a waste of time. The second position is the classical philosophy of consciousness, which claims that consciousness exists but it is something fascinating with such a mysterious nature that it cannot be fully explained by empirical science. These interpretations of consciousness were bound together by the concept of the *Hard Problem of Consciousness*, which roughly claims that empirical science especially neuroscience will never be able to give a satisfactory answer to how and why conscious phenomenal qualities arise from physical processes of the brain (Chalmers, 1996, 1998). The last position is "neurophilosophy" or "empirically oriented philosophy". Adherents of this new position consider consciousness to be a cognitive or neural process of the brain without any mysterious or intractable nature.

From this open minded basis and without any fundamental restrictions we constantly strive to explain issues of the philosophy of the mind using actual empirical data, measurements, observations and neuroscientific conclusions. From this combination we can expect valid empirical answers to questions about the nature of consciousness. What are the main questions of the science of consciousness? We can name the basic ones: *What are we conscious of? How do we become conscious? Why are we conscious?* and *Who is conscious?* (Prinz, 2005). All of the answers to these questions are related to the *neural correlates of consciousness* that are considered by Chalmers to be "arguably the cornerstone of the recent resurgence of the science of consciousness" (Chalmers, 2000, pp. 17).

In this review we will swiftly go through the proposed theories of consciousness. We will highlight which neural correlates they offer, what these theories are based on, and what their common features are. This review will also show that the science of consciousness based solely on these theories is missing a very important piece of the puzzle. This missing piece is *conscious resting states* that are currently widely associated with the *default mode network* (DMN) and its *endogenous brain activity* (Gusnard, Akbudak, Shulman, & Raichle, 2001; Raichle & Snyder, 2007; Raichle et al., 2001). This large-scale resting network is associated with a wide range of cognitive states but it is seldom considered from the perspective of the neural correlate of conscious experience.

The organization of this review is following. At first we will introduce three types of consciousness – *Background States of Consciousness*; *General Stream of Consciousness* and *Specific States of Consciousness.* Then we will show their correlates, first in evoked brain activity. Evoked brain activity represents so called reactive states of brain which are induced by stimulation. These states are also associated with active attention which is necessary for immediate responding to the environment. After that this review extensively describes DMN and shows its neglected correlates of three types of consciousness. Evoked brain activity is in anti-correlated position with activity of DMN which is most active during the absence of external stimulation and is responsible for spontaneous internally oriented mental states (Gusnard & Raichle, 2001; Gusnard et al., 2001; Raichle & Snyder, 2007; Raichle et al., 2001). And finally this review discusses and proposes precuneus as a new cerebral celebrity of consciousness.

2. Three types of consciousness whose correlates we will seek

Studying consciousness is anything but easy, not only because it is a very difficult scientific theme but also because there are many meanings of this concept. So the first thing we have to do is make it very clear what we do and do not mean by the term consciousness. We will not in any case be defending the *Hard Problem of Consciousness*. Even though we believe that the Hard Problem should not be entirely avoided it can be left alone for a while so it does not pollute every discussion about consciousness and subjective experience. John Bickle summed it up pretty nicely: "Zealous guardians of 'the hard problem' in the philosophy of consciousness should loosen up. Philosophers aren't only ones respectful or in pursuit of the full glory of Mind" (Bickle, 2003, pp. 213). So we take the liberty to think about consciousness as being something very similar to the "representational property of representations or a cognitive property of the system that processes representations" (Brooks, 2005, pp. 401).

I believe that we have cleared up our position about consciousness pretty quickly and I also believe that we can skip most of the other connotations of consciousness and restrict ourselves here to just three: *Background States of Consciousness*; *General Stream of Consciousness*; *Specific States of Consciousness.*

Background States of Consciousness are states of being awake, being asleep, states of dreaming, and being in a coma or in a vegetative state. These states are not part of conscious experience but some of them are crucial for its emergence. This includes states of being awake or arousal which is a key factor for the occurrence of conscious experience. On the other hand being in a state of dreamless sleep or coma makes it impossible to have ongoing conscious experience (Searle, 1990) even though this state is accompanied by cortical information processing (Daltrozzo et al., 2009).

By *General Stream of Consciousness* we mean a general stream of mental states and ongoing subjective experience. Finding correlates of *General Stream of Consciousness* means finding specific regions that are involved in the neural representations of mental states and also finding specific principles, conditions or mechanisms (e.g. specific neural oscillations or neural synchrony) that must be met to make this specific mental state conscious. Stream of consciousness therefore has to be distinguished from other unconscious neural representations which fail to meet these special conditions. However, these neural representations which are not part of the conscious experience can still have influence on the mental states. For example the well-known phenomena of blind-sight. Blind-sight emerges due to lesion in striatum, the primary visual cortex (V1). Despite the fact patients with this type of lesion consider themselves blind they can still determine shape, color, size of various objects and also can orient and navigate themselves in the space.

Neglect can also serve as another example of unconscious neural representation that has substantial influence on mental states. Neglect is usually the consequence of the lesion of inferior parietal lobe (IPL) (Vallar & Perani, 1986) which causes that subject neglects contralesional side of space. In well-known study two cards were presented to the patient with neglect. Cards showed same two houses however one had flames on the left side. If asked whether two images are same or different patient replied that they were the same. However, if patient was asked in which house she would prefer to live she repeatedly preferred the house which was not on fire (Marshall & Halligan, 1988). Patients with neglect still have well preserved mechanisms for information processing which means that only thing that is missing is awareness (Mattingley, 1999). This finding leads some to the conclusion that neglect is actually attention disorder and attention is the necessary condition for the emergence of conscious experience (Prinz, 2005, 2012).

Many neural representations occur without awareness and are not part of the stream of consciousness. There seems to be special neural mechanisms responsible for the information to be thrown into stream of consciousness and such mechanisms represent the neural celebrities in the discussions of stream of conscious experience. If these specific mechanisms or conditions are present in the brain it would be possible to say that the subject has ongoing *conscious experience*.

The third and last are *Specific States of Consciousness.* This concept refers to the specific mental states or contents of consciousness that occur in the Stream of Consciousness thus fulfilling the necessary conditions for conscious access. Finding a correlate of Specific State of Consciousness means directly identifying a neural location or sets of locations that if active or co-active represent a specific mental state. These specific states are "the most interesting states of consciousness (...): the fine-grained states of subjective experience that one is in at any given time. Such states might include the experience of a particular visual image, of a particular sound pattern, of a detailed stream of conscious thought, and so on" (Chalmers, 2000, pp. 19).

These are the three types of *consciousness* whose correlates we will seek in this study. Firstly, we will look through the conclusions and theories of 20th century neuroscience that were established based on stimulation experiments – namely visual experiments. Then we will look at the newly established and rapidly growing field that investigates the so-called endogenous activity of the brain that is in an anti-correlated position to the evoked activity of the brain, which is present during the stimulation of subjects or during attention demanding tasks.

3. Correlates of the background states of consciousness

The Background States of Consciousness refers to "an overall state of consciousness such as being awake, being asleep, dreaming, being under hypnosis, and so on" (Chalmers, 2000, pp. 18). We can also speak about disorders of consciousness such as a coma, vegetative state or a minimally conscious state as specific background states of consciousness. All of the above-mentioned states have a certain level of *arousal* (wakefulness, alertness, vigilance, etc.) or *being awake*, which is the primary building block that stands in the background of any higher cognitive state. Arousal in the meaning of waking state is a matter of degree. Conscious wakefulness has a high degree of arousal while vegetative state or coma have lowest degree of arousal. The degree of arousal can be measured with Glasgow Coma Scale (Teasdale & Jennett, 1974) or can be assessed by behavioral observation which focuses on the degree and awareness of the patient (Schnakers et al., 2008).

The opposite of arousal is unconsciousness, which may take a various forms such as syncope, concussion associated with loss of consciousness, other states of transient unconsciousness and coma which is defined as complete of nearly complete loss of vigilance, conscious experience and attention (Gosseries et al., 2011). Wakefulness is the most important background state of consciousness needed for the occurrence of the stream of subjective experience. This background state of consciousness can be described as an upward stream of neural activity that starts in more primitive brain structures and consequently activates higher brain areas (Zeman, 2001). If we are looking for correlates of arousal we can look for brain activity in "critical structures in the brainstem, thalamus and basal forebrain" (Lin, 2000; Schiff, 2008; Zeman, 2001, pp. 1267).

Correlates of some background states of consciousness can also be captured with the help of EEG. Brain rate, which is equal to the electrical activity generated by brain structures, shows us that arousal or wakefulness is associated mainly with beta rhythm, which represents a conscious state with open eyes and an alert state, and alpha rhythm, which represents a relaxed conscious state with closed eyes. On the other hand, theta and delta rhythms are associated with drowsiness and sleep. Gamma oscillations are a highly debated theme and are universally associated with high peak cognitive performance (Pop-Jordanova, 2011; Teplan, 2002; Zeman, 2001). Alpha, beta and gamma oscillations seem to be better candidates for correlation with wakefulness and arousal while delta and theta oscillations don't. However, this is not entirely easy because most of the EEG patterns are not specific (Young, 2000) and they cannot be reliably used for differentiation between conscious and unconscious brain processing (Gosseries et al., 2011). For example gamma can be correlated with wakefulness and high peak cognitive performance but it can also be found during sleep and dreaming (Llinás & Ribary, 1993). Sleep and anesthesia are usually accompanied by low frequencies but again gamma power can persist during loss of consciousness induced by propofol (Murphy et al., 2011).

4. Theories proposing neural correlates of the stream of consciousness

Consciousness for some is a link between arousal and awareness (Zeman, 2001). However, arousal is still a necessary building block of conscious experience because arousal can exist without awareness (i.e. a minimal conscious state or vegetative state) but awareness cannot be considered without wakefulness (Gosseries et al., 2011). Awareness can be defined as the ability of oneself to be aware of her environment and the self (Gosseries et al., 2011) but that doesn't mean that self-awareness and reflection upon one's internal states are necessary prerequisites for the emergence of conscious experience.

Even though arousal is a key factor for conscious experience it cannot be considered to be a reliable correlate of the stream of conscious experience. In the history of the science of consciousness there have been several theories that tried to explain what consciousness actually is by proposing neural correlates of the stream of consciousness. We can name a few. Probably the most well-known theory comes from Crick and Koch, who believed that synchronization of gamma oscillations in the cerebral cortex is the key for binding and conscious experience (Crick & Koch, 1990). Another theory came from Gerald Edelman, who considered consciousness to be a product of thalamo-cortical reentrant loops (Edelman, 1989; Edelman, 2005). Joseph Bogen believed that conscious awareness is necessarily connected to the activity of intralaminal nuclei of each thalamus (Bogen, 1995). Rodolfo Llinás and his colleagues also believed that cognition and consciousness rise due to synchronization of thalamocortical activity below 40 Hz (Llinás, Ribary, Joliot, & Wang, 1994). Bernard Baars also speaks in several of his articles about the thalamus and its reticular nucleus, which should be considered the central hub for consciousness and conscious attention (Newman & Baars, 1993). More recently, Jesse J. Prinz proposed his neurofunctional theory, which states that consciousness arises when information becomes available to working memory through attention associated with gamma oscillations (Prinz, 2005, 2012).

Theories that propose correlates of the stream of conscious experience consider two things. The first is the location of a specific neural part that when active is directly responsible for the stream of consciousness. The second is a specific principle that guarantees that specific information will be thrown into the stream of consciousness and will become a conscious mental state.

According to the above theories it seems that the thalamus and gamma activity are kinds of neural celebrities when it comes to consciousness. Moreover, the thalamus was proposed to be the central region of consciousness much sooner in the works of Wilder Penfield: "All parts of the brain may well be involved in normal conscious processes but the indispensable substratum of consciousness lies outside of the cerebral cortex, probably in the diencephalon" (Penfield, 1937, pp. 241).

There are of course some theories of consciousness that do not concern themselves so much with the thalamus. For example, the hypothesis of Stuart Hameroff and Roger Penrose that consciousness is quantum coherence in the microtubules (Hameroff & Penrose, 1996).

It is not at all surprising that the thalamus is considered to be one of the most important brain centers in relation to consciousness. The thalamus is responsible for gaiting sensory inputs and perceptual processing and lesions of thalamic nuclei lead to the impairment of consciousness. From the mass of evidence we know that retinal inputs are not processed directly to the cortex but go through parts of the thalamus, which presents a very interesting question: "Why do we have thalamic relays at all?" (Guillery & Sherman, 2002, pp. 169). Thalamic centers also receive information from the entire cortex and send it to other regions of the brain, predominantly the prefrontal cortex and the striatum. It is therefore considered a relay station from which all neocortex areas receive their inputs and it also keeps all of higher brain areas informed about ongoing motor instructions from subcortical areas (Guillery & Sherman, 2002).

5. Neural correlates of specific states in the stream of consciousness

In the previous chapter we focused on generally accepted theories of the stream of consciousness that propose specific correlates of the stream of consciousness and the necessary conditions for subjective experience. These theories not only propose correlates but also the necessary conditions for a valid claim that animal has a stream of subjective experience and has or is in some kind of subjective mental state.

Subjective experience is the most interesting and enigmatic topic in the science of consciousness, it was profoundly discussed by philosophers since Thomas Nagel showed how mysterious and unreducible subjectivity is using the metaphor of a bat's mind (Nagel, 1974). Many philosophers came to the conclusion that subjective experience cannot be explainable by empirical science, which led to the formulation of the 'hard problem of consciousness' (Chalmers, 1996). The new wave of neurophilosophy does not try to triumphantly explain all aspects of subjective experience and finally dismiss the hard problem, but it leaves the hard problem aside (e.g. Prinz, 2005). However, proponents as well as rejecters of the hard problem are in consensus about the fact that subjective experience is formed by specific content – images, colors, shapes, sounds, pain, thoughts, emotions, etc. This content of subjective experience can be called *specific states of consciousness* or *atomic states of consciousness* (Brooks, 2005). These specific states are the uppermost theme of the science of consciousness but the science of consciousness should in no way start to explain the nature of consciousness based on these states (Brooks, 2005, pp. 401). Finding, locating and correlating these states to specific neural activity is the highest peak of endeavor of the science of consciousness, but it is necessary to use this as the final piece and not as the basis for studying the nature of consciousness.

In the history of neuroscience there have been several endeavors that tried to underpin neural correlates of specific states of consciousness, especially states of visual consciousness. A considerable amount of work has been done on the functions of the visual cortex and today we know which parts of the occipital lobe are responsible for various functions like recognition of patterns, colors, depths, motion, and separation of object from the ground, etc.

Classes of neurons of the cat's visual cortex have been identified that respond only to horizontal and/or vertical stimuli that are moving slowly (Leventhal & Hirsch, 1977). Another study identified cells with the smallest receptive fields, which prefer either vertical or horizontal lines moving slowly (Pettigrew, Nikara, & Bishop, 1968), and a study by Blackmore and Van Sluyters found cells in the cat's visual cortex preferring vertical and horizontal lines (Blakemore & Van Sluyters, 1975). Another study presented evidence that these cells preferring slow moving stimuli receive projections from the lateral geniculate cortex (LGC). X-cells of LGC send inputs for slow moving stimuli while Y-cells of LGC seem to prefer rapid moving stimuli (Stone & Dreher, 1973). This again supports the claim that the thalamus and its parts play a major role in consciousness.

Logothetis performed several studies using paradigm of the binocular rivalry with trained monkeys. These studies established that certain neurons are active when specific stimuli are presented and therefore certain neurons are responding to certain stimuli. Then they presented to the monkeys two stimuli under conditions of binocular rivalry. The monkey "told" which of the stimulus it actually saw by pressing a bar. Surprisingly, the main region for vision V1 is not considered to be a correlate of consciousness. V1 cells fire for both stimuli but only one of them actually finds its way to conscious experience. Logothetis speaks about the inferior temporal cortex and the superior temporal sulcus, which discharge all of their neurons in the presence of dominant stimuli during binocular rivalry (Sheinberg & Logothetis, 1997). This evidence can be considered to be a very good arbiter as to whether specific states are truly in the conscious stream or whether they are only an unconscious neural representation. According to Logothetis' studies we can only speak about a correlate of consciousness during activity of the inferior temporal cortex.

However, Delphine Pins and Dominic ffytche came to another conclusion. Their study tried to determine whether visual consciousness relates to a network of frontal and parietal regions or whether visual consciousness relates to the activity of individual areas. During stimulation, twelve volunteers were required to press two buttons indicating – *Yes I saw*/or/*No, I did not see*. At first the fMRI results indicated that the neural correlate would lay within a distributed network; however, parallel evoked potential measures showed that measures of *Yes* and *No* trials varied in their timing. The measurements led Pins and ffytche to conclude that a primary correlate of conscious perception is in the occipital lobe at $\sim$100 ms after presenting a stimulus (Pins and ffytche, 2003).

In the previous chapters we highlighted three important categories of consciousness. However, we must realize that theories of the general stream of consciousness and also studies of specific states of consciousness are almost without exception based on visual stimulation and therefore they follow visual consciousness and its visual representations.

> "Vision is the most intensely investigated capacity in consciousness studies, and for sighted people, it is the most important sense modality" (Prinz, 2012, pp. 50).

or

> "We chose visual consciousness rather than other forms, because humans are very visual animals and our visual percepts are especially vivid and rich in information. In addition the visual input is of the highly structured yet easy to control" (Crick & Koch, 1998, pp. 97).

Science of consciousness has built its understanding of consciousness around the results of stimulations and the brain processes that relay these stimulations. Therefore, it is understandable that they consider the thalamus to play an important role in conscious experience because the thalamus is the relay point for all perceptual processing. We believe that focusing on research of visual consciousness is very productive; however, we consider that it represents only one side of the coin. We are worried that conclusions about visual consciousness will not generalize for every aspect of conscious experience.

> "Some researchers worry that the focus on vision in consciousness studies will result in theories that lack adequate breadth. They worry that lessons from vision will not generalize" (Prinz, 2012, pp. 50).

Visual consciousness is surely the most studied form of conscious experience which is evoked by the stimulation. Stimulation (and non-invasive observation) of specific activations of brain areas was the main research method of last century neuroscience. Even though this tradition brought very important knowledge about the brain it looked at brain mostly from the position of stimulation and mostly followed only reactive brain functioning. Marcus Raichle said: "Unfortunately, the success of studying evoked activity has caused us to lose sight of the possibility that our experiments reveal only a small fraction of the actual functional activity performed by our brain" (Raichle, 2010a, 2010b, pp. 180). Consequently, another conscious stream that was mostly left out is the stream of spontaneous cognition. Examples of this type of cognition could be self-referential thinking (Gusnard et al., 2001) or mind-wandering (Manson et al., 2007) which are now widely associated with activity of DMN. We believe it is necessary to dig deeper into this form of internally oriented conscious experience that is not bound to intensive stimulation. Studying internal streams of consciousness will provide us with an additional understanding of consciousness and conscious experience.

In no way do we want to accuse anyone of neglecting this internal cognition and internally focused conscious experience because the grounds for its studying were not stable until 2001 when the default mode network and endogenous neural activity came into the scientific field.

6. Default mode network

The default mode network (DMN) is currently characterized as a large network of the brain consisting of specific brain regions: medial prefrontal cortex (mPFC); ventral medial prefrontal cortex (vMPFC); medial temporal lobes (mTL); posterior cingulate cortex (PCC); precuneus and posterior inferior parietal lobule (pIPL). The very idea of an endogenous/intrinsic/resting state network was established based on regular observations of identical decreases in the activity of the mPFC and PCC. These two areas representing the core regions of this network are partially deactivated at times when the subject goes into states of reactive (evoked) activity which is induced by stimulation or during states of active attention necessary for an immediate response to the demands of an environment (Gusnard & Raichle, 2001; Gusnard et al., 2001; Raichle & Snyder, 2007; Raichle et al., 2001). According to Buckner, Andrews-Hanna, and Schacter (2008) these deactivations are the result of the competition between DMN and attentional systems. DMN is reduced when attention is focused on the specific event and is active when attention is broader, relaxed and internally focused (Buckner et al., 2008). Task induced deactivation might be therefore explained as the allocation of resources and/for attention (Raichle et al., 2001). The important influence on these deactivations has so called salience network (SN) which consists of the anterior insula and the anterior cingulate cortex. Main functions of SN lie in 'detecting salience stimuli' and in 'dynamical switching' between DMN and central executive network which is associated with evoked brain activity (Menon & Uddin, 2010).

DMN activity is now widely accepted as the *baseline* of neural activity – hence the name default mode of brain function (Raichle et al., 2001). Yet the specific function of this network is still an open question. However, there are authors proposing that DMN activity can be considered not only a physiological baseline of neural activity but also a psychological baseline (Manson et al., 2007). Marcus Raichle has claimed on several occasions that this wide endogenous network could become a key tool in the research of consciousness (Raichle M. E. & A. Z., 2009; He & Raichle, 2009; Raichle, 2010a, 2010b).

The best way to measure the activity of this network is during resting behavioral states with eyes closed. It is also possible to induce this endogenous brain activity by passive observation of stimulus (e.g. optical cross), which must not stimulate the subject and therefore engage reactive functions of the brain. Activity of DMN is at its highest in the moments when the subject is in the phase of behavioral peace and is without experimentally induced stimulation that would commence responsive aspects of brain activity universally associated with the brain network called the *attention system* (a term used by e.g. Carhart-Harris & Friston, 2010) or *executive networks* (a term used by e.g. Menon & Uddin, 2010). The endogenous activity is anti-correlated with reactive activity of the brain which is represented by attention systems. If one is active then the other is partially disengaged and vice versa (Gusnard & Raichle, 2001; Raichle & Snyder, 2007; Raichle et al., 2001).

Interestingly, van den Heuvel, Mandl, Kahn, and Hulshoff (2009) elucidated the structural anatomical substrate of the DMN (van den Heuvel et al., 2009). This pivotal study utilized the complementary knowledge from resting fMRI and diffusion tensor imaging (DTI). DTI is a relatively novel MRI technique which makes it possible to evaluate the organization and integrity of white matter fiber tracts, the structural highways of the brain enabling information to travel quickly from one brain region to another region. Authors showed in a very elegant way that robust anatomical white matter tracts interconnect all of the components of the DMN (and the majority of other resting state networks). These findings suggest that the functionally linked DMN fully reflects the underlying anatomical architecture of the brain. In other words, the DMN has its own underlying structural core and it is 'hard-wired' in the brain by anatomical white matter pathways. It is reasonable to speculate about the idea that the existence of the structural core of the DMN represents an inherited precondition for all functions related to DMN activity. If this assumption is true, it is also interesting that the DMN and its structural core consisting of white matter tracts has also been recently identified in other non-human vertebrate species such as monkeys (Mantini et al., 2011) and even in the mouse brain (Nasrallah, Tay, & Chuang, 2014). Even though DMN activity is apparently responsible for the self-referential thinking (Gusnard et al., 2001) it is too soon to claim that even rats have conscious sense of self. However, DMN regions are memory regions (Buckner et al., 2008) which encourages speculations whether rats could have some degree of conscious mind-wandering (based on memories) which could increase their chances of survival (Lu et al., 2012).

Most contemporary neuroscientists consider the precuneus and PCC to be the central region of the DMN (Fransson & Marrelec, 2008; Utevsky & Smith, 2014). The precuneus is considered to be a specialized nexus for the DMN. According to one of the first studies, the precuneus takes about 35 percent more glucose than other neural regions in the brain, which puts it in the first place in metabolic activity of the DMN (Gusnard & Raichle, 2001). Furthermore, the precuneus is considered as one of the most important neural region of the entire human brain which makes a significant contribution to a great number of neural and cognitive processes such as autobiographical and episodic memory retrieval (Lundstrom, Ingvar, & Peterssona, 2005; Maddock, Garrett, & Buonocore, 2001) monitoring of reward outcome (Hayden, Nair, McCoy, & Platt, 2008) and emotional stimulus processing (Maddock, Garrett, & Buonocore, 2003). The results of the recent study show that the precuneus is highly connected to the other regions of the DMN but is also connected with other task positive networks which are responsible for autobiographical memory (Utevsky & Smith, 2014). Due to the fact that no direct connections of precuneus with primary sensory regions have been reported it is reasonable to say that precuneus is not directly processing external stimuli (Cavanna & Trimble, 2006) which is in line with the behavior of DMN. Lu et al. (2012) came to the conclusion about function of DMN which is crucial for evaluation of 'the internal and external milieu of the body by integrating interoceptive and exteroceptive information from multiple modalities' (Lu et al., 2012, pp. 3982).

Even though DMN activity represents a physiological baseline (Gusnard & Raichle, 2001; Raichle et al., 2001) of neural activity this knowledge should not evoke the belief that endogenous activity is perhaps "pure" neural activity that is absolutely unchanging and in a fixed position in all subjects. Endogenous activity is highly variable and is influenced by many factors. A constantly reoccurring theme is for example the issue of resting state with or without closed eyes. Opening eyes will vary the endogenous activity and highly decrease the coherence of endogenous activity in the occipital lobes (Bianciardi et al., 2009). Because of this, some authors even propose that endogenous activity should be measured only in absolute darkness and without any stimuli (Logothetis et al., 2009). The mood of the subject is another factor that affects endogenous activity. A sad mood alters the lower functional connectivity of the superior and inferior posterior cingulate cortex, bilateral angular gyrus, inferior medial frontal cortex, caudate nucleus and putamen (Harrison et al., 2008). Another known factor is obesity. Data show that obese people have a visible alteration in the activity of the DMN and the temporal lobe. Obese subjects had higher functional activity of the precuneus/PCC, while they had greatly reduced activity in the anterior cingulate cortex (ACC) (Kullmann et al., 2012). Another study performed on obese subjects that were exercising showed that exercise associated with losing fat is correlated with reduced activity of the precuneus (McFadden, Cornier, Melanson, Bechtell, & Tregellas, 2013).

Elderly subjects also have reduced connectivity in the overall DMN and especially within connectivity between the precuneus and hippocampi (Sheline et al., 2010). On the other hand, young children have endogenous networks but these networks are not completely developed and the DMN as a complex network is not yet formed (Fransson et al., 2007). Another factor that alters DMN connectivity is simply quitting smoking (Cole et al., 2010).

The above list of factors that vary endogenous activity is in no way exhaustive. These factors, however, help to refute the idea that endogenous activity presents stable and constant activity that could be used at any time for direct correlates of consciousness or conscious experience. Nevertheless, it does not mean that a consequent study of the correlates of endogenous consciousness would be a lost cause. Absolutely not. This chapter should only prevent us and future studies of science of consciousness from making exaggerated claims.

This should be enough for a basic understanding of the DMN and for the first hint that there is another side of neural activity that is not tied to stimulation – visual or other. In the previous chapters we have shown some general theories of the stream of consciousness and correlates of specific states of consciousness linked to the reactive aspects of neural activity. Now we will concentrate on endogenous activity and its correlates of Background States of Consciousness, Specific Streams of Consciousness and Specific States of Consciousness.

7. Background states of consciousness and DMN

The initial interpretations of the DMN that talked about self-referential thoughts (Gusnard et al., 2001) provided the first step towards the question: How is DMN activity related to consciousness? If endogenous activity of the DMN is responsible for self-referential mental states then activity of this network could naturally be considered as a direct correlate of self-referential oriented processes. Furthermore, the DMN is in anti-correlated position with *attention systems* or *executive networks* that represent the reactive functions of the brain. Therefore, the DMN could present a new and interesting correlate of the *endogenous stream of subjective experience* composed of self-directed cognitive content. Last but not least, the DMN, a wide brain network with specific regions, and the central area of the precuneus/PCC could also be correlated with various background states of consciousness.

Sleep is one of the well documented background states that can be put into correlation with activity of DMN. Reduction of vigilance and subsequent sleep will substantially reduce functional connectivity between frontal and posterior parts of the DMN (Sämann et al., 2011). Also during sleep cycles, the DMN is divided in such a way that frontal parts are functionally altered while the posterior parts of the brain will increase their neural connectivity (Horovitz et al., 2009).

However far more interesting were the results of the study that reported how activity of DMN correlates with various levels of consciousness. Although it was not the main objective of the study, it unknowingly showed how endogenous activity is connected to the various *background states of consciousness*.

The study was conceived around fourteen healthy volunteers and fourteen patients who had been diagnosed with brain injury. All of the data were obtained by direct non-invasive observation of brain activity and emphasis was placed on the functional connectivity of the nodes of the DMN (Vanhaudenhuyse et al., 2010). "In all subjects, 10 min resting state fMRI were acquired on a 1.5 T magnetic resonance scanner (Siemens, Germany). Two hundred multislice T_2^*-weighted fMRI images were obtained with a gradient echo-planar sequence using axial slice orientation (Vanhaudenhuyse et al., 2010, pp. 163)."

The study provided two important conclusions. *Firstly*, there is a direct correlation between the functional connectivity of the specific nodes of the DMN and levels of consciousness:

> "Default network connectivity correlates with the level of consciousness, ranging from healthy controls, to minimally conscious, vegetative then comatose patients" (Vanhaudenhuyse et al., 2010, pp. 167).

and

> "In controls, the DMN could be reproducibly identified as a set of areas encompassing the posterior cingulate cortex (PCC)/precuneus, temporo-parietal junction, medial prefrontal cortex, parahippocampal gyri, superior frontal sulci and thalamus" (Vanhaudenhuyse et al., 2010, pp. 166).

Secondly, the central region for correlation between the functional connectivity of nodes of the DMN and consciousness is the precuneus/PCC, which is in consensus with a many other studies that propagate the central role of the precuneus and the PCC in the DMN (Fransson & Marrelec, 2008; Utevsky & Smith, 2014).

> "In all analyses, the peak area of significance for the correlation between connectivity and consciousness was found to be the PCC/precuneus. PCC/precuneus connectivity was also found to differentiate minimally conscious from unconscious patients" (Vanhaudenhuyse et al., 2010, pp. 166).

The study showed that the lower the functional connectivity of nodes of the DMN, correlates with the lower the level of consciousness. Control subjects with an intact level of consciousness have high levels of connectivity of nodes of the DMN, while connectivity of these nodes in comatose patients is almost unnoticeable. Moreover, results show linear correlation between DMN connectivity and levels of consciousness (Giacino, Fins, Laureys, & Schiff, 2014; Vanhaudenhuyse et al., 2010). Observation of the functional connectivity of the DMN can be used to identify other levels of consciousness not just for coma and intact levels of consciousness. It could become indicator of a patient's level of consciousness in addition to EEG and behavioral observation, based wholly on the strength of DMN connectivity. Noninvasive observation of the endogenous activity of the DMN thus constitutes a clear measurement of the level of consciousness of a patient, which is very helpful, for example, for patients who are not able to communicate (Vanhaudenhuyse et al., 2010).

> "[...] connectivity strength within DMN could possibly be a reliable indicator of a patient's level of consciousness, differentiating unconscious patients such as those in a coma or vegetative state from minimally conscious and locked-in syndrome patients" (Vanhaudenhuyse et al., 2010, pp. 168).

8. Neural correlates of specific streams of consciousness during endogenous activity

Conditions necessary for endogenous activity and activity of the DMN are a resting state without stimulation that would initiate the reactive activity of the brain and partially disable activity of the DMN. As was mentioned above precuneus is the central region of DMN (Fransson & Marrelec, 2008; Utevsky & Smith, 2014). It has no connection with primary sensory regions and is considered as one of the associative areas of brain (Cavanna & Trimble, 2006). A closer look at the regions of the DMN will tell us that this network is not composed of motor or sensory regions. It is composed of the temporal cortex (which is associated with memory), the medial and ventral prefrontal cortex (which is associated with higher cognitive functions) and most importantly the precuneus/PCC (which is associated with many functions and still is a great mystery). Based on this, we can say that the DMN does not consist of sensory or motor regions but it is composed of memory regions (Buckner et al., 2008). Also can be mentioned that associative areas (precuneus) are connected with other cortical and subcortical areas that might permit integration of external and also self-referential information for posterior medial parietal cortex (Cavanna & Trimble, 2006). This suggests that DMN activity is cut off from the actual environment which gives us a hint about to the nature of endogenous cognition and endogenous stream of consciousness.

Specific dimensions of endogenous thought have been described to-date such as *self-referential thinking* (Gusnard et al., 2001), *imagining future* (Buckner et al., 2008), *mind wandering* (Manson et al., 2007), *remembering and imagining future* (Addis, Wong, & Schacter, 2007), *social cognition* (Mars et al., 2012), *theory of mind* (Buckner et al., 2008; Nekovarova, Fajnerova, Horacek, & Spaniel, 2014), *spontaneous cognition* (Andrews-Hanna, Reidler, Huang, & Buckner, 2010), *mental time travel* (Østby et al., 2012), *internal train of thought* (Smallwood, Brown, Baird, & Schooler, 2012), etc. Current interest in the internally and self-referentially oriented mental states also confirms fact that several researches are now analyzing content and form of spontaneous thoughts with help of questionnaires of spontaneous cognition (Delamillieure et al., 2010; Diaz et al., 2013, 2014; Gorgolewski et al., 2014).

In the very first articles about the DMN the dorsal medial prefrontal cortex and its endogenous activity are posited as a neural correlate of self-referential thinking (Gusnard et al., 2001; Raichle et al., 2001). It is not wrong to consider activity of frontal regions to play an important role in self-referential thinking because, according to the evidence, lesions of these regions lead to mental emptiness associated with the loss of spontaneous speech and spontaneous thoughts (Manson et al., 2007; Damasio, 1983). Correlating self-referential thinking to the activity of the prefrontal cortex is also not wrong; however, it is so wide and vague that it cannot be considered as a direct and exhaustive correlate. Later the study provides a very detailed description of these correlates when describing mind-wandering. Mind-wandering referrers to very similar kinds of mental phenomena to the self-referential thinking that accompanies endogenous activity. Neural correlates for these stimulus independent thoughts are bilateral regions of the mPFC; the superior frontal gyri; the anterior and posterior cingulate, the precuneus; the insula; the left angular gyrus; the left superior temporal, the right superior temporal and the left middle temporal gyri (Manson et al., 2007). Activity of these regions can be considered as a correlate of the stream of consciousness, which contains stimulus independent thoughts; however, stimulus independent thoughts, mind-wandering and self-referential thinking are rather ambiguous terms that can mean basically anything and can refer to a very broad spectrum of mental states.

Nevertheless, we have correlates for an endogenous stream of stimulus independent thoughts and now we can distinguish specific streams of endogenous consciousness by the nature of their mental states. What naturally comes to mind when speaking of self-referential thinking or mind-wandering are *memories* and *imaging the future*. General conclusions are that imagining the future and the recollection of memories are associated with DMN activity or with network that substantially overlaps with DMN (Andrews-Hanna et al., 2010; Smallwood et al., 2012; Østby et al., 2012). All of the regions that are responsible for the recollection of memories are also responsible for imagining the future – the additional regions recruited for both tasks are the hippocampus and the middle occipital gyrus. However, during recollection of memories and imagining the future specific regions are recruited for each of these tasks. When imaging the future additional regions i.e. the right frontopolar cortex and left ventrolateral PFC are recruited. The hippocampi also play an important role not only during the recollection of memories but also when imaging the future, but only the right hippocampus is active when imaging the future. The left hippocampus is usually active during the recollection of memories while only the right hippocampus is activated only in the event of predicting the future (Addis et al., 2007). Several other studies reported this right lateralization of activity of hippocampus during imagining future (Addis, Cheng, Roberts, & Schacter, 2011; Addis & Schacter, 2012; Martin, Schacter, Corballis, & Addis, 2011; Weiler, Suchan, & Daum, 2010) and according to Buckner hippocampus maybe be understood as neural mechanism for predictions about upcoming events due to its adaptive and forward-oriented perspective (Buckner, 2010).

These findings of addition regions are very interesting for identifying neural correlates of two specific endogenous streams of consciousness – *imaging the future* and *recollection of memories*. In this way, we can identify specific streams of consciousness by the nature of their mental states and we can further identify their correlates and distinguish them from the universal stream of stimulus independent thoughts.

Another stream of consciousness of endogenous activity can identified for *social cognition.* Mental states of social cognition are stimulus independent thoughts but we can have some doubts about their self-referential nature. During these specific mental phenomena, mental states are concerned with gathering, searching and processing information about mental states of other individuals. Study has shown that natural connections exist between the DMN and social cognition. During this type of cognition a subject's neural activity is very similar to the activity of the DMN except for various small differences. Social cognition tends to activate a larger area of the medial frontal cortex and apparently the lateral temporoparietal seemed to be extended less dorsally during social cognition than during rest (Mars et al., 2012). These findings also give us valuable knowledge about neural correlates of yet another specific stream of consciousness.

However, the function of the DMN has not yet been completely elucidated. One of the first proposed functions of the DMN was the *Sentinel*, which claimed that endogenous activity is for monitoring the external environment and for animals to always be in an alert state to be ready for unexpected things from the external environment (Gusnard & Raichle, 2001). We can see this active network in other species. There are very similar endogenous networks of the DMN for example in rodents (Lu et al., 2012) and in nonhuman primates (Mantini et al., 2011). All of which leads us to an interesting question about the evolutionary importance of the function of the DMN. There are proposals starting from primitive functions such as monitoring of internal and external milieu, and gathering information for avoidance of predators, etc. (Mantini, 2011), and in the case of humans and nonhuman primates the DMN can be considered to play a higher role, for example for social cognition (Mars et al., 2012). Basically, all of the proposed functions of the DMN can be summarized and put under the universal proposal of the *Bayesian brain,* which in the case of endogenous activity states that living biological agents that are in equilibrium with their environment have to constantly reduce their own entropy (analogical to surprise) to increase their own chance of survival (Friston, 2010).

Anyway, the purpose of this chapter is not to discuss the function of the DMN but to provide an indication of the neural correlates of *specific states of consciousness*.

9. Correlates of specific states of consciousness during endogenous activity

Above we described the neural correlates between the activity of the DMN and background states of consciousness and also correlates of specific streams of endogenous consciousness. The next step is to identify the correlates of the content of consciousness during endogenous brain activity. It is no surprise that we are still a long way from identifying direct correlates of specific states of consciousness because there are two main methodological problems. First of all, we cannot stimulate the brain to find these correlates because stimulating the brain leads to the deactivation of endogenous activity; secondly, we cannot inhibit endogenous activity because it leads to the loss of arousal necessary for endogenous mental states to occur (Havlik & Marvan, 2015).

According to above we can find endogenous activity that correlates with specific streams of consciousness e.g. predicting or recollecting memories. But these correlates do not tell us anything about the specific content of consciousness. We can identify that a person is predicting but we cannot identify the content of their predictions. We can find out that a person is remembering but we have no direct correlate for what they are remembering. Perhaps in the future it will be possible to analyze patterns of the neural activity in more detail and predict specific contents of conscious experience. However we should always be aware of the methodological and logical problems of reverse inference (Poldrack, 2006).

Although identifying these correlates will be very hard and also a new method of testing will be needed (Havlik & Marvan, 2015) the first steps have already been taken. A recent study showed that it is possible to identify correlates of specific states of consciousness during endogenous activity. This study wanted to find out where in the brain are stored the specific modules of other people's personalities. For this localization subjects tried to predict behavior of various people during phases of resting state. Predictions can be understood as mental simulations that consist of maintaining the scene, individuals with various personalities, etc. Regions that are crucial for these predictions according to the study are the PCC, MTls, IPL and mPFC – central nodes/hubs of DMN (Hassabis et al., 2013).

Apparently the most important part of the whole study was the prescan training, during which subjects learned in detail about the personalities of four people (e.g. Patrick, Dave, etc.) with two personality traits – *Agreeableness* and *Extraversion*. Subsequently, they were asked to imagine four different locations that should be entirely original and were not to be constructed from the subject's memories. During the scanning the subjects were asked to imagine and predict how a specific person would behave under specific circumstances in the specific location (Hassabis et al., 2013).

"For example: 'in a bar — someone spills their drink — Dave'" (Hassabis et al., 2013, pp. 1980).

The subjects were then given ten seconds to predict the mental states, intentions, behavior etc. of the specific person. After this scanning the subjects were asked to imagine the empty scene without anyone there. Later they were asked to imagine themselves in exactly the same situation as the person who was the center of their predictions.

Analysis of these three simulations proved (and was in accordance with other studies) that mental simulations are correlated with an increased BOLD signal in the regions of the DMN, i.e. the medial prefrontal cortex (mPFC), posterior cingulum (PCC), medial temporal lobes (MTL), lateral temporal cortex (LTC), temporal pole, inferior parietal lobe (IPL), and superior and inferior frontal gyri (Hassabis et al., 2013). However, the most important results were obtained from the comparative analysis between predictions of behavior of a specific person and between simulations of an empty scene. This comparison showed that during mental simulations of predicting a person's behavior (against an empty scene) regions of the ventral, dorsal, and anterior mPFC, pCC, the temporal poles, and occipital cortex were active (Hassabis et al., 2013).

Another question was where in the brain modules of identities and personalities of specific persons are situated. Comparative analysis showed that persons with high and low extraversion were differentiated by differences in the PCC. Different types of personalities were associated with unique and detectable patterns of neural activity in the mPFC. These differences in the mPFC were used to differentiate between specific persons whose behavior was predicted in the mental simulation. Agreeableness were associated with unique patterns of BOLD in the dorsal mPFC and LTC, while extraversion persons were associated with the PCC (Hassabis et al., 2013).

By the end of the study Hassabis claims:

"In other words, based on brain activation patterns alone, we were able to infer which of the 4 protagonists the participants were imagining" (Hassabis et al., 2013, pp. 1984).

This study showed that localization of a specific person in the brain is possible and therefore, it showed that finding direct neural correlates of specific conscious mental states in endogenous activity is possible.

10. New cerebral celebrity in the science of consciousness and further implications

In Section 4 we presented some of the generally accepted theories of consciousness. A comparison of these theories of consciousness with our contemporary knowledge of the default mode network and its regions will point out one important finding – conscious experience is possible without the thalamus! The thalamus is not part of the DMN and is not active during *specific endogenous streams of consciousness* and neither during activity that is in correlation with *specific endogenous states of consciousness*.

Joseph Bogen says at the beginning of his work Locating the Subjectivity Pump: The Thalamic Intralaminar Nuclei:

"It is here proposed that subjectivity is engendered by neuronal activity in and immediately around the intralaminar nuclei (ILN). Falsification of this proposal is straightforward: find someone with essentially complete, bilateral destruction of ILN whom we would consider conscious. [...] without C (subjectivity) there is no consciousness" (Bogen, 1998, pp. 237).

According to a study by Burk and Mair, lesions in the intralaminar thalamic nuclei seem to lead to no sensor loss or attentional dysfunction (Burk & Mair, 2001); however, consciousness is a slightly trickier problem. Finding a person with these kinds of lesions is even more difficult. But we could make a slight alteration to the above-mentioned proposal and ask if consciousness, subjectivity and subjective experience can occur without activity of the thalamus. Based on the previous chapters about the DMN and endogenous activity, we would have to say that it is possible to have conscious experience without the thalamus. As we mentioned above, the thalamus is engaged during perception, stimulation and during evoked (reactive) cerebral activity that reacts to the immediate demands of the environment. During resting states with or without eyes closed, activity of the thalamus is not necessary for stimulus independent thoughts and specific endogenous streams of consciousness. Therefore, we could on the one hand falsify Bogen's strong proposition about the necessity of intralaminar nuclei in consciousness or on the other hand adjust it for responsive activity of the brain and conscious perception. However, this falsification or adjustment is just a proposition because this article is not about falsification of specific hypotheses but about *endogenous correlates of consciousness* which represent *missing piece of a puzzle in the science of consciousness*.

Earlier we talked about two cerebral celebrities that the science of consciousness revolves around – *Thalamus* and *Gamma oscillations*. In the light of the knowledge described above we can ask an interesting question as to whether these cerebral celebrities are still the most prominent ones and whether there are other candidates, for example some regions of the DMN.

We believe that the thalamus is losing its position as the key region of consciousness due to its inactivity during endogenous subjective experience. Endogenous streams of consciousness with their correlates were described in Section 8. Studies that reported self-referential thinking (Gusnard et al., 2001), imagining future (Buckner et al., 2008), mind wandering (Manson et al., 2007), remembering and imagining future (Addis et al., 2007), social cognition (Mars et al., 2012), theory of mind (Buckner et al., 2008; Nekovarova et al., 2014), spontaneous cognition (Andrews-Hanna et al., 2010), mental time travel (Østby et al., 2012), internal train of thought (Smallwood et al., 2012) have one thing in common. None reported activity of thalamus which should be, considering the theories of consciousness described in Section 4, the most important region in discussions of the conscious experience. Finding of asynchronous thalamo-cortical deactivations can also be used as additional evidence for the argument that conscious experience is possible without thalamus. While falling asleep thalamic deactivation precedes the cortex. During this phase hypnagogic hallucinations or hypnagogic experiences are present while thalamus is already deactivated (Magnin et al., 2010).

Thalamus plays the crucial role in transmitting of information from the external environment to the cortex, since it receives relatively little other input (Saalmann & Kastner, 2011). However, despite the fact that cortex depends on thalamus activity it doesn't necessary mean that thalamus has to be active in states of rest and during the cognition (and conscious experience) which correlates with the activity of memory regions (DMN). Thalamus may play the important role during evoked activity however it doesn't have to be present during the spontaneous cognition and its various forms. Role of thalamus in conscious experience was also questioned in the recent article of Koch, Massimini, Boly, and Tononi (2016) and as the correlate of the conscious experience was proposed posterior cortical hot zone (Koch et al., 2016) which is very similar to Vogt and Laureys proposition (2005) that precuneus and posterior cingulate cortex are the pivotal candidates for conscious cognitive information processing (Vogt & Laureys, 2005).

We can now ask, with the knowledge of endogenous activity, what its successor as the new cerebral celebrity of consciousness should be. According to the many articles, the precuneus/PCC seems to be a very likely choice. The precuneus/PCC is considered to be the central region for endogenous activity and the core region of the DMN. Precuneus/PCC has many connections with other regions, namely association areas and paralimbic areas, and is responsible for a high degree of information integration (Leech & Sharp, 2014).

Another possible choice would be the mPFC, which is the second most important region of the DMN. However, we believe that the precuneus/PCC should still be considered more important in the science of consciousness because it is located in the sensory parts of the brain and according to *restrictivism* all consciousness is perceptual (for more see Prinz, 2012, chapter 5). We consider the mPFC as an important region for the content of consciousness but we believe that PCC activity may even play the role of the second cerebral celebrity (gamma synchrony), which is believed to be the neural process of becoming conscious.

Gamma synchrony was reported in several studies. Gamma synchrony correlates with stimulus selection under the paradigm of binocular rivalry (Engel, Fries, Brecht, & Singer, 1999). It is related to the conscious detection of stimulus in masking experiments (Gaillard et al., 2009; Summerfield, Jack, & Burgess, 2002), supposedly accompanies deviant auditory stimuli (Edwards, Soltani, Deouell, Berger, & Knight, 2005), visual working memory tasks (Holz, Glennon, Prendergast, & Sauseng, 2010) and also occurs during dreaming (Llinás & Ribary, 1993). Doesburg, Green, McDonald, and Lawre (2009) proposed that large-scale gamma-band synchrony constitutes an oscillatory substrate for the stream of consciousness. Lucia Melloni, Wolf Singer and others understand the synchrony of oscillatory activity at the gamma frequency range as the critical process behind conscious perception (Melloni & Singer, 2010; Melloni et al., 2007). Jesse J. Prinz proposed his neurofunctional theory of consciousness suggesting that consciousness arises when and only when information becomes available to working memory through attention that is associated with gamma synchronization (Prinz, 2005, 2012). Filipe De Brigar claims that internal attention which is associated with gamma frequency is not only necessary for conscious recollection but also is the necessary mechanism which render the memories conscious (De Brigard, 2012). And most important regions for this conscious recollection are prefrontal cortex, medial-temporal lobes and parietal cortex (De Brigard, 2012), parts of DMN.

Recently there has been a proposition about the relation of precuneus/PCC with attention (Leech & Sharp, 2014). The PCC could be an important region for balancing internal and external attentional focus. Authors also consider the function of the PCC in three aspects. *Firstly*, it is a highly important region for the state of arousal. *Secondly*, the PCC is responsible for the balance between the external and internal focus of attention. And *thirdly*, the PCC is responsible for the breadth of attention that can be either broad or very narrow (Leech & Sharp, 2014). They also consider different parts to be responsible for different focuses of attention as well as its breadth. The key component for external narrow attention seems to be the dorsal PCC with the coactive dorsal attention network and the fronto-parietal control network (FPCN). Authors also predict that the dorsal PCC and FPCN are important for external broad attention. On the other hand, a key neural component for internal and narrow attention (that we can associate with internal cognition) is considered to be activity of the ventral PCC. And similarly during broad attentional internal focus, the ventral PCC is in an anti-correlated pattern of activity to the dorsal attention network (Leech & Sharp, 2014). These hypotheses and predictions about the attentional functions of the PCC basically state that dorsal parts of the PCC are responsible for external attention to the environment and ventral parts of the PCC are responsible for internal attention.

The relationship between consciousness and attention is under discussion in contemporary cognitive science and neurophilosophy. One of the central questions of this discussion is whether consciousness can exist without attention or whether attention is necessary for the existence of subjective experience. Supporters of the claim that attention is not necessary for consciousness and that consciousness and attention can exist separately include for example Christopher Koch and Naotsugu Tsuchiya (e.g. Koch & Tsuchiya, 2007). The other side is represented by Jesse J. Prinz, who presupposes that the relationship between consciousness and attention is so strong that consciousness cannot occur without attention (Prinz, 2005, 2011, 2012).

Prinz's very recent theory of consciousness is called *Attended Intermediate Representation (AIR) theory of consciousness*. It is a very interesting hybrid of neuroscience, cognitive science and psychology with *Attention* at its center. Prinz claims that "consciousness arises when and only when intermediate-level representations are modulated by attention" (Prinz, 2012, p. 89). Intermediate-level representations are sensory information that represent object features such as boundaries and contours. Representations of this level are associated with areas of occipital lobe such as V2, V3, V4, V5 and others. Low-level representations are information that represent edges and orientations of the object and are anatomically localized in the primary visual cortex (V1). High-level is associated with object recognition and is associated with inferior temporal cortex, superior temporal sulcus, lateral occipital complex and ventral/posterior interparietal areas (Prinz, 2012).

Intermediate-level representations are the answer to the question *What are we conscious of?* However, intermediate-level is not an answer to the question *How do we become conscious?* Consciousness emerges when such states are modulated by attention which makes them available to working memory. For Prinz, attention is a necessary process that stands behind the phenomenon that we can become conscious of a specific mental state. *How do we become conscious*? – *We attend* or more technically we go through a process that can be basically described as increased activity of our inhibitory interneurons that fire in *gamma synchrony,* which allows representations to become available to working memory (Prinz, 2011, 2012).

In the event that the foregoing predictions about the role of the PCC in attention (Leech & Sharp, 2014) were verified, the precuneus/PCC would not only be the central region for internal stream of consciousness but its activity would be the key component for the emergence of subjective experience. Prinz's AIR theory is built on evoked brain responses only and does not deal with endogenous activity; however, if gamma oscillations (which represent attention in Prinz's theory) would be found in the precuneus/PCC during stimulus independent thought it would be a great asset for a universal theory of consciousness that would apply for both evoked and endogenous activity of the brain.

If we take a closer look at the measurements of electrical activity of the DMN and endogenous activity we must say that the findings are still ambiguous. One of the first studies associated high metabolic activity of the DMN with beta waves:

> "We identified power in the 17- to 23-Hz beta band as a signature of activity in the brain network that underlies this default mode network" (Laufs et al., 2003, pp. 11057).
>
> and later:
>
> "Default mode fMRI resting state oscillations have been found to correlate with power in different EEG frequency bands including (during eyes-closed rest) with spatially averaged alpha and beta, posterior B2" (Laufs et al., 2008, pp. 766).
> "Mantini et al. additionally found spatially averaged alpha power co-vary with BOLD activity in the resting state network" (Laufs et al., 2008, pp. 765–766).

Another study presented more detailed EEG measurements of endogenous activity during periods of closed eyes that were associated with:

> "[...] large low-frequency delta activity within prefrontal area, theta activity at fronto-central area, alpha-1 activity at the anterior-posterior area, alpha-2 and beta-1 at the posterior area, and high-frequency beta-2 and gamma activities at the prefrontal area" (Chen, Feng, Zhao, Yin, & Wang, 2008, pp. 571).
>
> and
>
> "[...] Default mode network at rest with eyes-closed of the dominant spectral field powers entails a constellation of large low-frequency delta activity at the prefrontal area, much smaller theta activity at fronto-central area, compared to the eyes-open resting state, the delta filed power is enhanced at the prefrontal area while the theta, alpha-1, alpha-2 and beta-1 powers are reduced in the respective areas" (Chen et al., 2008, pp. 571).

The foregoing studies do not report the observation of gamma oscillations. However, it is true that none of the studies tried to involve stimulus indented thoughts during scanning, which could also make a difference. One study reported gamma oscillations during an experiment with mindful meditation:

> "Mindfulness meditation (MM) affects self-referential processing [...] we first identified the electrophysiological changes associated with the transition from resting state to a simple time production task – lower gamma power over frontal and midline regions. [...] MM practitioners exhibited lower frontal gamma activity mainly right-lateralized, related to narrative self-reference and default mode network activity. In addition we have identified state increases in temporal and parieto-occipital gamma power, largely lateralized to the right [...] an increase in right parieto-occipital gamma power was also found in the MM practitioners compared to controls, during the resting state, indicating a trait effect [...]" (Berkovich-Ohana, Glicksohn, and Goldstein 2012, pp. 708).

Although these findings are very interesting and provide an observation of gamma activity during endogenous activity, we must not forget that meditation is something that requires training and these techniques are not common to ordinary people. We need to know what neural processes are present in a normal brain and which processes accompany endogenous conscious experience.

Sadly, so far the measurements of electrical activity of endogenous activity are very fragmented and no study that would be primarily interested in the necessary conditions for endogenous streams of consciousness using simultaneously fMRI and EEG has been performed. Therefore, it is too early for any crucial conclusion (falsification/verification) about the foregoing hypotheses about the DMN, attention and consciousness.

Concluding remarks

This review shows exhaustively how important the DMN and endogenous activity are for the science of consciousness and that they are not only an interesting addition to the science of consciousness but a whole new theme that deserves our full attention. DMN activity represents a *Baseline* of brain activity and solely for this reason it cannot be ignored in the discussion about *conscious experience*.

Secondly, we showed how the DMN and endogenous activity correlate with various categories of consciousness. DMN activity directly correlates with *background states of consciousness* and could be used as another method for determining levels of consciousness. Endogenous activity and the DMN also correlate with *specific streams of consciousness*, whose content is the stimulus independent thought. We also showed correlates of specific persons, whose behavior was predicted by subjects, which is an excellent example of the identification of *specific states of consciousness*.

Thirdly, we showed that the thalamus is not part of the DMN and we attempted to refute the idea that the thalamus is the cerebral celebrity of consciousness. On the other hand, we proposed a new aspirant to this position of the cerebral celebrity of consciousness – the precuneus/PCC.

Fourthly, we highlighted the fact that more research needs to be performed on neural oscillations of the DMN and endogenous activity, which would give us new data about internally focused attention and gamma oscillations during endogenous activity.

The DMN and endogenous activity should be included when specifying the true nature of subjective experience and we also believe that this review uncovered a little about endogenous activity and the DMN and that they are no longer a missing piece of the puzzle in the science of consciousness.

Funding

This work was supported by the Czech Science Foundation – Czechia (GACR) Grant No. 17-23718S, and by the NPU I project "NPU4NUDZ" No. LO1611 from the MEYS CR.

Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Acknowledgements

The author would like to acknowledge support from the Department of Applied Neurosciences and Brain Imaging at the National Institute of Mental Health. The author would also like to thank all reviewers for their insightful comments and valuable suggestions that significantly improved the manuscript.

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