

*Below is the unedited draft of the article that has been accepted for publication
(© Cognitive Processing, 2016, Volume 17, Issue 1, P. 27-37.)*

Long-Term Meditation Training Induced Changes in the Operational Synchrony of Default Mode Network Modules During a Resting State

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Abstract:

Using theoretical analysis of self-consciousness concept and experimental evidence on the brain default mode network (DMN) that constitutes the neural signature of self-referential processes we hypothesized that the anterior and posterior subnets comprising the DMN should show differences in their integrity as a function of meditation training. Functional connectivity within DMN and its subnets (measured by operational synchrony) has been measured in 10 novice meditators using an electroencephalogram (EEG) recording in a pre-/post-meditation intervention design. We have found that while the whole DMN was clearly suppressed, different subnets of DMN responded differently after four months of meditation training: The strength of EEG operational synchrony in the right and left posterior modules of the DMN decreased in resting post-meditation condition compared to a pre-meditation condition, whereas the frontal DMN module on the contrary exhibited an increase in the strength of EEG operational synchrony. These findings combined with published data on functional-anatomic heterogeneity within the DMN and on trait subjective experiences commonly found following meditation allow us to propose that the first-person perspective and the sense of agency (the witnessing observer) are presented by the frontal DMN module, while the posterior modules of the DMN are generally responsible for the experience of the continuity of ‘I’ as embodied and localized within bodily space. Significance of these findings is discussed.

Keywords:

Meditation; yoga; electroencephalogram (EEG); mind–body practice; self; self-referential processing; self-consciousness; functional connectivity; operational synchrony; operational modules; DMN

Abbreviations:

Quantitative electroencephalogram – qEEG; default mode network – DMN; operational module – OM; operational synchrony – OS; rapid transitional period – RTP; synchrocomplex – SC.

1. Introduction

For a long time the topic of self-consciousness (or self-awareness) was the exclusive domain of philosophy and only recently has it begun to take a more prominent place in the cognitive neuroscience and neuroimaging studies under the umbrella term of ‘*self-referential processing*’ (Musholt, 2013). Northoff et al. (2006) have argued that self-referential processing is common to distinct concepts of self in different knowledge domains. In this context the self-referential processing is the core of what constitutes the ‘*experiential self*’. The accumulation of empirical data in neuroscience (Craig et al., 1999; Kircher et al., 2000; Gusnard et al., 2001; Gusnard, 2005; Spreng and Grady, 2010; Fingelkurts and Fingelkurts, 2011; Qin and Northoff, 2011), including the study of direct causal relationship between brain activity and self-consciousness (Lou et al., 2010; Chen et al., 2013), has lead researchers to a suggestion that the brain *default mode network* (DMN) is a most probable neural correlate for the sense of self¹ (Christoff et al., 2003; Wicker et al., 2003; Gusnard, 2005; Buckner and Carroll, 2007; Schilbach et al., 2008; Fingelkurts et al., 2012).

The DMN is commonly defined as a set of interacting cortex areas, encompassing mostly left and right middle frontal gyri, bilateral frontal medial areas, left and right middle temporal and occipital gyri, and left and right precuneus, that are mostly active and functionally synchronized across a wide variety of self-related tasks and during the resting state when participants are engaged in self-generated thoughts and mind-wandering (Gusnard et al., 2001; Newen and Vogeley, 2003; Christoff et al., 2003; Northoff et al., 2006; Schilbach et al., 2008; Fingelkurts and Fingelkurts, 2011; Andrews-Hanna et al., 2014).

Capitalizing on these studies it has been suggested that the practice of meditation (which aims at reducing the prevalence of self-related thought chains and valuation) should reduce the activity of or synchrony within the DMN (Fell, 2012). In the initial attempts to verify this hypothesis it was indeed found that meditation inhibits activity of the DMN (Pagnoni et al., 2008; Ott et al., 2010; Brewer et al., 2011) and reduces functional connectivity between areas within DMN (Faber et al., 2004; Brewer et al., 2011; Lehmann et al., 2012; Taylor et al., 2013; Berkovich-Ohana et al., 2014). However, such findings might be biased by treating the entire DMN as a cohesive unit (where the dynamics of separate modules of DMN is masked). Indeed, in most DMN studies this network was considered as a single and homogenous unit that functions as a single whole (Uddin et al., 2009). At the same time, it

¹ This conclusion is further supported by evidence that DMN structured interactions do not exist in preterm infants (Fransson et al., 2007, 2009), are underdeveloped in infants (Gao et al., 2009) and develop an adult-like structural patterns only by age 7–9 (Fair et al., 2008; Thomason et al., 2008). The role of the DMN in supporting self-conscious experience is also confirmed by empirical evidence from patients with disorders of consciousness (Laureys 2005; Vanhaudenhuyse et al., 2010; Fingelkurts et al., 2012), as well as during anesthesia (Greicius et al., 2008) and brain death (Boly et al., 2009).

seems very unlikely that multiple spatially distinct regions that comprise DMN are responsible for just one function, being essentially redundant (Andrews-Hanna et al., 2014). Much more plausibly, different DMN regions serve complementary functions that in combination give rise to a large variety of self-related mentations and processes (for example, self-location, first-person perspective and agency, self-reflection, self-referential narrative thinking, autobiographical thoughts, planning aspects of personal future, and so on).

Recent evidence suggests that the DMN is indeed a heterogeneous brain system composed of at least three separable yet interacting components or subnets (Uddin et al., 2009; Andrews-Hanna et al., 2010; Spreng and Grady, 2010; Leech et al., 2011; Fingelkurts and Fingelkurts, 2011). In our own previous studies we have found three subnets (or operational modules – OMs, as we call them) within DMN (Fingelkurts and Fingelkurts, 2011): two symmetrical occipito-parieto-temporal OMs and one frontal OM. Comparing healthy fully-conscious subjects with patients in vegetative and minimally conscious states, we also documented that these modules react in a slightly different manner as a function of self-consciousness presence (Fingelkurts et al., 2012): While the strength of functional connectivity decreased dramatically in vegetative patients (who are unconscious) in all three OMs, it was minimal within the frontal OM that nearly ceased to exist. Such strength was intermediate in patients who were in a minimally conscious state when compared to patients in vegetative state and healthy fully conscious subjects (Fingelkurts et al., 2012). Moreover, only frontal OM could reliably predict recovery of self-consciousness six years later (Fingelkurts et al., in press). Based on the functional distinctions between these three DMN OMs (Fingelkurts and Fingelkurts, 2011), one could predict that the anterior and posterior OMs comprising the DMN should show differences in their integrity as a function of meditation training.

Therefore, **the aim of this study** was to analyze the DMN OMs individually to reveal whether there are important trait differences in the resting-state functional connectivity within different OMs in a pre-/post- meditation intervention design. Given the functional specialization of frontal and parietal OMs (Fingelkurts and Fingelkurts, 2011), we hypothesized that after long-term meditation training the strength of integrity (functional connectivity) within the frontal OM should increase, while it should decrease in the occipito-parieto-temporal OMs. Furthermore, we expected to see much stronger decrease of the functional connectivity strength in both posterior OMs, than increase of integrity in the single frontal OM, thus resulting in an overall decrease (in congruence with the previous studies: Faber et al., 2004; Brewer et al., 2011; Lehmann et al., 2012; Berkovich-Ohana et al., 2014) in the functional connectivity of the DMN taken as a whole.

EEG is informationally rich signal and there are many EEG characteristics that could be measured pre- and post-meditation, but our interest in this particular study was to investigate how

operational synchrony within three separate modules of DMN will be affected by the long-term meditation training.

2. Methods

2.1. Subjects

Ten (average age = 51.7 ± 10.9 , four males) healthy, right-handed subjects participated in the study. The authors recruited participants (novices) from a four-month training course in meditation who have passed inclusion/exclusion criteria. The subjects had no history of head trauma, no current/past psychiatric disorders, no psychoactive medication or drug use, and also had normal or corrected to normal vision. Inclusion criteria to be recruited for this study were (a) be in good general, neurological and psychological/psychiatric health, (b) never practice any meditation technique before entry to the study. Exclusion criteria comprised (a) stressful events during the course of meditation training, (b) change of job, place of residence, or preoccupation during the course of meditation, (c) change of life-style or a diet during the course of meditation training, (d) any serious disorder during the course of meditation.

Participants signed an informed consent form after the experimental procedures were explained, prior to electroencephalogram (EEG) scanning. The study complied with the Code of Ethics of the World Medical Association (Declaration of Helsinki) and standards established by the organization Review Board. The use of the data for scientific studies was authorized by means of written informed consent of the subjects approved by the Review Board.

2.2. EEG Recording and Trial Design

The subjects' EEG was recorded with a 21-channel EEG data acquisition system (Mitsar, St. Petersburg, Russian Federation). EEG data were collected (linked earlobes as a reference electrode; 0.5–30 Hz bandpass; 50 Hz notch filter ON; 250 Hz sampling rate; 6 min closed eyes) in subjects during a waking resting state with eyes closed from 19 electrodes positioned according to the International 10–20 system (i.e., O₁, O₂, P₃, P₄, P_z, C₃, C₄, C_z, T₃, T₄, T₅, T₆, F_z, F₃, F₄, F₇, F₈, F_{p1}, F_{p2}). The impedance of recording electrodes was always below 5-10 kΩ. Eye movements was registered with an electrooculogram (0.5–70 Hz bandpass), which was recorded alongside the EEG.

All EEG recordings were done in late morning for all subjects. The subjects were asked to relax and engage in no specific mental activity, and to not apply any specific relaxation or meditation techniques during the EEG recording. The first EEG recording (marked as a *pre-meditation*) was recorded within one week before meditation training course commenced. Meditation training lasted

four months and required 20 minutes of daily meditation. We were not interested in the specific and immediate effects of different meditation techniques ('state' effect²) but rather in a general and long-lasting effect ('trait' effect³) common for any meditation such as entering into a relaxed and at the same time alert state of mind where one feels to be really present in the moment and is able to observe his/her body, emotions and thoughts (or physiological, emotional and mental contents) in a fresh and approving manner (see also, Fischer, 1971; Goleman, 1996; Hinterberger et al., 2011; Raffone et al., 2014). For that purpose, initially all of the participants were given the basics of an ancient Kriya yoga practice which contains various meditational methods like following the breath, noticing certain points in the body, recitation and visualization (Nash and Newberg, 2013). Within the first week of supervised training by the experienced instructor, participants found and chose their preferred technique/method for the rest of the course. The second EEG (marked as a *post-meditation*) was recorded within one week after 4-month meditation training has been terminated. Parameters and conditions of this second EEG recording were identical to those of the first EEG recording.

Such design of the study allowed us to avoid the multiple control conditions for possible confounding factors and specific meditation techniques that would make this study unfeasible. All unstructured factors (such as different life-styles, diets, stress levels, specific meditation techniques) that did not systematically relate to a general (and common) trait effect of meditation on DMN would cancel out when averaged between different subjects. Trait features of the resting-state condition associated with DMN and influenced by meditation would stand out because the meditation (irrespective of a concrete technique) is the only common factor among all subjects during very long time (four months). Additionally, the resting-state condition permits assessment of "pure" self-relevant brain activity (Koenig et al., 2002) such as spontaneous processing of an internal mental context (top-down processing) (Von Stein and Sarnthein, 2000), related episodic memory (Shulman et al., 1997), imagery (Fletcher et al., 1995), internal 'narrative,' and 'autobiographical' self (Gusnard et al., 2001; Johnson et al., 2002; Buckner and Carroll, 2007).

2.3. EEG-Signal Data Preprocessing

The presence of an adequate EEG signal was determined through visual inspection of the raw signal. Epochs containing artefacts due to eye movement/opening, significant muscle activity, and movements on EEG channels, as well as drowsy and sleep episodes were marked and then automatically rejected from further analysis.

² State effect refers to altered sensory, cognitive, and neurophysiological effects that can arise during meditation practice (Cahn and Polich, 2006).

³ Trait effect refers to lasting changes in altered sensory, cognitive, and neurophysiological effects that persist in the meditator irrespective of being actively engaged in meditation at the moment (Cahn and Polich, 2006).

A full EEG stream for each subject free from any artifacts was fragmented into consecutive 1-min epochs (5-6 one-minute EEG epochs for different subjects). The division of the EEG stream into a 1-min intervals permitted us to obtain a relatively large number of the analysis epochs (within which we searched for the naturally accruing quasi-stationary segments, see subsection 2.4. below) – this was important for the unbiased estimate of the operational synchronicity index (its computation requires enough data samples). Such an approach is justified because there are no fixed positions in the EEG, and we can therefore divide it into any number of epochs with a length appropriate for the particular experiment and analysis. More details and justifications could be found in Fingelkurts and Fingelkurts (2008). Further data processing was done separately for each 1-minute epoch of the signal.

Due to the technical requirements of the tools used to process the data, EEGs were re-sampled to 128 Hz. This procedure should not affect the results since 128 Hz sampling rate meets the Nyquist Criterion (Faulkner, 1969) of a sample rate greater than twice the maximum input frequency for the alpha activity, thus avoiding aliasing and preserving all the information about alpha activity in the input signal. This method was considered sufficient since the sampling rate of the source signals was significantly higher than required.

After re-sampling and prior to further processing procedures, each EEG signal was bandpass-filtered (Butterworth filter of the sixth order) in the alpha (7–13 Hz) frequency band. Phase shifts were eliminated through forward and backward filtering. The alpha frequency band was chosen for several reasons. First, it has been repeatedly demonstrated that the DMN has significant positive correlation with alpha rhythm⁴ (Laufs et al., 2003; Mantini et al., 2007; Jann et al., 2009) and that the alpha band independent component of EEG-signal showed the highest spatial correlation to the DMN template when compared to other EEG bands (Knyazev et al., 2011). Second, alpha oscillations dominate EEG of humans in the absence of external stimuli when internal life (mind-wandering and spontaneous thoughts) is most pronounced (Shaw, 2003; Palva and Palva, 2007; Klimesch et al., 2007; Basar and Guntekin, 2009; Fingelkurts and Fingelkurts, 2010, 2014). Thirdly, it has been shown that operational connectivity within the DMN (identified by EEG alpha band) was smallest or even absent in patients in vegetative state, intermediate in patients in minimally conscious state and highest in healthy fully self-conscious subjects (Fingelkurts et al., 2012).

⁴ Though there are some studies where correlation of DMN with other frequency bands has been found (Berkovich-Ohana et al., 2012, 2014; Neuner et al., 2014), the positive correlation of DMN with alpha band is the most reproducible.

2.4. Estimation of DMN OMs and Their Strength

As it has been proposed in our earlier study (Fingelkurts and Fingelkurts, 2011) and confirmed in subsequent work (Fingelkurts et al., 2012) a constellation of nine operationally synchronized cortical areas indexed by 3 distinct OMs (*frontal OM*: F₃-F_z-F₄; *left posterior OM*: T₅-P₃-O₁; and *right posterior OM*: T₆-P₄-O₂) could account, in large part, for the DMN. Therefore, in this study the following EEG positions (and correspondent to them cortical areas, Koessler et al., 2009) were used to estimate the operational synchrony within such OMs: EEG positions F₃ and F₄ (left and right middle frontal gyri or Brodmann's area 8), EEG position F_z (bilateral medial areas or Brodmann's area 6), EEG positions T₅ and T₆ (left and right middle temporal gyri or Brodmann's area 21), EEG positions P₃ and P₄ (left and right precuneus or Brodmann's area 19), and EEG positions O₁ and O₂ (left and right middle occipital gyri or Brodmann's area 18). The anatomical correlations of EEG electrode positions used were taken from the reference study of Koessler et al. (2009), where a clear match between the EEG electrode positions and anatomical areas of the cortex was clearly established and verified through an EEG-MRI sensor system and an automated projection algorithm (see also Kaiser, 2000 for the correlations between EEG activity in a given electrode position and its correspondent cortical area).

In order to estimate the operational synchrony and its strength within given DMN OMs as well as within the 'whole DMN', several stages of data processing are required. The details of these procedures could be found elsewhere (Fingelkurts and Fingelkurts, 2008, 2015). Therefore, here we provide only a brief overview of main steps. At the **first step**, each local EEG signal was reduced to a temporally organized sequence of nearly stationary (quasi-stationary) segments of various duration (~300 ms in average for alpha rhythm). To uncover these quasi-stationary segments from the complex nonstationary structure of local EEG signals, an *adaptive segmentation procedure* was used (Fingelkurts and Fingelkurts, 2008, 2015). The aim of the segmentation is to divide each local EEG signal into naturally existing quasi-stationary segments by estimating the intrinsic points of 'gluing' – rapid transitional periods (RTPs). An RTP is defined as an abrupt change in the analytical amplitude of the signal above a particular threshold which is computed based on statistical procedures which have been experimentally established in modeling and empirical studies (Fingelkurts and Fingelkurts, 2008, 2015). The RTPs themselves are very short in duration when compared to the quasi-stationary segments, and therefore can be treated as a point or near-point (Fingelkurts and Fingelkurts, 2008, 2015). It has been proposed that each homogeneous segment in the local EEG signal corresponds to a temporary stable microstate – an *operation* executed by a neuronal assembly (Fingelkurts et al., 2010). The temporal coupling (synchronization) of such segments among several local EEG recordings then, reflects the synchronization of operations (i.e. *operational synchrony*) produced by

different neuronal assemblies, which are located in different cortex regions, into integrated and unified patterns responsible for complex mental operations (Fingelkurts et al., 2010).

Estimation of operational synchrony signifies the **second step** of analysis. Measurement of operational synchrony estimates the statistical level of RTP temporal coupling between two or more local EEG recordings (Fingelkurts and Fingelkurts, 2008, 2015). The measure tends toward zero if there is no synchronization between EEG segments derived from different EEG channels and has positive or negative values where such synchronization exists. Positive values (above upper stochastic threshold) 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 a computer simulation), whereas negative values (below lower stochastic threshold) mark ‘active’ decoupling of segments (synchronization of EEG segments is observed significantly less than expected by chance as a result of random shuffling during a computer simulation) (Fingelkurts and Fingelkurts, 2008, 2015). The *strength of EEG operational synchrony* is proportional to the actual (absolute) value of measure: The higher this value, the greater the strength of functional connection.

Using pair-wise analysis, operational synchrony was identified in several (more than two) channels – synchrocomplexes (SC); these define operational modules – OMs. The criterion for defining an OM is a sequence of the same synchrocomplexes (SC) during each 1-min epoch, whereas a SC is a set of EEG channels in which each channel forms a paired combination with valid values of synchrony with all other EEG channels in the same SC; meaning that all pairs of channels in an SC have to have statistically significant synchrony linking them together (Fingelkurts and Fingelkurts, 2008, 2015).

The measure of operational synchrony is sensitive to the morpho-functional organization of the cortex rather than to volume conduction and is independent of the signal power (Fingelkurts and Fingelkurts, 2008, 2015).

2.5. Statistics

The strength of functional connectivity within the DMN and individual DMN OMs was assessed using EEG operational synchrony (see previous subsection). The differences in strength of operational synchrony between different conditions (pre-meditation and post-meditation) were assessed using Wilcoxon Matched Pairs Test, which is used in the majority of functional connectivity studies (for the overview, see Weiss and Rappelsberger, 2000). At first, all strength values of EEG operational synchrony were averaged within each OM for all 1-min EEGs of all subjects per condition (pre-meditation or post-meditation). During the final stage an average of operational

synchrony strength values for the whole DMN (includes all three OMs) was calculated for each condition.

3. Results

We observed a significant decrease ($p < 0.01$) in the average strength of EEG operational synchrony within the DMN taken as a whole in post-meditation condition compared to a pre-meditation condition (Fig. 1). Analysis of separate subnets of DMN (indexed as OMs) revealed that while right and left posterior OMs had a significant decrease in the strength of EEG operational synchrony in post-meditation condition compared to a pre-meditation condition ($p < 0.001$ for the right OM; $p < 0.01$ for the left OM), the frontal OM on the contrary exhibited a mild but statistically significant increase ($p < 0.05$) in the strength of EEG operational synchrony (Fig. 1).

Decreases or increases in the operational synchrony (congruent with a group level) have been found in 9 participants from 10 (though, for different OMs the single participant who did not show difference between pre-post conditions was always different). Note that the topological distribution was always the same – three modules for each participant.

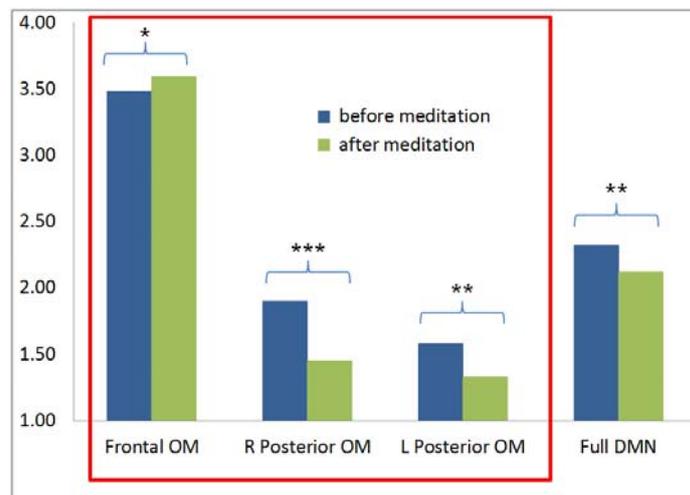


Figure 1. EEG operational synchrony strength within the DMN and its subnets (OMs) as a function of meditation training. DMN – default mode network; OM – operational module; R – right; L - left. Y-axis indicates the strength of EEG operational synchrony. * – $p < 0.05$; ** – $p < 0.01$; *** – $p < 0.001$. Due to very small values of standard error for all means, their values presented in the legend and not on the graph. Standard error of the means: Frontal OM before meditation: 0.01 / after meditation: 0.01; Right posterior OM before meditation: 0.02 / after meditation: 0.03; Left posterior OM before meditation: 0.02 / after meditation: 0.02; Full DMN before meditation: 0.02 / after meditation: 0.02.

4. Discussion

Using operational synchrony analyses of resting-state EEG data, we examined differentiation of functional connectivity of subnets within the DMN as well as dynamics of the functional connectivity of the whole DMN in a pre-/post- meditation training design. Our results indicated that while there was an overall decrease in the functional connectivity of the whole DMN after 4-month meditation training, – a finding compatible with previous studies (Faber et al., 2004; Brewer et al., 2011; Lehmann et al., 2012; Taylor et al., 2013; Berkovich-Ohana et al., 2014), – a significant functional differentiation of separate DMN OMs was present (Fig. 1). Only right and left posterior OMs had decreased strength of EEG operational synchrony in post-meditation condition compared to a pre-meditation condition, whereas the frontal OM on the contrary had increased strength of EEG operational synchrony (Fig. 1). These findings reveal that the phenomenon of DMN-change as a function of meditation is more complex than previously thought. They pointed to a conclusion that *the DMN is comprised of multiple subsystems, each contributing to specific processes that characterize different aspects or qualities of self-referential thought*. Given the functional-topographical heterogeneity of OMs within the DMN (Fingelkurts and Fingelkurts, 2011; see also Uddin et al., 2009; Andrews-Hanna et al., 2010, 2014; Doucet et al., 2011; Yeo et al. 2011) combined with meditation training induced specific changes in the functional connectivity within separate OMs (Fig. 1), and keeping in mind that the phenomenon of self-awareness is multi-faceted (Musholt, 2013), one could speculate about the specific qualities that contribute to different aspects of self-referential thought and the sense of self.

The major finding that deserves explanation is the functional connectivity increase found in the frontal OM of the DMN as a result of meditation training. To understand this result we need to consider multiple aspects of the self. It could be plausibly divided into *being a self* (i.e., being a subject of self-conscious experience) and *being cognitive of being a self* (i.e., being able to represent and reflect on oneself) (Musholt, 2013). While the former consists in having a first-person perspective, the latter requires the ability to think about oneself as such and to explicitly represent one's own perspective, including autobiographical memories (Musholt, 2013). Based on the available data from literature, we argue that the first-person perspective and the sense of agency⁵ (the

⁵ Even though some researchers attribute to the term 'agency' just the active (volitional) control or action, the term is much broader. Starting from the early phenomenologists like Merleau-Ponty or Husserl, the agency is understood as 'mines', or the 'sense of ownership' of thoughts, perceptions, and actions relevant to selfhood (Metzinger, 2004; de Vignemont and Fournier, 2004; Hohwy, 2007; Blanke and Metzinger, 2009). In other words agency means the sense that it is 'I' who is undergoing an experience in its implicit first-person mode of givenness (Gallagher, 2000; Zahavi, 2005). It is this 'self-ownership' that has been claimed to be the most fundamental aspect of phenomenal selfhood

witnessing observer) are presented by the frontal OM, while the posterior OMs are generally responsible for the experience of the continuity of ‘I’ as embodied and localized within bodily space (Fingelkurts and Fingelkurts, 2011).

Indeed, the brain structures participated in the frontal OM have been shown to be involved in a complete self-consciousness (Uhtomskiy, 1966; Andrews-Hanna, 2012; Moran et al., 2013), where one feels directly present as the center of an externalized multimodal perceptual reality (for instance, the objects in one’s environment or phenomenal emptiness are always presented in a certain distance and orientation from oneself) (Sims, 2003; Revonsuo, 2006; Trehub, 2007). Interestingly, the sense of such a ‘center’ is never lost even in deep meditation (or sleep) and is repeatedly described as ‘the unbroken experience of existence attained by the still mind’ or a ‘samadhi’ state and is the highest aim of many different meditation techniques (Nash and Newberg, 2013, Raffone et al., 2014). From this perspective it is not surprising that long-term meditation leads to an increased integrity in the frontal OM of the DMN. Several other functions of the areas involved in the frontal OM could also explain its enhancement after the course of meditation training.

Many studies documented that meditators report the development of an unconditional feeling of loving-kindness and compassion as a result of meditation training (Ricard et al., 2014). It is the frontal DMN subnet that has been repeatedly shown to be involved in these experiences (Lutz et al., 2008; Davidson, 2010; Travis and Shear, 2010; Mascaro et al., 2013; Li et al., 2014). Furthermore, a number of neuroimaging studies have demonstrated the crucial role of the frontal brain areas in empathy (Eslinger, 1998), positive affect (Nitschke et al., 2004; Phan et al., 2004) and extreme joy (Blood and Zatorre, 2001; Arnow et al., 2002; Hagerty et al., 2013) all of which are reported to emerge as the meditation effects⁶ (Nash and Newberg, 2013; Ricard et al., 2014).

The chief role of the frontal DMN OM in self-referential processing was documented in the study of patients with disorders of consciousness (those who are in vegetative or minimally conscious states) (Fingelkurts et al., 2012). It was demonstrated that the frontal DMN OM had the strongest decrease in operational synchrony strength as a function of self-consciousness loss, when compared with the posterior DMN OMs. As the result of these findings it has been proposed that the frontal DMN module most likely provides a critical self-related context (experience of agency) for all human behaviors and activities (Fingelkurts and Fingelkurts, 2011). This conclusion is also in line with the fact that the frontal brain areas are reciprocally connected with nearly all other cortical, subcortical,

(Gallagher, 2000; Aspell et al., 2009; Blanke and Metzinger, 2009). In such conceptualization the agent could be a passive observer, who just witnesses events, perceptions or thoughts in its implicit first-person mode of givenness.

⁶ While usually meditation effects considered to be positive and beneficial, they could become maladaptive and negative if overexpressed in individuals with a particular set of constitutional neurophysiological characteristics (for a detailed analysis see Fingelkurts et al., 2015).

and brainstem structures (Fuster, 1993; Noack et al., 2012), and thus, represent some kind of a hub which integrates motivational, emotional, sensory, motor, and mnemonic information (Barbas, 2000), serving as the ‘observing self’ to maintain any conscious state (Baars et al., 2003; Fingelkurts and Fingelkurts, 2011; Qin and Northoff, 2011; Noack et al., 2012).

Another finding of the present study that fully confirmed our prediction was the marked decrease in the integrity of posterior DMN subnets (Fig. 1). The following interpretation of this result could be suggested based on the available literature about subjective experiences of meditators. Many meditators report the sense of ‘absolute unitary being’ or ‘self-boundarylessness’, or loss of bodily perceptions (Newberg et al., 2001; Newberg and Iversen, 2003). We suggest that such subjective experiences when practiced systematically in the course of meditation training may result in the long-lasting diminished integrity (measured by functional connectivity) of the occipito-temporal-posterior DMN subnets (indexed as posterior OMs) as was found in the present study. More specifically, we propose that decreased functional connectivity within these posterior OMs is responsible for diminished experience of embodiment and localization of the continuity of ‘I’ within bodily space. Indeed, the brain areas comprising the left and right posterior OMs have been shown to be involved in the body self-consciousness (Haggard et al., 2003; Jeannerod, 2007) as well as interoceptive and exteroceptive bodily sensory processing (Damasio, 1999; Critchley et al., 2004); and the dysfunctions in such areas have been causally associated with out-of-body experiences (Blanke et al., 2002; Ionta et al., 2011). Such conceptualization is in line with the studies of subjective experience during the acute intensive meditation. It has been documented that in the acute intensive meditation some meditators have reported achieving a state of complete loss of body ownership, where the body no longer being perceived as belonging to the ‘self’ (Dor-Ziderman et al., 2013), which is strikingly similar to the subjective experiences during de-personalisation syndrome (Berlucchi and Aglioti, 1997).

Furthermore, since the temporal areas that participate in the posterior OMs have been shown to contribute to the integration of an object or self into a situation model, including a particular time, place, and context, including autobiographical memories (Patterson et al., 2007; Walker et al., 2007; Binder and Desai, 2011; Múnera et al., 2014), we may propose that the lack of functional integration of such areas with other areas of the posterior OMs found in the present study as a result of meditation training is consistent with frequently reported subjective feelings of meditators such as peaceful state of mind, diminishing of ego borders and narrative thoughts⁷, transcending, expanded consciousness, all-oneness, etc (Fischer, 1971; Goleman, 1996; Hinterberger et al., 2011). Such

⁷ Interestingly, narrative thoughts and mind wandering has been linked to negative emotions (Smallwood et al., 2009) and a sense of unhappiness (Killingsworth and Gilbert, 2010; Fell, 2012).

subjective effects of meditation are considered useful to cope with stress and responsible for the fact that today, elements of meditation have been implemented in several therapeutic systems, such as stress reduction (Ludwig and Kabat-Zinn, 2008) or cognitive therapy (Shonin et al., 2014).

To summarize, it is important to keep in mind that these separate modules of DMN *persistently exist in parallel* (Fingelkurts and Fingelkurts, 2011) suggesting that these three OMs are functionally integrated with one another within the common neuronal spatial–temporal network (i.e., DMN), and they are likely to interact or co-occur during many self-generated experiences (Andrews-Hanna, 2012) to support much of the mental content underlying self-referential mentation or thought and form a *coherent framework of a sense of self* (Uddin et al., 2009; Fingelkurts and Fingelkurts, 2011; Andrews-Hanna et al., 2014).

5. Conclusion, Significance and Limitations

The study of self is very broad due to the multi-faceted nature of self-consciousness phenomenon itself (Musholt, 2013). The accumulated evidence suggests that the core of the experiential self is constituted by self-referential processes (Northoff et al., 2006), that are represented (neurophysiologically) through operationally integrated DMN of the brain (Christoff et al., 2003; Wicker et al., 2003; Gusnard, 2005; Buckner and Carroll, 2007; Schilbach et al., 2008; Qin and Northoff, 2011). It is further suggested that such DMN could be a ‘neural signature’ of self-referential processes with a control function of the overall behavior from a first-person perspective (Fingelkurts and Fingelkurts, 2011); meaning that the DMN maintains a first-person perspective for any information or stimuli for perceiving, interpreting, responding to, remembering and even predicting environmental demands or envisioning the future (Raichle, 2006).

Since the practice of meditation aims to reduce the prevalence of self-related thought chains and dissolution of ego borders, it is commonly hypothesized that it should reduce the activity of or synchrony within the DMN (Fell, 2012). At the same time, in light of the recent evidence on DMN heterogeneity (Uddin et al., 2009; Andrews-Hanna et al., 2010; Spreng and Grady, 2010; Leech et al., 2011; Fingelkurts and Fingelkurts, 2011; Salomon et al., 2014) we expected that while the whole DMN should be clearly suppressed, it is possible for different subnets of DMN to respond differently to the meditation training. Considering the functional differentiation of separate DMN subnets (Andrews-Hanna et al., 2010, 2014; Doucet et al., 2011; Yeo et al. 2011; Fingelkurts and Fingelkurts, 2011) we specifically predicted that functional connectivity within the frontal DMN module should increase, while the functional integrity of bilateral posterior modules of DMN should decrease as a function of four-month meditation training.

The results of the present study fully support our predictions (Fig. 1). Such opposing changes induced by the meditation training in the functional connectivity within the frontal and posterior modules of DMN integrated with published data on functional-anatomic heterogeneity within the DMN and on trait subjective experiences commonly found following meditation allow us to propose that the first-person perspective and the sense of agency (the witnessing observer) are most likely represented by the frontal DMN OM, while the posterior OMs are generally responsible for the experience of the continuity of ‘I’ as embodied and localized within bodily space. Specifically, increased integrity of the frontal and decreased integrity of posterior DMN modules may give a neural explanation to the well-known subjective experiences of meditation training as ‘the unbroken experience of existence attained by the still mind’ (Nash and Newberg, 2013), avoidance of intruding unintended thoughts with simultaneous unconditional feeling of loving-kindness and compassion (Ricard et al., 2014) and decreased disturbing interoceptive and exteroceptive bodily sensations (Newberg et al., 2001; Newberg and Iversen, 2003).

Our analysis of the putative functions served by separate DMN modules suggests that such a net comprises multiple but interacting subsystems, each contributing specific functions or qualities characterizing self-referential processing. These findings have several implications.

In the *theoretical domain*, our findings add more evidence that the DMN consists of functionally differentiable but interacting subdivisions or subnets and that analyzing each subnet (or module) individually will lead to a richer understanding of the functions of the DMN and the phenomenon of self. In the *clinical domain*, characterization of each of the subnets of the DMN in various clinical populations may provide greater insights into which region of the default mode is compromised the most in clinically impaired individuals, and thus provide further information about the underlying neuropathology of a concrete pathological condition.

The main limitation of the present study is the lack of subjective reports reflecting the phenomenological experience of the participants. The interpretations of the current findings were done based on the published data about the trait subjective experiences commonly found following meditation. Even though such approach is valid, future studies should adopt a neurophenomenological study design (Lutz and Thompson, 2003), incorporating both EEG recordings and first-person descriptions of the same subjects. Another limitation is the small sample of participants; thus, the results of the present study warrant replication in a larger group. Additionally it would be interesting to perform the same analysis of separate DMN subnets as in the present study but separately for different meditative traditions.

Yet another potential limitation could be the absence of a control group. The design of the study makes such a group unnecessary. Our study was longitudinal – subjects were required to meditate 20

min daily for a period of 4-month training course. Considering such a long period and completely different life-styles of participants, as well as the multitude of inter-subject independent events happening during this period, the only common factor was a daily meditation. Since all possible other (not related to meditation) factors are random (in relation to the aims of the present study, as well as among the subjects) it is very unlikely that they may produce any common effect. On the contrary, they should cancel effect of each other at the group level. The fact that we have got statistically significant result (in fact 9 from 10 subjects show decreases/increases in the same direction as for the group level for each studied OM), which confirms the initial hypothesis, signifies that the effect is related to a mediation (the only common factor present during very long period in all subjects) and not to a random interference of other possible factors.

Acknowledgments

The authors did not receive funding for this study. The authors would like to thank Dmitry Skarin for language editing and all participants of the meditation training course. Special thanks go to Tapio Saarinen with whom the authors discussed DMN-related aspects, which then motivated the authors to conduct this study.

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