Persistent Operational Synchrony within Brain Default-Mode Network and Self-Processing Operations in Healthy Subjects

Andrew A. Fingelkurts [a],* and Alexander A. Fingelkurts [a]

[a] *BM-Science – Brain and Mind Technologies Research Centre, Espoo, Finland*

Abstract
Based on the theoretical analysis of self-consciousness concepts, we hypothesized that the spatio-temporal pattern of functional connectivity within the default-mode network (DMN) should persist unchanged across a variety of different cognitive tasks or acts, thus being task-unrelated. This supposition is in contrast with current understanding that DMN activated when the subjects are resting and deactivated during any attention-demanding cognitive tasks. To test our proposal, we used, in retrospect, the results from our two early studies (Fingelkurts, 1998; Fingelkurts et al., 2003). In both studies for the majority of experimental trails we indeed found a constellation of operationally synchronized cortical areas (indexed as DMN) that was persistent across all studied experimental conditions in all subjects. Furthermore, we found three major elements comprising this DMN: two symmetrical occipito-parieto-temporal and one frontal spatio-temporal patterns. This new data directly supports the notion that DMN has a specific functional connotation − it provides neurophysiologic basis for self-processing operations, namely first-person perspective taking and an experience of agency.

Key words: alpha rhythm, EEG, brain operations, metastability, neurophysiological pattern, resting state, default mode, synchronization, functional connectivity.

1. Introduction

In the end of XXth and the beginning of new XXIst century a team of researchers from the Washington University and Mallinckrodt Institute of Radiology, using quantitative positron emission tomography (PET), discovered that in the cortex there are some areas which were activated when the subjects are resting and deactivated in a task-independent manner during any attention-demanding cognitive tasks (Shulman et al., 1997; Raichle, et al., 2001). Latter this consistent set of cortical areas was called a 'Default-Mode Network' (DMN) (Gusnard and Raichle, 2001). The name was used rather in a metaphorical sense, since to reveal the set of brain areas is not sufficient to prove whether the activated areas are actually functionally connected within an intrinsically correlated network. Direct evidence for temporal coherence of resting-state neural activity between regions in this hypothetical network was lacking. However, detection of temporal coherence in such a network would provide more direct evidence for the existence of a DMN, and generally enhance our understanding of neural activity of brain states.

Recently, Greicius with colleagues (2003), using a functional connectivity MRI analysis, were the first to show that the default regions are indeed functionally connected[1]. Since then this result has been replicated multiple times (Fox et al., 2005; De Luca et al., 2006; Fair et al., 2008; van den Heuvel et al., 2008; Greicius et al., 2008, 2009; Uddin et al., 2009; Honey et al., 2009). Majority of these neuroimaging studies characterize the DMN as a homogenous single network; however, each brain area participating in the DMN may have different functional specialization, suggesting much greater heterogeneity within this network than it is commonly appreciated. Uddin with coauthors (2009) found that there is indeed some heterogeneity in the DMN; particularly this network consists of two relatively independent major nodes – frontal and parietal. Functional specialization of regions within DMN subsystems has been also documented by Spreng and Grady (2010).

Patterns of functional connectivity in the brain (Friston et al., 1993) are believed to reflect the patterns of interaction between transient neuronal assemblies (Fingelkurts et al., 2005) and to be associated with attention, perception, cognition (Bressler, 1995; Gray and Singer, 1995; Varela et al., 2001) and eventually with consciousness (Fingelkurts and Fingelkurts, 2001, 2005, 2006; Fingelkurts et al., 2009, 2010). In connection to this, there is healthy skepticism as to how closely functional connectivity with MRI estimates actual connectivity among neuronal assemblies (Maldjian, 2001).

---

[1] As far as in 1998 Fingelkurts with coworkers observed the consistent functional connectivity between electroencephalographic (EEG) signals registered from the constellation of particular cortical areas (Fingelkurts, 1998), which later began to be known as the DMN. In that time the authors did not interpret this set of functionally connected cortical areas as DMN, since the concept was not yet been introduced. Several years after Fingelkurts with coworkers have found exactly the same set of functionally connected areas in another EEG study (Fingelkurts et al., 2003).

All hemodynamically based methods (PET, fMRI, and Optical Imaging) determine functional connectivity of neuronal assemblies *indirectly* by evaluating the correlation in hemodynamic activity between two regions. What is obtained is the information about how changes in such hemodynamic activity in one region are related to that in other regions (Horwitz et al., 1999). However, the common factor that underlies several types of functional brain imaging is the electric current of masses of dendrites, which can be measured *directly* by means of electroencephalography (EEG) (Freeman et al., 2009). In this context, brain functional connectivity is usually discussed in terms of how neural (EEG) activity in one brain area is related to neural (EEG) activity in other areas (Fingelkurts et al., 2005). Such EEG based measures of brain synchrony have an advantage over hemodynamically based measures because they reflect a true functional connectivity between different neuronal assemblies (Fingelkurts and Fingelkurts, 2008). While there is some evidence that several different source configurations can generate the same distribution of potentials and electro-magnetic fields on the scalp (for a review see Fender, 1987), the converse is also valid: different scalp topographies of electro-magnetic fields *must* have been generated by different configurations of brain sources (Michel et al., 2004). Capitalizing on this fact, and as will be discussed further in detail below (see Section 3.2), whether and when different neuronal populations are synchronized, could be identified by EEG functional connectivity measures sensitive to differences in scalp topographies (Fingelkurts et al., 2005).

In the present study we will formulate hypothesis (see Section 2) about EEG functional connectivity persistence within DMN along different conditions and will review the converging theoretical and experimental evidences to support it. To our knowledge at present there are no EEG studies of functional connectivity within DMN besides research of Fingelkurts et al. (Fingelkurts, 1998; Fingelkurts et al., 2003) and the current study[2]. Such electrophysiological studies are critical to refute claims that DMN observations constitute an epiphenomenon not of neuronal origin (Birn et al., 2008). Additionally they hold the potential to advance our understanding of the neural correlates and mechanisms of the DMN.

Recently DMN attracted increased attention of many researchers and especially philosophers and psychologists, because it was suggested that this network may represent the neural correlate of the stream of consciousness (Mason et al., 2007). For the purposes of current study we need to have a closer look at the DMN role. What function do DMN subserves?

---

[2] Sometimes the work of Chen at al. (2008) is cited as a reference of EEG functional connectivity in DMN. However, in that study authors did not study functional connectivity between different brain areas that may comprise the DMN, but rather they analyzed the correlation of distributed EEG field powers between different frequency bands.

2. Function(s) of DMN

Initially some researchers associated this network with engaging in functionally important processing such as continuously monitoring the external world (Gusnard and Raichle, 2001). However, it may also make a vital contribution to the off-line processing of recent experiences and consolidation of memories: processing of internal signals such as monitoring one's own mental state, or one's intended speech and actions (Miall and Robertson, 2006; see also Gusnard and Raichle, 2001).

Nowadays researchers tend to associate this DMN either with the stimulus-independent thought, mind-wandering and the internal "narrative" (Gusnard et al., 2001; Mason et al., 2007), or with the "autobiographical" self (Gusnard et al., 2001; Buckner and Carroll, 2007), remembering one's past and planning one's future (Andrews-Hanna et al., 2010; Spreng and Grady, 2010), and "chronic" self-evaluation (Beer, 2007), or even with "being a self," or having self-consciousness (Vogeley et al., 2004; Gusnard, 2005; Schilbach et al., 2008). *However, this interpretation (especially latter ones) would "work" only if the DMN would persist all the time, at least during periods of wakefulness (and dreaming).* At the same time, it is currently accepted that DMN deactivated each time when the subject is involved in attention-demanding cognitive tasks (Raichle, et al., 2001; Gusnard and Raichle, 2001).

Self-consciousness has been defined as the implicit and explicit awareness of one's own mental and/or bodily states (Newen and Vogeley, 2003); and it is difficult to imagine that in normal healthy humans there can be situation of losing this kind of awareness during wakefulness and also in the dream state (Windt and Metzinger, 2007). In its absence, our experience of ourselves and our world becomes kaleidoscopic and the whole life chaotic (Flanagan, 1995; Zahavi, 2002). Besides, if the 'being a self' is supposed to be a *primary* function of DMN and if the DMN stops to be active during some periods of time (attention-demanding cognitive tasks), there would be no explanation for something about self-consciousness which has been clearly established. That is that the sense of 'being a self' (probably in an implicit form) is active not only during resting wakefulness, but even during realization of any cognitive or other task, independently of its complexity (Sims, 2003; Trehub, 2007). Indeed, subject that experiences phenomenal self-consciousness always feels directly present in the center of an externalized multimodal perceptual reality (Revonsuo, 2006; Trehub, 2007). This well known (from the first-person-perspective) fact would be then unexplainable if we accept that DMN transiently stops to exist functionally each time we are engaged in some activity.

Furthermore, it is suggested that apart from being a self 'at a given moment', being a self 'across time' might provide exactly those internal representations of self-awareness continuity, which allow the person subjectively experience the integrity of self-related mental states (Metzinger, 2003). So, in this perspective, and considering that the dynamic structure of cognition and even consciousness is instantiated in the dynamic structure of functionally connected brain network(s) (for the complete argumentation, see Fingelkurts et al., 2009, 2010), *we hypothesize that the spatio-temporal pattern of functional connectivity within the DMN should persist* **unchanged** *across a variety of different cognitive and any other tasks or acts, thus being* **task-unrelated**.

Here we would like to clarify our position: we speak only about EEG functionally connected pattern of brain areas; the metabolically measured activity of these areas can be deactivated. Although it appears that there is a relationship between neuronal activity integrated over time and the amplitude of the hemodynamic response (Gratton et al., 2001), this relationship does not necessarily imply a close relationship between patterns of increased blood flow and electro-magnetic sources (Nunez and Silberstien, 2000). As reviewed by Gevins (2002), "whether synaptic activity is detectable at the scalp depends on the degree to which it is additive, which in turn requires that synapses be activated synchronously and that such synchronous activation occurs in a population of cells that has an architecture such that current flows summate rather than cancel and that has a geometric orientation that supports propagation to the scalp. Relative synchrony in activation does not necessarily imply a relative increase in metabolic activity, and metabolic intensity is not necessarily closely related to the presence or absence of laminar architecture or a suitable orientation". The discrepancy between electrophysiological and metabolical methods was shown experimentally (Ullsperger and Debener, 2010). For example, hypocarbia does not alterate the metabolic support, but task performance and electrical activity are altered (Halgren et al., 1977). Epileptic spikes in EEG which unequivocally represent an increase in synchronized neuronal activity can be associated with negative BOLD in the locus of the epileptic focus (Gotman, 2008; Vulliemoz et al., 2009). Further, it has been shown that BOLD effects associated with large vessels are not closely correlated with actual site of neuronal (electrical) activity (Ugurbil, 2002).

It would be important to test our proposal and to analyze (i) whether the postulated network indeed exists *persistently* through the resting condition and externally cued cognitive tasks, (ii) which brain regions are linked in the network, and (iii) how this links are modulated during performance of cognitive tasks.

To address these questions, we used, in retrospect, the results from our two earlier studies (Fingelkurts, 1998; Fingelkurts et al., 2003). Full details concerning the paradigm and data acquisition of each study can be found therein. We provide only the essential details here.

3. Methodological aspects

We studied electroencephalograms (EEG) to examine brain functional connectivity in a group of 12 Russian subjects during rest and visual working memory task (Fingelkurts, 1998) and in a group of 9 Finnish subjects under rest and auditory working memory task (Fingelkurts et al., 2003). In both studies the working memory task has had several stages: (i) active waiting, (ii) stimulus presentation and memorizing, (iii) keeping the memorized image in a mind, and (iv) identification of the memorized image.

In the Russian study (Fingelkurts, 1998) 16-channel EEGs were recorded for 12 healthy, right-handed adult subjects (aged 19-26) during resting condition and the multistage visual memory task (waiting, memorizing of the actual visual matrix object, and retention of the perceptual visual image). The visual stimuli presented in front of the subjects to memorize were non-verbalisable matrices composed of nine square elements presented on a matrix screen. The combination of the squares was selected quasi-randomly and presented on the screen for 20-sec by lighting with bottom-mounted red light diodes. Raw EEG signals were recorded with a frequency band of 0.3-30 Hz. The impedance of recording electrodes was monitored for each subject and it was always below 5 kΩ. The presence of an adequate EEG signal was determined by visual inspection of the raw signal on the computer screen. Total number of EEGs (across all subjects) for resting conditions was 96 (for open and closed eyes separately); and total number of EEGs for the memory task was 288 (for each of three memory stages).

In the Finnish study (Fingelkurts et al., 2003) 20-channel EEGs were recorded for 9 healthy, right-handed adult subjects (aged 20–29) during the modified Sternberg's memory task. The memory set (encoding) consisted of four auditorily presented stimuli. The stimuli consisted of 24 auditory verbs (spoken with a female voice). A total of 192 four-verb memory sets were constructed such that each of the verbs had to occur with equal frequency and only once in the same memory set. In 50% of the cases, the frame set verb was among the previously presented four-stimulus block. In total, there were 192 trials, which were presented to the subjects in a pseudorandomized order. The experiment was designed in such a way that it was possible to test separately resting, waiting, encoding, keeping-in-mind, and identification short-term periods of the memory task. Raw EEG signals were recorded with a frequency band of 0.3-70 Hz. The impedance of the recording electrodes was always below 5 kΩ. The full EEG streams were split into 5 distinct segments: resting period, waiting period, encoding period, keeping-in-mind period, and identification period.

In both studies we then applied an Operational Architectonics (OA) methodology (Fingelkurts and Fingelkurts, 2001, 2008) to the alpha frequency band of the EEG in order to estimate the spatio-temporal patterns of *functionally connected* cortical areas. The approach to study coordinated activity between different brain areas which we have used is very different from conventional methods (such as coherence, phase synchrony, and others; see Fingelkurts et al., 2005). It fits into a more general class of nonlinear interdependencies between dynamic systems, in which rapid transients in one system can be directly mapped to a second system. In general, this measure belongs to the class of methods estimating synchronization between non-identical (structurally nonequivalent) systems. The main benefit of this synchrony over the ones quantifying coherence, correlation, and phase synchronization is a conceptual one (Fingelkurts and Fingelkurts, 2001, 2004). Contrary to findings of previous EEG studies on functional connectivity, our measure is well suited to extract information about discrete operations of neuronal assemblies from EEG recordings and to estimate the level of inherent synchrony of these operations appearing simultaneously and locally in different cortical areas. It can therefore quantify a broader range of the coordination processes, especially metastable and non-static nonlinear phenomena (Fingelkurts et al., 2005; Fingelkurts and Fingelkurts, 2004, 2008).

The alpha frequency band (7-13 Hz) was chosen for the current study because it has been demonstrated that the DMN has significant positive correlation with alpha rhythm (Mantini et al., 2007). Additionally, for the purpose of the present study it is important that alpha activity is expected to play the leading part in organization of conscious (specifically human) interactions with the environment (Knyazev, 2007). Furthermore, it has been estimated that 90% of people have alpha activity in resting but awake EEG and in 60% of people EEG alpha rhythm is dominant (Stern and Engel, 2005). Therefore, alpha activity is the most common component of the human brain's electrical activity (Basar and Guntekin, 2006), which is highly correlated with mind wondering and spontaneous thoughts (Shaw, 2003).

3.1. A brief introduction to Operational Architectonics (OA) methodology

OA theory explores the temporal structure of information flow and the inter-area interactions within a network of dynamical, transient, and functional neuronal assemblies (which activity is "hidden" in the complex non-stationary structure of EEG signal; see Kaplan et al., 2005) by examining topographic rapid transition processes (on the millisecond scale) in local EEGs (Fingelkurts and Fingelkurts, 2001, 2005, 2008). The rapid transitional processes (RTPs) occurring in the amplitude of a continuous EEG activity mark the boundaries between quasi-stationary segments

for this activity. RTP is defined as an abrupt change in the analytical amplitude of the signal above a particular threshold established experimentally for each local EEG in modeling studies (see Fingelkurts and Fingelkurts, 2008). According to the OA framework each homogenous segment in EEG signal corresponds to a temporary stable microstate – an operation executed by a neuronal assembly (Fingelkurts and Fingelkurts, 2001, 2005). The transition from one segment to another reflects then the moment of abrupt switching from one neuronal assembly to another (see the example in Fingelkurts and Fingelkurts, 2008).

The general statistical principles of the *microstate segmentation* have been described extensively elsewhere (Fingelkurts and Fingelkurts, 2001, 2005, 2008; Kaplan et al., 2005). Therefore, here we only provide a brief overview of this approach (see Fig. 1). The RTPseg toolkit (BM-Science, Finland) was used for automatic segmentation of the local EEG signals within the multichannel EEG record. This method is based on the automatic algorithm of moving double window screening along each separate EEG signal. The ongoing amplitude values in the test window are compared with amplitude values averaged in the level window (test window << level window). If, in accord with the given level of probability of false alert, the value averaged in the level window is exceeded by the highest among the test window value, the time point with the highest amplitude is considered as a preliminary RTP. In order to exclude false alerts caused by anomalous peaks in amplitude, another condition must be fulfilled: the statistically significant difference must be detected between an amplitude value averaged across five consecutive time points following the preliminary RTP and the amplitude value averaged across the level window. If these two criteria are met, the RTP is considered as actual (real). Thereafter, both windows are shifted from this RTP on one time-point, and the procedure is repeated until the whole sequence of statistically proven RTPs is determined (Fig.1; Fingelkurts and Fingelkurts, 2008).

Temporal *synchronization* of multiple brain operations executed by different local and transient neuronal assemblies (operational synchrony) gives rise to a new level of brain abstractness – metastable brain states (Fingelkurts and Fingelkurts, 2001, 2005). These metastable brain states or functional Operational Modules (OMs) (Fig. 2B), as we name them, underlie the realization of brain complex macrooperations: cognitive percepts, phenomenal objects, and reflective thoughts within the operational space-time continuum (Fingelkurts and Fingelkurts, 2010). Each OM is metastable spatial-temporal pattern of brain activity, because the neuronal assemblies which constitute it produce different operations/functions and each does its own inherent "job" (thus expressing the autonomous tendency), while still at the same time been temporally entangled among each other (and thus expressing the coordinated tendency) in order to execute common complex operation or cognitive act of a higher hierarchy (Fingelkurts and Fingelkurts, 2004; Fingelkurts et al., 2009). As has been

proposed by Kelso (1995) metastability relates exactly to the constant interplay between these autonomous and interdependent tendencies (for further discussion see Bressler and Kelso, 2001; Kelso and Engstrøm, 2006).
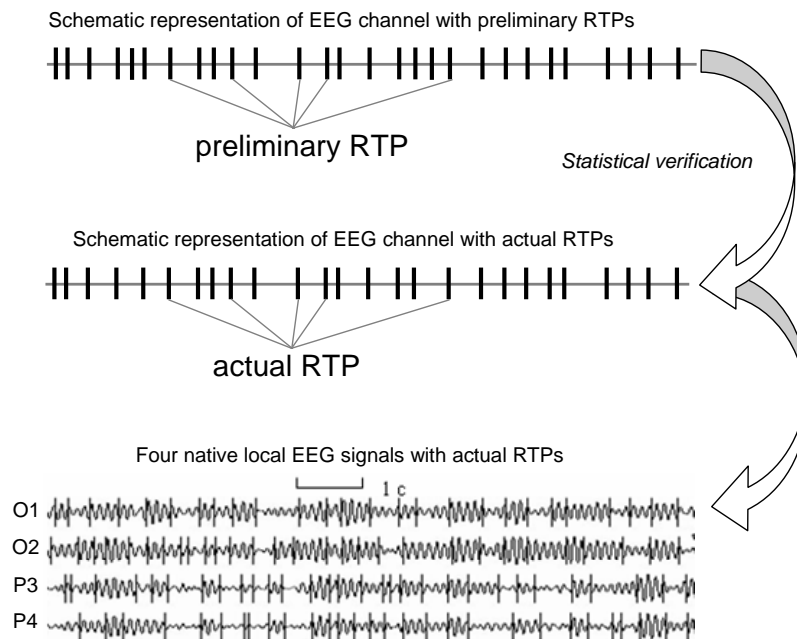
Figure 1. EEG segmentation. An example of four local EEG signals with rapid transition periods (RTPs) and the schematic representation of one channel (O1) and RTPs (Notice that after statistical verification of preliminary RTPs some of these RTPs do not present among the actual RTPs). EEG was registered in resting condition (closed eyes) and then filtered in the alpha frequency band (7-13 Hz).

At the EEG level the OM phenomenon is expressed in the synchronization of EEG quasi-stationary segments (indexed by Structural Synchrony, ISS) obtained from different brain locations (Fingelkurts and Fingelkurts, 2001, 2008) and measured by means of RTPsyn toolkit (BM-Science, Finland). As the details of this technique are beyond the scope of this article, we will only concentrate on some essential aspects.

The criterion for defining an OM is a sequence of the same synchrocomplexes (SC), whereas SC is a set of EEG channels in which each channel forms a paired combination with high values of ISS with all other EEG channels in the same SC; meaning that all pairs of channels in an SC have to have statistically significant ISS (Fig. 2A). RTP in the *reference* EEG channel (the channel with the minimal number of RTPs from any pair of EEG channels) is surrounded by a short "window" (ms). Any RTP from another (*test*) EEG channel is considered to coincide if it fell within this window (Fig. 2A). The ISS tends towards zero where there is no synchronization between the EEG segments located in different EEG channels and has positive or negative values where such synchronization

exists. Positive values indicate 'active' coupling of EEG segments (synchronization of EEG segments is observed significantly more often than expected by chance as a result of random shuffling during computer simulation), whereas negative values mark 'active' decoupling of segments (synchronization of EEG segments is observed significantly less than expected by chance as a result of random shuffling during computer simulation).

3.2. Volume conduction and brain activity sources problem

Although it is often claimed that volume conduction is the main obstacle in interpreting EEG data in terms of brain connectivity, it has been shown previously through empirical and modeling experiments that the values of the operational synchrony index are sensitive to the morpho-functional organization of the cortex rather than to the volume conduction and/or reference electrode (for relevant details we refer the reader to Kaplan et al., 2005; Fingelkurts and Fingelkurts, 2008). These findings also suggested the existence of statistical heterogeneity (anisotropy) of electro-magnetic field in regard to the processes of mutual stabilization of quasi-stable periods in regional EEGs. In addition and contrary to other EEG measures of functional connectivity, the operational synchrony measure, which was used in the current study is based on temporal point-to-point coincidences of RTPs (even for the remote cortex areas) and does not require a shared EEG rhythm or activity in different EEG channels (it is this similarity of EEG signals on the scalp that is determined to a large degree by volume conduction or a common activity source). Thus the measure based on temporal coincidences of RTPs does not required implicit or explicit source model for the interpretation of its results (Kaplan et al., 2005).

Even though the discussion of this issue is outside the scope of the present paper, it is worthwhile to mention experimental evidences about sensitivity of topographic EEG mapping which are commonly neglected. The accuracy of topographic EEG mapping for determining local (immediately under the recording electrode) brain activity was experimentally shown with radioactive marker (Cook et al., 1998; for further argumentation see Bullock, 1997; Kaiser, 2000; Freeman, 2003). Further, experimental findings demonstrated that the probabilities of firing of neurons observed singly and in small groups simultaneously are in close statistical relationship to the EEG recorded in the near vicinity (Eeckman and Freeman, 1990, 1991). It has been shown also that EEG and MEG (which is free from volume-conduction effects) offer comparable spatial resolutions on the order of several millimeters (Cohen et al., 1990; Ingber, 1991). Therefore the EEG can provide an experimental basis for estimating the local mean field of contributory neurons (Pascual-Marqui, 2009) located in cortical regions near the recording electrodes (Gevins, 2002).
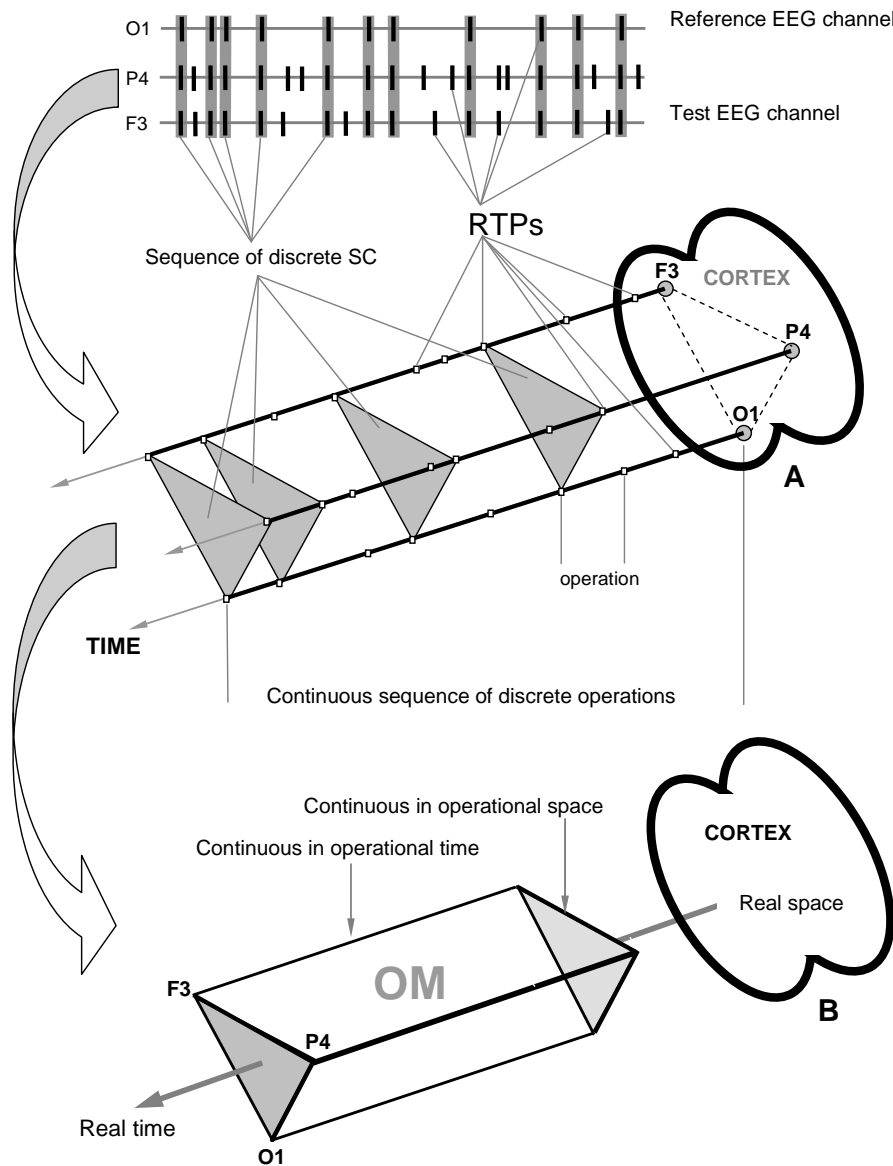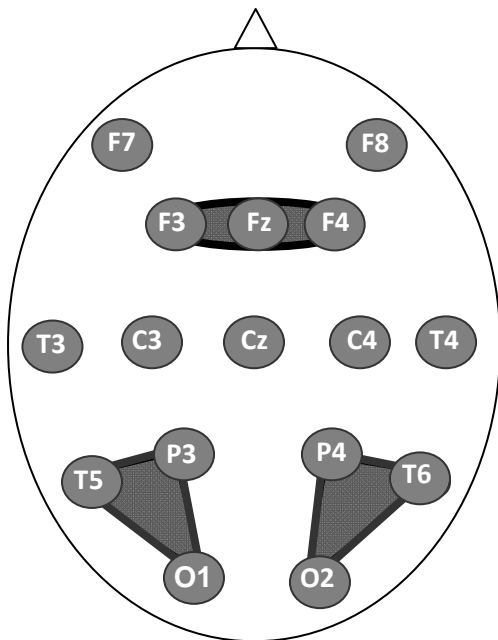
Figure 2. EEG operational synchrony (schematic presentation). A: Technical estimation of functional connectivity applying operational synchrony measure. B: Illustration of brain Operational Module (OM). Each OM exists in its own space and time, which exclude other possible time and space scales present simultaneously in the brain. In other words, all neural assemblies that do not contribute to a particular, given OM are temporarily and spatially excluded from this OM.

Notice that in these studies there are no inferences about primary generators (sources) of the EEG activity in different cortex areas. It is obvious that state and behavior of each cortex area is affected (influenced/modulated) by a mixture from multiple primary sources. However, considering that each cortex area is an active system and in each time instant it has its own state, all activities (influences) from multiple primary sources are not just summed or averaged in a given cortex area, but are integrated within the current state (activity) of this area. It is this integrated (modified or modulated) state (activity) in a given cortex area that is registered predominantly by the nearest EEG electrode as

it was demonstrated in the experimental studies cited above. In these sense local EEG represents a *'functional source'*, which is defined as the part or parts of the brain that contribute to the activity recorded at a single sensor (Stam, 2005; Wackermann and Allefeld, 2007). A functional source is an operational concept that does not have to coincide with a well defined anatomical part of the brain, and is neutral with respect to the problems of localization of primary source and volume conduction (Stam, 2005; Wackermann and Allefeld, 2007).

## 4. Results and discussion: persistent synchrony within DMN

In both studies (Fingelkurts, 1998; Fingelkurts et al., 2003) for the majority of experimental trails we have found a constellation of operationally synchronized cortical areas (indexed by 3 OMs) that was *persistent* across all studied experimental conditions (rest and different stages of working memory), thus being *task-unrelated* (Fig. 3)[3]. It is interesting that despite different subjects' population samples (Russian and Finnish) and different sensory modalities (visual and auditory) the obtained task-unrelated set of OMs was robust and consistent through all studied phases of cognitive tasks (Fig. 3). As it is seen from Figure 4, the strength of connectivity within OMs did not change significantly along with changes in cognitive states.

Figure 3. Persistent (task-unrelated) EEG operational synchrony spatio-temporal patterns (indexed as Operational Modules, OMs). The statistically significant ($p < 0.05$) values of operational synchrony among EEG locations that occur in majority of experimental trials across all subjects are mapped onto schematic scalp map as dark grey shapes, which indicates OMs. Figure is modified from Fingelkurts et al., 2003, NeuroImage[©].

---

[3] Simultaneously, different diverse sets of transient OMs, which were specific to different phases of cognitive activity (thus being *task-related*), have been also found. Since they are not in the focus of the present study, we refer interested reader to the previous publications (Fingelkurts, 1998; Fingelkurts et al., 2003) where these OMs are described and discussed in detail.

The following scalp EEG positions and correspondent to them cortical areas (Koessler et al., 2009) were involved in the operational synchrony process (Fig. 3): EEG positions F_3 and F_4 (left and right middle frontal gyruses or Brodmann's area 8), EEG position F_z (bilateral medial areas or Brodmann's area 6), EEG positions T_5 and T_6 (left and right middle temporal gyruses or Brodmann's area 21), EEG positions P_3 and P_4 (left and right precuneus or Brodmann's area 19), and EEG positions O_1 and O_2 (left and right middle occipital gyruses or Brodmann's area 18). These anatomical correlations of EEG electrode positions were taken from the reference study of Koessler et al. (2009), where matching between EEG electrode positions and anatomical areas of the cortex was clearly established and analyzed using a new EEG-MRI sensor system and an automated projection algorithm (see also Kaiser, 2000). The extensive overlap between found in the present study set of synchronized cortical areas and the proposed DMN (Shulman et al., 1997; Raichle, et al., 2001) suggests that this identified network of synchronized cortical areas (Fig. 3) accounts, in large part, for the DMN.
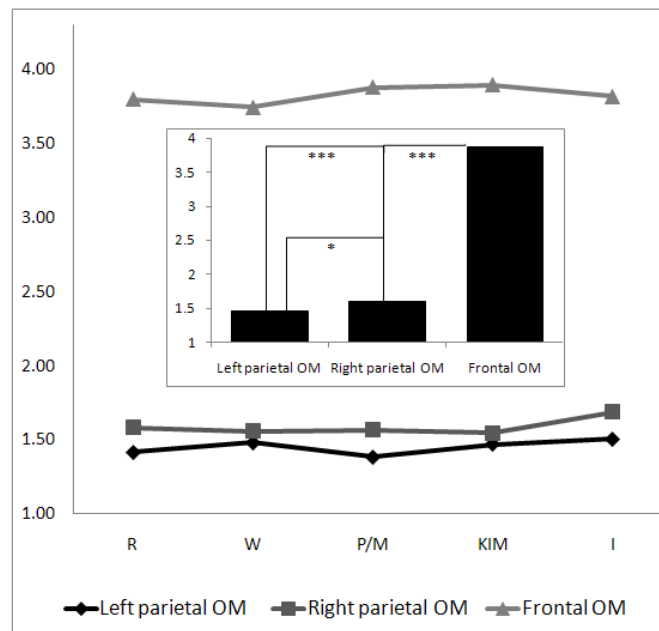
Figure 4. Mean strength of operational synchrony within each Operational Modules (OMs). *X*-axis presents different experimental conditions: *R* – rest; *W* – active waiting; *P/M* – stimulus presentation and its memorizing; *KIM* – keeping in mind the image of memorized stimulus; *I* – identification (test). *Y*-axis presents the mean values of strength of operational synchrony. At the insertion graph, in the center of figure, the comparison between mean strength of operational synchrony within OMs is shown. * – $p < 0.05$ and *** – $p < 0.001$, Wilcoxon *t*-test.

Although the DMN was thought to be most active (metabolically) during the resting state (Raichle and Snyder, 2007), our analysis has consistently show that operationally *synchronized* cortical areas within DMN may also persist unchanged during different cognitive tasks (Fig. 4). Besides direct evidence for the existence of operationally synchronized cortex areas within DMN, this finding also pointed to the conclusion that the brain is able to *divide its functional resources* between processing of the immediate external stimuli and the functioning of the default system, spatial-temporal pattern of which should be continuously available if it is responsible for the self-consciousness (see Section 2). This conclusion is congruent with the view recently suggested by Buckner et al. (2008).

One may argue that the fact that the strength of synchrony in DMN OMs is almost completely unaffected by cognitive states could be explained by the measurement artifact and/or volume conduction. However, this is unlikely since in both studies (Fingelkurts, 1998; Fingelkurts et al., 2003) the large set of task-dependent transient OMs (some of which partly overlap with the DMN OMs) was identified. This provides evidence against the possibility that the task-independence of alpha-band coupling in only three OMs is due to an artifact and/or volume conduction.

Since the functionally connected DMN appears to persist unchanged during several cognitive tasks, our initial hypothesis that DMN should be persistent irrespectively on the functional state and/or cognitive task is confirmed. Therefore, we could speculate that the classical interpretation (see Section 2) that DMN is responsible (i) for the self-awareness and (ii) for the continuity of this subjective experience over time is now valid. In this context, even during periods of engaging in some task-demanding activity the DMN is still supporting stimulus-independent thoughts/operations (mostly self-relevant or related to self-agency; see Spreng and Grady, 2010); in other words DMN is their neurophysiological substratum. Indeed in several studies of complex cognitive tasks relative fMRI activity increase rather than decrease in the default network has been observed (for reviews see Svoboda et al., 2006; Buckner and Carroll, 2007; Hassibis and Maguire, 2007; Buckner et al., 2008). If DMN could be persistent, how then the need for the re-allocation of the resources to those brain areas which are differentially needed for cognitively effortful, stimulus-dependent processing (McKiernan et al., 2006) can be explained?

According to the Operational Architectonics framework (Fingelkurts and Fingelkurts, 2001, 2005, 2006, 2008) there are multiple, simultaneously occurring interactions between different cognitive operations, which are subserved by simultaneous presence of transient neuronal assemblies as autonomous entities and OMs (synchronized neuronal assemblies) of different complexity (Fingelkurts et al., 2009, 2010). Because of the composite polyphonic character of the electrical brain field (EEG), this field can be presented as a mixture of many time-scale processes (Nunez, 2000;

Basar et al., 2001; Basar, 2004). Consequently, a large number of functionally distinct OMs can *co-exist simultaneously* on different time-scales and even between them (Fig. 5; for experimental support, see Fingelkurts, 1998; Kaplan and Shishkin, 2000; Fingelkurts, et al., 2004). Hence, in this perspective, the immediately needed cognitive (or mental) operation within a *particular time-scale* can be presented by immediately emerged specific OM on the same time-scale without the need to disassemble the persistent OM which exists on a *different time-scale* (Fingelkurts et al., 2003; see also Fingelkurts et al., 2009; 2010). This mechanism allows brain to present multiple multimodal stimulus, objects, actions and/or tasks by distant functional OMs. The same conclusion can be drawn from the study of Calhoun et al. (2002).
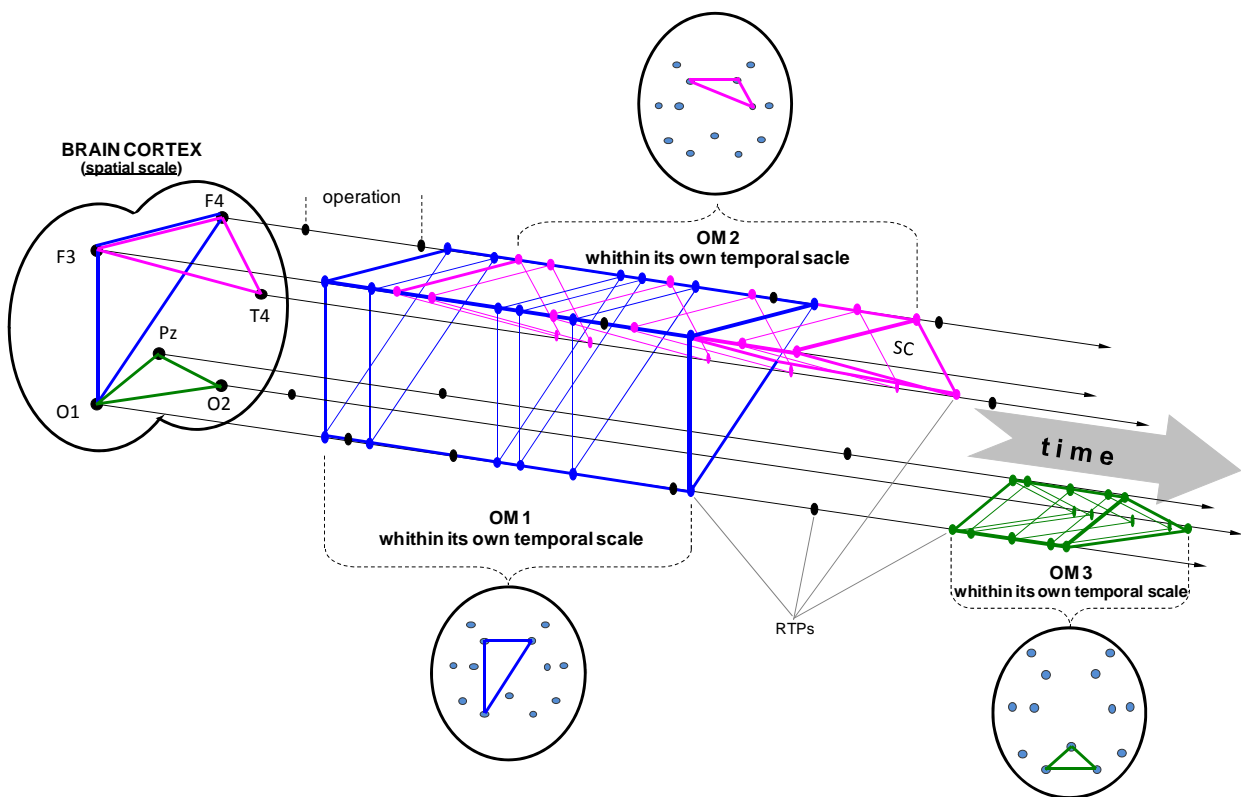
Figure 5. Schematic illustration of synchronous coexistence of multiple Operational Modules (OMs). As one can see, each OM exists in its own spatial-temporal scale, which is "blind" to other possible time and space scales present simultaneously in the brain "system". In other words, all neural assemblies that do not contribute to a particular OM are temporarily and spatially "excluded" from the spatial-temporal scale of that particular OM. RTP – rapid transitional processes (boundaries between quasi-stationary EEG segments); SC – momentary synchrocomplexes (synchronization of RTPs between different, but particular, local EEGs at the particular time instants); F3 – the left frontal cortical area; F4 – the right frontal cortical area; O1 – the left occipital cortical area; O2 – the right occipital cortical area; T4 – the right temporal cortical area; Pz – the central parietal cortical area. As an example, it is shown that neural assemblies in these areas could synchronize their operations on three different (even though partially intertwined) spatial-temporal scales, thus forming three separate OMs each having its own operational space-time. Figure is modified from Fingelkurts et al., 2010, Physics of Life Reviews[©].

The interpretation that DMN is responsible for the self-awareness could, however, further be challenged by the fact that awareness usually divided into two components: self-awareness and external awareness (Boly et al., 2008a). Self- and external awareness are believed to behave in an anti-correlated manner: when someone is engaged in self-related processes, he/she is less receptive to environmental demands, and vice versa (Duval and Wicklund, 1972; Boly et al., 2007). One, then, needs to suppose that in awake healthy subjects, self- and external awareness' OMs should show non-correlated patterns of activity[4]. Such non-correlated behavior between DMN OMs (self-awareness) and specific OMs which are induced by the external stimuli (external awareness), have indeed been observed during a number of perception and cognitive tasks (Fingelkurts, 1998; Fingelkurts et al., 2003). In this context self-consciousness (indexed by DMN OMs) has only a control function for the behavior (Leontyev, 1975), while the concrete cognitive tasks are supported by the specific and transient OMs, which are responsible for the transient focus of conscious attention for the external immediate stimuli and/or tasks.

5. Heterogeneity of synchronicity within DMN

Another interesting aspect that we have observed was the fact that DMN consisted of functionally differentiable subdivisions or separate OMs (Fig. 3). We found three major elements comprising DMN: two symmetrical occipito-parieto-temporal OMs and one frontal OM. Furthermore, the strength of operational synchrony was different in these OMs with the highest values found in the frontal OM and lowest values in the left parietal OM (see an insertion in the Fig. 4). Topographic organization of these OMs (together with the strength values) strongly suggests their functional specificity.

The high values of operational synchrony within the frontal OM of the DMN can be explained by the important known functions of the cortical areas which are involved in this OM. The recruitment of frontal lobe areas has been described to be associated with (i) top-down attentional control (Levine et al., 2004), (ii) personal identity and past personal experiences (Luria, 1973), (iii) coordination of basic drives and with other influences on goal-directed behaviors (Raichle and Gusnard, 2005) and (iv) complete self-consciousness (Uhtomskiy, 1966). Furthermore, as it follows from the lesion

---

[4] Here it is worth to note that we are speaking precisely about "non-correlation" and not about "anti-correlation". In the frame of the Operational Architectonics theory, anti-correlations are expressed in the presence of negative values of the index of EEG operational synchrony (for a detail, see Section 3.1. and Fingelkurts and Fingelkurts, 2008). These negative values reflect the active process of decoupling between operations executed by distant neuronal assemblies. However, we did not observe such negative values of operational synchrony between persistent task-unrelated OMs of DMN and specific task-related OMs. Therefore, in contrast to some MRI studies (Fox et al., 2005; Fransson, 2005) we could not conclude that task-unrelated DMN OMs and task-related OMs are actively anti-correlated.

studies, the medial frontal cortex might be involved in "affective shifting," that supposed to be important to adjust one's responses to a change of the reinforcement value of a given stimulus or tasks (Rolls, 2000; Fellows and Farah, 2003). Thus, we can suggest that this frontal OM most likely provides a critical self-related context (experience of agency) for all human behaviors and activities.

The areas participated in the symmetrical parietal OMs of the DMN are usually involved in realization of more specific cognitive and behavioral functions; therefore, they should intensively participate in multiple OMs. This is probably the reason why these areas have had weaker functional connections within parietal OMs than the areas within the frontal OM (see insertion at Fig. 4). The functions which are attributed to these areas include (but not limited to) visuospatial and mental imagery, episodic memory retrieval, social interaction and self-related processing (Shulman et al., 1997; Cavanna and Trimble, 2006; Schilbach et al., 2006). Larger strength of functional connections within the right parietal OM can be explained by slightly stronger involvement of the right than left hemisphere in self-awareness. For example, in several studies it has been shown that right temporal-parieto-occipital regions of the cortex are responsible for the sense of self-ownership for perceptions of objects (Zahn et al., 2008) and are selectively active in explicit self-reference (Lou et al., 2004) and during physical first-person perspective (Vogeley and Fink, 2003).

Despite the evidence that DMN consisted of functionally differentiable subdivisions or separate OMs (Fig. 3), the fact that all three OMs persistently existed in parallel through many studied experimental conditions (Fingelkurts, 1998; Fingelkurts et al., 2003) suggests that these three OMs might be functionally integrated with each other within the common neuronal spatial-temporal network (i.e., DMN) over a much longer (minuets or even hours) time-scale (see Fig. 6). In this sense the DMN still represents the integrated network as a whole, which does not support the immediate task goals. Indeed, as stated by Buckner and Vincent (2007), "we spend most of our time directed away from the environment in processing modes that consolidate the past, stabilize brain ensembles, and prepare us for the future." Parallel existence of frontal and parietal operationally synchronized spatio-temporal patterns within the same neuronal network has been related to a conscious perception, self-programming and self-control (Leontyev, 1976; Chuprikova, 1985; Pavlova and Romanenko, 1988).

6. Concluding discussion

Our findings on the operational synchrony within the DMN extend previous studies on the DMN showing that *operationally synchronized* DMN may persist unchanged through both rest and experimental (cognitively demanding) periods, although the level of metabolic activity may vary.

This new data supports the notion that DMN has a specific functional connotation – it provides neurophysiologic basis for self-processing operations, namely first-person perspective taking and an experience of agency (Schilbach et al., 2008). This suggestion is compatible with the fact that both functionally connected DMN and self-awareness are persistently present through wakefulness (during rest and cognitive tasks) in healthy subjects. The overall emphasis is on the importance of the ability of both persistent non-specific OMs (which constitute the DMN) and transient specific OMs (which support immediate tasks) to create hierarchical patterns of brain activity, which are hypothesized to allow full-fledged conscious experience of self and outside world (Fingelkurts et al., 2010).
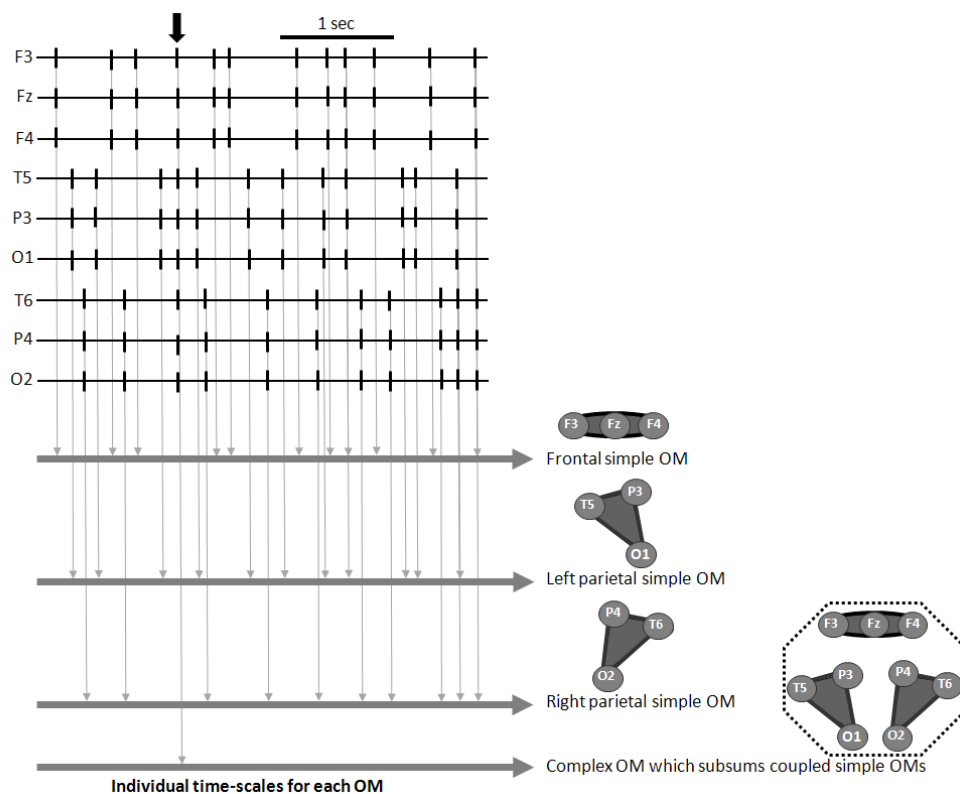
Figure 6. Schematic presentation of synchronization of three OMs within the same integrated network. Horizontal lines represent EEG recordings labeled with EEG IDs. Short black vertical bars indicate the boundaries between quasi-stationary EEG segments, which correspond to rapid transition periods (RTPs). Vertical grey arrows pointed to the particular time-scales on which several EEGs (recorded from different cortical areas) are operationally synchronized. Short black arrow at the top of the figure marks the point on a given time-scale, which corresponds to a synchronization of RTPs among all recorded EEG channels. Grey shapes correspond to individual operational modules (OMs).

The fact that DMN may present not only in normal resting and task-demanding conditions but also during anesthesia (Greicius et al., 2008) and in vegetative patients (Laureys et al., 1999), in whom conscious mental activity is thought to be absent, may point to a more fundamental or intrinsic property of DMN (for a similar conclusion see Britz et al., 2010). It can be responsible for the need of

the organism (even being unconscious) to integrate the internal representations and/or operations within so-called *self-model* to make them available for further selective resource allocation and processing (Metzinger, 2007). In this sense, such self-model may be unconscious (Metzinger, 2007). This latter conclusion is supported by the fact that the main anatomical nodes of the DMN are already present at birth (Fransson et al., 2007) and that they supposed to form the structural core (some sort of connectivity hubs; Sporns et al., 2007) of the cerebral cortex (Hagmann et al., 2008). Remarkably, the locations of these hubs are present across passive and active task states, suggesting that they reflect some stable property of brain network architecture (Buckner et al., 2009).

The present study does not directly investigate relation of EEG functional connectivity within DMN and levels of self-consciousness. At the same time, fMRI findings on (i) the absence of DMN functional connectivity in brain death (Boly et al., 2008b); (ii) the extremely low connectivity within DMN during anesthesia (Greicius et al., 2008), in coma and in vegetative patients (Boly et al., 2008b; Cauda et al., 2009); (iii) the DMN underconnectivity in minimally conscious patients (Boly et al., 2008b); (iv) decreased connectivity within DMN in children (Fair et al., 2008) and autistic patients (Cherkassky et al., 2006), who is lacking of self-representation and (v) increased DMN connectivity in schizophrenic patients, who have an exaggerated focus on self (Whitfield-Gabrieli et al., 2009), clearly support the view that DMN *is* involved in self-consciousness. The schematic representation of relations between the levels of self-consciousness and fMRI-based DMN functional connectivity are shown in Figure 7.

The present set of analyses taken together allow us to conclude that when functionally integrated in healthy subjects, DMN persists as long as subject is engaged in an active, complex, flexible and adaptive behavior. The fact that self-agency is ongoing, and that it is present even when we are processing stimuli from the outside world, makes the concept of ongoing brain activity (indexed by DMN) not only plausible but crucial. As it is stressed by Schilbach et al. (2008) such mode of DMN functioning can, therefore, "help to integrate self-referential information, facilitate perception and cognition and provide a social context or narrative in which events become personally meaningful." Indeed, rather than passively "stand by" and "wait" to be activated by sensory input, it is proposed that the integrated DMN is continuously busy generating predictions about the immediate present and the relevant future by deriving analogies from the past and sensory information that link input with representations in memory (Bar, 2007).

At the more methodological level, this study extends conventional activation (indexed by fMRI and/or PET) analyses to the notion of networks, emphasizing functional interactions between the activity (indexed by EEG) of regions *independently of whether or not they are metabolically activated* (indexed by fMRI and/or PET). Indeed, operational synchrony analysis revealed differences

in the brain functional organization not detectable with direct comparisons of activated states (indexed by fMRI and or PET). For instance, the same regions may be activated in two or more conditions, but there may be differences between these two (or more) conditions in the spatial-temporal pattern and strength of functional connections between the areas involved (Fingelkurts et al., 2005).
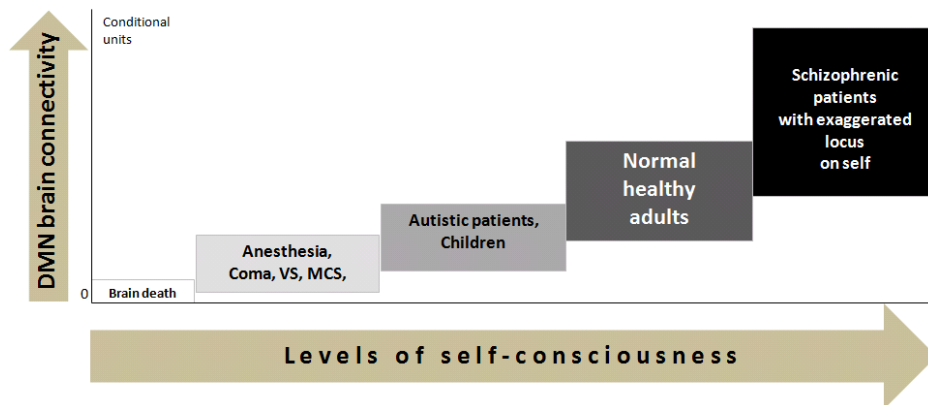
Figure 7. Schematic presentation of the relations between the levels of self-consciousness and fMRI-based DMN functional connectivity.

Furthermore, OA methodology does not consider functional connectivity with respect to a single region only, as it is done in the seed voxel fMRI approaches, but gives rise to a whole network structure which, in contrast to most fMRI connectivity studies, is not chosen in a priori manner, but emerges as a result of data analysis. To our knowledge, the present study (i) is the first presentation of *condition-independent* EEG functional interactions within DMN and (ii) enables to examine the structure of EEG functional connectivity among cortical areas as a whole.

Critically, the EEG-level persistent functional connectivity presented here extends a number of fMRI-based studies of DMN functional connectivity (e.g., Greicius et al., 2003,,2008, 2009; Fox et al., 2005; Uddin et al., 2009; Honey et al., 2009; Spreng and Grady, 2010) and strongly argues against the DMN being an epiphenomenon (Birn et al., 2008). Future studies should enable more detailed EEG mapping of DMN functional connections, but precise mapping will require higher resolution EEG data (as for example in Chen et al., 2008) and more diverse set of experimental conditions. Additionally, to make the suggested hypothesis about putative relation of DMN and self-consciousness stronger, further work is needed to show experimentally that the EEG functional connectivity within DMN structures is lost or weakened in circumstances when self-awareness was lost or weakened.

Acknowledgments

References:

Andrews-Hanna, J., Reidler, J., Sepulcre, J., Poulin, R., & Buckner, R. (2010). Functional–anatomic fractionation of the brain's default network. *Neuron, 65*, 550–562.

Bar, M. (2007). The proactive brain: Using analogies and associations to generate predictions. *Trends in Cognitive Sciences, 11*, 280–289.

Basar, E. (2004). Macrodynamics of electrical activity in the whole brain. *International Journal of Bifurcation and Chaos, 14*, 363–381.

Basar, E., & Guntekin, B. (2006). The key role of alpha activity in "creative evolution". *International Journal of Psychophysiology, 61*, 313–314.

Basar, E., Basar-Eroglu, C., Karakas, S., & Schurmann, M. (2001). Gamma, alpha, delta, and theta oscillations govern cognitive processes. *Journal of Psychophysiology, 39*, 241–248.

Beer, J. S. (2007). The default self: Feeling good or being right? *Trends in Cognitive Sciences, 11*, 187–189.

Birn, R. M., Murphy, K., & Bandettini, P. A. (2008). The effect of respiration variations on independent component analysis results of resting state functional connectivity. *Human Brain Mapping, 29*, 740–750.

Boly, M., Balteau, E., Schnakers, C., Degueldre, C., Moonen, G., Luxen, A., Phillips, C., et al. (2007). Baseline brain activity fluctuations predict somatosensory perception in humans. *Proceedings of the National Academy of Sciences of the United States of America, 104*, 12187–12192.

Boly, M., Phillips, C., Tshibanda, L., Vanhaudenhuyse, A., Schabus, M., Dang-Vu, T. T., Moonen, G., Hustinx, R., Maquet, P., & Laureys, S. (2008a). Intrinsic brain activity in altered states of consciousness. How conscious is the default mode of brain function? *Annals of the New York Academy of Sciences, 1129*, 119–129.

Boly, M., Vanhaudenhuyse, A., Tshibanda, L., Bruno, M-A., Boveroux, P., Noirhomme, Q., Schnakers, C., et al. (2008b). Resting state connectivity integrity in the Default Network reflects the level of consciousness impairment in brain-injured patents. An fMRI study in brain death, coma, vegetative state, minimally conscious state and locked-in syndrome. Proceedings of 12th Annual Meeting of the Association for the Scientific Study of Consciousness. June 19-22, Taiwan, pp. 39-40.

Bressler, S. L. (1995). Large-scale cortical networks and cognition. *Brain Research: Brain Research Reviews, 20*, 288-304.

Bressler, S. L., Kelso, J. A. S. (2001). Cortical coordination dynamics and cognition. *Trends in Cognitive Sciences, 5*, 26-36.

Britz, J., Van De Ville, D., Michel, C. M. (2010). BOLD correlates of EEG topography reveal rapid resting-state network dynamics. *NeuroImage, 52*, 1162-1170.

Buckner, R. L., & Vincent, J. L. (2007). Unrest at rest: Default activity and spontaneous network correlations. *NeuroImage, 37*, 1091-1096.

Buckner, R. L., & Carroll, D. C. (2007). Self-projection and the brain. *Trends in Cognitive Sciences, 11*, 49–57.

Buckner, R. L., Andrews-Hanna, J. R., & Schacter, D. L. (2008). The brain's Default mode network: Anatomy, function and relevance to disease. *Annals of New York Academy of Sciences, 1124*, 1-38.

Buckner, R. L., Sepulcre, J., Talukdar, T., Krienen, F. M., Liu, H., et al. (2009). Cortical hubs revealed by intrinsic functional connectivity: mapping, assessment of stability, and relation to Alzheimer's disease. *The Journal of Neuroscience, 29*, 1860-1873.

Bullock, T. H. (1997). Signals and signs in the nervous system: The dynamic anatomy of electrical activity. *Proceedings of the National Academy of Sciences of the United States of America, 94*, 1-6.

Calhoun, V. D., Pekar, J. J., McGinty, V. B., Adali, T., Watson, T. D., & Pearlson, G. D. (2002). Different activation dynamics in multiple neural systems during simulated driving. *Human Brain Mapping, 16*, 158–167.

Cauda, F., Micon, B. M., Sacco, K., Duca, S., D'Agata, F., Geminiani, G., & Canavero, S. (2009). Disrupted intrinsic functional connectivity in the vegetative state. *Journal of Neurology, Neurosurgery, and Psychiatry, 80*, 429-431.

Cavanna, A. E., & Trimble, M. R. (2006). The precuneus: A review of its functional anatomy and behavioural correlates. *Brain, 129*, 564–583.

Chen, C. A. N., Feng, W., Zhao, H., Yin, Y., & Wang, P. (2008). EEG default mode network in the human brain: Spectral regional field powers. *NeuroImage, 41*, 561–574.

Cherkassky, V. L., Kana, R. K., Keller, T. A., & Just, M. A. (2006). Functional connectivity in a baseline resting-state network in autism. *Neuroreport, 17*, 1687-1690.

Chuprikova, N. I. (1985). *Psychic and Consciousness as Function of the Brain*. Moscow: Nauka.

Cook, I. A., O'Hara, R., Uijtdehaage, S. H., Mandelkern, M., Leuchter, A. F. (1998). Assessing the accuracy of topographic EEG mapping for determining local brain function. *Electroencephalography and Clinical Neurophysiology, 107*, 408-414.

Cohen, D., Cuffin, B. N., Yunokuchi, K., Maniewski, R., Purcell, C., Cosgrove, G. R., Ives, J., Kennedy, J., Schomer, D. (1990). MEG versus EEG localization test using implanted sources in the human brain. *Annals of Neurology, 28*, 811-817.

De Luca, M., Beckmann, C. F., De Stefano, N., Matthews, P. M., & Smith, S. M. (2006). fMRI resting state networks define distinct modes of long-distance interactions in the human brain. *NeuroImage, 29*, 1359–1367.

Duval, S., & Wicklund, R. (1972). *A Theory of Objective Self-awareness*. New York: Academy Press.

Eeckman, F. H., & Freeman, W. J. (1990). Correlations between unit firing and EEG in the rat olfactory system. *Brain Research, 528*, 238-244.

Eeckman, F. H., Freeman, W. J. (1991). Asymmetric sigmoid nonlinearity in the rat olfactory system. *Brain Research, 557*, 13-21.

Fair, D. A., Cohen, A. L., Dosenbach, N. U. F., Church, J. A., Miezin, F. M,, Barch, D. M., Raichle, M. E., Petersen, S. E., & Schlaggar, B. L. (2008). The maturing architecture of the brain's default network. *Proceedings of the National Academy of Sciences of the United States of America, 105*, 4028-4032.

Fellows, L. K., & Farah, M. J. (2003). Ventromedial frontal cortex mediates affective shifting in humans: Evidence from a reversal learning paradigm. *Brain, 126*, 1830–1837.

Fender, D. H. (1987). Source localization of brain electrical activity. In A. S. Gevins, & A. Remond (Eds.), *Handbook of Electroencephalography and Clinical Neurophysiology, Vol. 1. Methods of Analysis of Brain Electrical and Magnetic Signals*. (pp. 355–399). Amsterdam: Elsevier.

Fingelkurts, An. A. (1998). *Time-Spatial Organization of the Human EEG Segmental Structure*. Ph.D. Dissertation., Moscow: MSU press, 401 p. (in Russian).

Fingelkurts, An. A., & Fingelkurts, Al. A. (2001). Operational architectonics of the human brain biopotential field: Towards solving the mind-brain problem. *Brain and Mind, 2*, 261-296.

Fingelkurts, An. A., & Fingelkurts, Al. A. (2004). Making complexity simpler: multivariability and metastability in the Brain. *International Journal of Neuroscience, 114*, 843-862.

Fingelkurts, An. A., & Fingelkurts, Al. A. (2005). Mapping of the brain operational architectonics. In F.J. Chen (Ed.), *Focus on Brain Mapping Research. Chapter 2* (pp. 59-98). Nova Science Publishers Inc, 59-98.

Fingelkurts, An. A., & Fingelkurts, Al. A. (2006). Timing in cognition and EEG brain dynamics: discreteness versus continuity. *Cognitive Processing, 7*, 135-162.

Fingelkurts, An. A., & Fingelkurts, Al. A. (2008). Brain-mind Operational Architectonics imaging: technical and methodological aspects. *Open Neuroimaging Journal, 2*, 73-93.

Fingelkurts, An. A., Fingelkurts, Al. A., & Kähkönen, S. (2005). Functional connectivity in the brain – is it an elusive concept? *Neuroscience and Biobehavioral Reviews, 28*, 827-836.

Fingelkurts, An. A., Fingelkurts, Al. A., & Neves, C. F. H. (2009). Phenomenological architecture of a mind and Operational Architectonics of the brain: the unified metastable continuum. *Journal of New Mathematics and Natural Computation, 5*, 221-244.

Fingelkurts, An. A., Fingelkurts, Al. A., & Neves, C. F. H. (2010). Natural world physical, brain operational, and mind phenomenal space–time. *Physics of Life Reviews, 7*, 195–249.

Fingelkurts, An. A., Fingelkurts, Al. A., Krause, C. M., Kaplan, A. Ya., Borisov, S. V., & Sams, M. (2003). Structural (operational) synchrony of EEG alpha activity during an auditory memory task. *NeuroImage, 20*, 529-542.

Fingelkurts, An. A., Fingelkurts, Al. A., Kivisaari, R., Pekkonen, E., Ilmoniemi, R. J., & Kähkönen, S. A. (2004). Local and remote functional connectivity of neocortex under the inhibition influence. *NeuroImage, 22*, 1390–1406.

Flanagan, O. (1995). *Consciousness Reconsidered*. Cambridge, MA: MIT Press.

Fox, M. D., Snyder, A. Z., Vincent, J. L., Corbetta, M., Van Essen, D. C., & Raichle, M. E. (2005). The human brain is intrinsically organized into dynamic, anticorrelated functional networks. *Proceedings of the National Academy of Sciences of the United States of America, 102*, 9673–9678.

Fransson, P. (2005). Spontaneous low-frequency BOLD signal fluctuations: an fMRI investigation of the resting-state default mode of brain function hypothesis. *Human Brain Mapping, 26*, 15–29.

Fransson, P., Skiöld, B., Horsch, S., Nordell, A., Blennow, M., Lagercrantz, H., & Aden, U. (2007). Resting-state networks in the infant brain. *Proceedings of the National Academy of Sciences of the United States of America, 104*, 15531–15536.

Freeman, W. J. (2003). The wave packet: An action potential for the 21st Century. *Journal of Integrative Neuroscience, 2*, 3-30.

Freeman, W. J., Ahlfors, S. P., & Menon, V. (2009). Combining fMRI with EEG and MEG in order to relate patterns of brain activity to cognition. *International Journal of Psychophysiology, 73*, 43-52.

Friston, K. J., Frith, C. D., Liddle, P. F., & Frackowiak, R. S. J. (1993). Functional connectivity: the principal-component analysis of large (PET) data sets. *Journal of Cerebral Blood Flow and Metabolism, 13*, 5–14.

Gevins, A. (2002) Electrophysiological imaging of brain function. In A.W. Toga & J.C. Mazzoitta (Eds.), *Brain Mapping. The Methods*. 2 edition (pp. 175–188). USA: Elsevier Science

Gotman, J. (2008). Epileptic networks studied with EEG–fMRI. *Epilepsia, 49*, 42–51.

Gratton, G., Goodman-Wood, M. R., Fabiani, M. (2001). Comparison of neuronal and hemodynamic measures of the brain response to visual stimulation: An optical imaging study. *Human Brain Mapping, 13*, 13–25.

Greicius, M. D., Krasnow, B., Reiss, A. L., & Menon, V. (2003). Functional connectivity in the resting brain: A network analysis of the default mode hypothesis. *Proceedings of the National Academy of Sciences of the United States of America, 100*, 253–258.

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

Greicius, M. D., Supekar, K., Menon, V., & Dougherty, R. F. (2009). Resting-state functional connectivity reflects structural connectivity in the default mode network. *Cerebral Cortex, 19*, 72-78.

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

Gusnard, D. A., Akbudak, E., Shulman, G. L., & Raichle, M. E. (2001). Medial prefrontal cortex and self-referential mental activity: Relation to a default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America, 98*, 4259–4264.

Hagmann, P., Cammoun, L., Gigandet, X., Meuli, R., Honey, C. J., Wedeen, V. J., & Sporns, O. (2008). Mapping the structural core of human cerebral cortex. *PLoS Biology, 6*, e159.

Halgren, E., Babb, T. L., & Crandall, P. H. (1977). Responses of human limbic neurons to induced changes in blood gases. *Brain Research, 132*, 43–63.

Hassabis, D., & Maguire, E. A. (2007). Deconstructing episodic memory with construction. *Trends in Cognitive Sciences, 11*, 299–306.

Honey, C. J., Sporns, O., Cammoun, L., Gigandet, X., Thiran, J. P., Meuli, R., & Hagmann, P. Predicting human resting-state functional connectivity from structural connectivity. *Proceedings of the National Academy of Sciences of the United States of America, 106*, 2035–2040.

Horwitz, B., Tagamets, M.-A., & McIntosh, A. R. (1999). Neural modeling, functional brain imaging and cognition. *Trends in Cognitive Sciences, 3*, 91-98.

Ingber, L. (1991). Statistical mechanics of neocortical interactions: A scaling paradigm applied to electroencephalography. *Physical Review A, 44*, 4017-4060.

Kaiser, D. A. (2000). QEEG. State of the art, or state of confusion. *Journal of Neurotherapy, 1530-017X*, 57-75.

Kaplan, A. Ya., & Shishkin, S. L. (2000). Application of the change-point analysis to the investigation of the brain's electrical activity. In B. E. Brodsky & B. S. Darkhovsky (Eds.), *Nonparametric Statistical Diagnosis: Problems and Methods* (pp. 333–388). Dordrecht, the Netherlands: Kluwer Academic Publishers.

Kaplan, A. Ya., Fingelkurts, An. A., Fingelkurts, Al. A., Borisov, S. V., & Darkhovsky, B. S. (2005). Nonstationary nature of the brain activity as revealed by EEG/MEG: Methodological, practical and conceptual challenges. *Signal Processing, 85*, 2190-2212.

Kelso, J. A. S. (1995). *Dynamic Patterns: The Self-Organization of Brain and Behavior*. Cambridge, MA: MIT Press.

Kelso, J. A. S., & Engstrøm, D. (2006). *The Complementary Nature*. Cambridge, MA: MIT Press.

Knyazev, G. G. (2007). Motivation, emotion, and their inhibitory control mirrored in brain oscillations. *Neuroscience and Biobehavioral Reviews, 31*, 377–395.

Koessler, L., Maillard, L., Benhadid, A., Vignal, J. P., Felblinger, J., Vespignani, H., & Braun, M. (2009). Automated cortical projection of EEG sensors: Anatomical correlation via the international 10-10 system. *NeuroImage, 46*, 64-72.

Laureys, S., Goldman, S., Phillips, C., Van Bogaert, P., Aerts, J., Luxen, A., Franck, G., & Maquet, P. (1999). Impaired effective cortical connectivity in vegetative state: Preliminary investigation using PET. *NeuroImage, 9*, 377-382.

Leontyev, A. N. (1975). *Activity. Consciousness. Self*. Moscow: Nauka.

Leontyev, A. N. (1976). *Perception and Activity*. Moscow: Nauka.

Levine, B., Turner, G. R., Tisserand, D., Hevenor, S. J., Graham, S. J., & McIntosh, A. R. (2004). The functional neuroanatomy of episodic and semantic autobiographical remembering: A prospective functional MRI study. *Journal of Cognitive Neuroscience, 16*, 1633–1646.

Lou, H. C., Luber, B., Crupain, M., Keenan, J. P., Nowak, M., Kjaer, T. W., Sackeim, H. A., & Lisanby, S. H. (2004). Parietal cortex and representation of the mental Self. *Proceedings of the National Academy of Sciences of the United States of America, 101*, 6827–6832.

Luria, A. R. (1973). The frontal lobes and the regulation of behavior. In K.H. Pribram & A.R. Luria (Eds.), *Psychophysiology of the Frontal Lobes* (pp. 3-26). New York: Academic Press.

Maldjian, J. A. (2001). Functional connectivity MR imaging: fact or artifact? *American Journal of Neuroradiology, 22*, 239-240.

Mantini, D., Perrucci, M. G., Del Gratta, C., Romani, G. L., & Corbetta, M. (2007). Electrophysiological signatures of resting state networks in the human brain. *Proceedings of the National Academy of Sciences of the United States of America, 104*, 13170–13175.

Mason, M. F., Norton, M. I., Van Horn, J. D., Wegner, D. M., Grafton, S. T., & Macrae, C. N. (2007). Wandering minds: the default network and stimulus independent thought. *Science, 315*, 393–395.

McKiernan, K. A., D'Angelo, B. R., Kaufman, J. N., & Binder, J. R. (2006). Interrupting the "stream of consciousness": An fMRI investigation. *NeuroImage, 29*, 1185–1191.

Metzinger, T. (2003). *Being No One. The Self-Model Theory of Subjectivity*. Cambridge, MA: MIT Press.

Metzinger, T. (2007). The self-model theory of subjectivity (SMT). *Scholarpedia, 2*, 4174.

Miall, R. C., & Robertson, E. M. (2006). Functional imaging: Is the resting brain resting? *Current Biology, 16*, R998-R1000.

Michel, C. M., Murray, M. M., Lantz, G., Gonzalez, S., Spinelli, L., & Grave de Peralta, R. (2004). EEG source imaging. *Clinical Neurophysiology, 115*, 2195–2222.

Newen, A., & Vogeley, K. (2003). Self-representation: searching for a neural signature of self-consciousness. *Consciousness and Cognition, 12*, 529–543.

Nunez, P. L. (2000). Toward a quantitative description of large-scale neocortical dynamic function and EEG. *Behavioral and Brain Sciences, 23*, 371–398.

Nunez, P. L., & Silberstien, R. B. (2000). On the relationship of synaptic activity to macroscopic measurements: Does co-registration of EEG with fMRI make sense? *Brain Topography, 13*, 79–96.

Pavlova, L. P., & Romanenko, A. F. (1988). *Systemic Approach to Psychophysiological Investigation of Human Brain*. Leningrad: Nauka.

Pascual-Marqui, R. D. (2009). Theory of the EEG inverse problem. In S. Tong & N.V. Thakor (Eds.), Quantitative EEG Analysis Methods and Clinical Applications, (pp. 121-140). Artech House.

Raichle, M. E., & Gusnard, D. A. (2005). Intrinsic brain activity sets the stage for expression of motivated behavior. *Journal of Comparative Neurology, 493*, 167–176.

Raichle, M. E., & Snyder, A. Z. (2007). A default mode of brain function: A brief history of an evolving idea. *NeuroImage, 37*, 1083–1090.

Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, G. L. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America, 98*, 676–682.

Revonsuo, A. (2006). *Inner Presence: Consciousness as a Biological Phenomenon.* Cambridge, MA: MIT Press.

Rolls, E. T. (2000). The orbitofrontal cortex and reward. *Cerebral Cortex, 10*, 284–294.

Schilbach, L., Wohlschlaeger, A. M., Kraemer, N. C., Newen, A., Shah, N. J., Fink, G. R., et al. (2006). Being with virtual others: Neural correlates of social interaction. *Neuropsychologia, 44*, 718–730.

Schilbach, L., Eickhoff, S. B., Rotarska-Jagiela, A., Fink, G. R., & Vogeley, K. (2008). Minds at rest? Social cognition as the default mode of cognizing and its putative relationship to the "default system" of the brain. *Consciousness and Cognition, 17*, 457–467.

Shaw, J. C. (2003). *The Brain's Alpha Rhythms and the Mind.* Elsevier Science BV.

Shulman, G. L., Fiez, J. A., Corbetta, M., Buckner, R. L., Miezn, F. M., Raichle, M. E., et al. (1997). Common blood flow changes across visual tasks. II. Decreases in cerebral cortex. *Journal of Cognitive Neuroscience, 9*, 648–663.

Sims, A. C. P. (2003). *Symptoms in the Mind: An Introduction to Descriptive Psychopathology.* Elsevier Health Sciences.

Singer, W., & Gray, C. M. (1995). Visual feature integration and the temporal correlation hypothesis. *Annual Review of Neuroscience, 18*, 555-586.

Sporns, O., Honey, C. J., Kôtter, R. (2007). Identification and classification of hubs in brain networks. *PLoS ONE, 2*, e1049.

Spreng, R. N., & Grady, C. L. (2010). Patterns of brain activity supporting autobiographical memory, prospection, and theory-of-mind and their relationship to the default mode network. *Journal of Cognitive Neuroscience, 22*, 1112–1123.

Stam, C. J. (2005). Nonlinear dynamical analysis of EEG and MEG: Review of an emerging field. *Clinical Neurophysiology, 116*, 2266–2301.

Stern, J. M., & Engel, J. Jr. (2005). *Atlas of EEG Patterns.* Lippincott: Williams & Wilkins.

Svoboda, E., McKinnon, M. C., & Levine, B. (2006). The functional neuroanatomy of autobiographical memory: a meta-analysis. *Neuropsychologia, 44*, 218 9–2208.

Trehub, A. (2007). Space, self, and the theater of consciousness. *Consciousness and Cognition, 16*, 310-330.

Uddin, L. Q., Kelly, A. M. C., Biswal, B. B., Castellanos, X., & Milham, M. P. (2009). Functional connectivity of default mode network components: Correlation, anticorrelation, and causality. *Human Brain Mapping, 30*, 625–637.

Uhtomskiy, A. A. (1966). *Dominanta.* Moscow-Leningrad: Nauka.

Ugurbil, K. (2002). High-field magnetic resonance. In A.W. Toga & J.C. Mazzoitta (Eds.), Brain mapping. The methods. 2 edition (pp. 291–313). USA: Elsevier Science.

Ullsperger, M, & Debener, S. (2010). *Simultaneous EEG and fMRI. Recording, Analysis, and Application.* Oxford University Press.

van den Heuvel, M., Mandl, R., Luigjes, J., Hulshoff, P. H. (2008). Microstructural organization of the cingulum tract and the level of default mode functional connectivity. *Journal of Neuroscience, 28*, 10844-10851.

Varela, F., Lachaux, J. P., Rodriguez, E., & Martinerie, J. (2001). The brainweb: phase synchronization and large-scale integration. *Nature Reviews Neuroscience, 2*, 229-239.

Vogeley, K., & Fink, G. R. (2003). Neural correlates of the first-person-perspective. *Trends in Cognitive Sciences, 7*, 38–42.

Vogeley, K., May, M., Ritzl, A., Falkai, P., Zilles, K., & Fink, G. R. (2004). Neural correlates of first-person-perspective as one constituent of human selfconsciousness. *Journal of Cognitive Neuroscience, 16*, 817–827.

Vulliemoz, S., Thornton, R., Rodionov, R., Carmichael, D. W., Guye, M., Lhatoo, S., McEvoy, et al. (2009). The spatio-temporal mapping of epileptic networks: combination of EEG–fMRI and EEG source imaging. *NeuroImage, 46*, 834–843.

Wackermann, J., Allefeld, C. (2007). On the meaning and interpretation of global descriptors of brain electrical activity. Including a reply to X. Pei et al. *International Journal of Psychophysiology, 64*, 199–210.

Whitfield-Gabrieli, S., Thermenos, H., Milanovic, S., Tsuang, M., Faraone, S., McCarley, R., Shenton, M., et al. (2009). Hyperactivity and hyperconnectivity of the default network in schizophrenia and in first degree relatives of persons with schizophrenia. *Proceedings of the National Academy of Sciences of the United States of America, 106*, 1279-1284.

Windt, J., & Metzinger, T. (2007). The philosophy of dreaming and self-consciousness: What happens to the experiential subject during the dream state? In D. Barrett & P. McNamara (Eds.), *The New Science of Dreaming. Volume 3: Cultural and Theoretical Perspectives* (pp. 193-247). Westport, CT & London: Praeger Imprint/Greenwood Publishers.

Zahavi, D. (2002). First-person thoughts and embodied self-awareness: some reflections on the relation between recent analytic philosophy and phenomenology. *Phenomenology and the Cognitive Sciences, 1*, 7-26.

Zahn, R., Talazko, J., & Ebert, D. (2008). Loss of the sense of self-ownership for perceptions of objects in a case of right inferior temporal, parieto-occipital and precentral hypometabolism. *Psychopathology, 41*, 397-402.