Research Report

The default mode network and EEG alpha oscillations: An independent component analysis

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ABSTRACT

The default mode network (DMN) has been principally investigated using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) and has received mixed support in electroencephalographic (EEG) studies. In particular, the existing evidence is too inconsistent to allow formulation of specific hypotheses linking DMN activity to traditional EEG frequency bands. In this study, we aimed to test whether blind decomposition methods are able to identify in EEG data spatial patterns resembling the DMN as it is described in PET and fMRI studies. Further we aimed to test a degree of task-relatedness of DMN patterns identified in the traditional EEG frequency bands. To answer these questions we collected data both in a resting state and during performance of two experimental tasks: an explicit judgment of facial affect and a social game task. Individual differences in amount of self-referential thoughts during the resting state were measured by a short self-report scale. Only alpha band spatial patterns simultaneously showed a considerable overlap with the DMN and high correlations with presumptive DMN function-related outcomes both in the resting state and during the social game task. Spontaneous self-referential thoughts were associated with enhanced alpha activity in the posterior DMN hub, whereas processing of DMN function-related external stimuli disrupted this activity and simultaneously caused partial alpha phase-locking to external events. This evidence implies that synchronization of internal mental processes, as opposed to the processing of external stimuli, might be the primary function of alpha oscillations which is bound to be related to activity of the DMN.

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1. Introduction

The default mode network (DMN) concept was first introduced in 2001 (Raichle et al., 2001) and has rapidly become a central theme in cognitive neuroscience. This concept comes from an emergent body of evidence showing a consistent pattern of deactivation across a network of brain regions that occurs during the initiation of task-related activity (Raichle et al.,...
The DMN includes the precuneus/posterior cingulate cortex (PCC), the medial prefrontal cortex (MPFC), and medial, lateral, and inferior parietal cortices. Although deactivated during task performance, this network is active in the resting brain with a high degree of functional connectivity between regions. The more demanding the task the stronger the deactivation appears to be (McKiernan et al., 2006; Singh and Fawcett, 2008). A notable exception to this general pattern of deactivation during goal-directed activity occurs in relation to tasks requiring self-referential thought and social cognition (Gobbini et al., 2007; Mitchell, 2006). Mitchell (2006) suggested that social cognition is one of the functions of the DMN. DMN was shown to be activated during social interaction task as compared to a non-social control task sharing many of the same features (Rilling et al., 2004; 2008). In spite of this body of evidence suggesting that some aspect of DMN activity may be related to social cognition, this needs to be also considered in light of other evidence, showing the robustness of coherent DMN activity fluctuations even under conditions of sedation and general anesthesia (e.g., Greicius et al., 2008; Vincent et al., 2007). Vincent et al. (2007) suggest that these coherent system fluctuations probably reflect an evolutionarily conserved aspect of brain functional organization that transcends levels of consciousness.

In order to draw out the relevant and appropriate implications from the above presented findings, the key methodological issues should be taken into account. The DMN has been principally investigated using functional magnetic resonance imaging (fMRI, e.g. Greicius et al., 2003; 2004; 2007), although positron emission tomography (PET, e.g. Raichle et al., 2001) and electrophysiology (e.g. Helps et al., 2008; Laufs et al., 2003b; Scheeringa et al., 2008) have also been employed. Although fMRI blood oxygen level dependent (BOLD) signal imaging is ideal for providing a representation of the spatial organization of brain function, it is as yet unclear how these changes relate to concurrent changes in the spatial extent and magnitude of neuronal events (Debener et al., 2006). The aspect of neuronal activity which best predicts changes in BOLD contrast (i.e., combined neuronal spiking, local field potentials, changes in spontaneous rhythms, etc.) has not been established definitely (Huettel et al., 2004). Hence there may be a degree of incongruence between hemodynamic and electrophysiological signals. Moreover, despite the excellent spatial resolution of fMRI, the temporal resolution is poor. In contrast, electroencephalogram (EEG) has excellent temporal resolution in which electrophysiological correlates of spontaneous or event-related changes in neuronal activity may be examined. Researchers have examined DMN activity in terms of traditional bands of EEG activity (Chen et al., 2008) and in terms of very slow EEG frequencies (Helps et al., 2008; Vanhatalo et al., 2004). Chen et al. (2008) compared the spatial distribution and spectral power of seven bands of resting state EEG activity, in eyes closed and eyes open condition. They termed the defined set of regional and frequency specific activity, the EEG default-mode network (EEG-DMN), and propose that the EEG-DMN should now be examined in the context of task-induced demands and in patient groups.

Simultaneous EEG–fMRI allows the empirical determination of the degree of overlap between EEG and fMRI BOLD signal. This growing body of literature has noted correlations between the DMN and gamma (Mantini et al., 2007), beta (Laufs et al., 2003b; Mantini et al., 2007), alpha (Laufs et al., 2003a; Mantini et al., 2007), and theta (Meltzer et al., 2007; Scheeringa et al., 2008). Mid-range beta (17–23 Hz) was strongly correlated with task-independent deactivations in PCC, precuneus, temporo-parietal and dorsomedial prefrontal cortex (Laufs et al., 2003b). In view of the lack of association between alpha and resting state brain activity, Laufs et al. (2003b) hypothesize that alpha may act as a baseline for specific brain structures associated with the attentional system, and more specifically the task-positive network (Laufs et al., 2006). In contrast, Mantini et al. (2007) reported positive correlations between beta (13–30 Hz) and alpha (8–13 Hz) with the PCC, precuneus, bilateral superior frontal gyrus and the medial frontal gyrus. Further, regions in the DMN associated with self-referential processing such as the medial prefrontal cortex (MPFC) were positively correlated with gamma (30–50 Hz; Mantini et al., 2007). In addition, medial frontal theta power changes were negatively correlated with the BOLD response in medial frontal regions, PCC/precuneus, and bilaterally in inferior frontal, inferior parietal and middle temporal cortices and the cerebellum (Scheeringa et al., 2008). Further, Meltzer et al. (2007) found that frontal-medial theta was most strongly negatively correlated with the MPFC, although negative correlations were also found with other DMN areas such as PCC.

The observed weak to moderate correlations between regions associated with the DMN and a variety of EEG frequency domain features do not necessarily support the idea that any feature in the EEG has the DMN as a specific source. Moreover, it might be questioned whether the DMN actually exists as a source in the EEG. Perhaps, as Chen et al. (2008) suggest, instead of trying to find out a correspondence between EEG features and DMN topography we should consider two different phenomena—the fMRI-DMN and the EEG-DMN. However, if we admit the existence of method-specific phenomena in the brain that do not correlate with each other, we should be very careful in considering their possible functional correlates. It is quite possible that some functional processes may have no reflection in the BOLD signal while they have a clear manifestation in EEG, and vice versa. However, functional processes that are ascribed to DMN, such as self-referential thought and social cognition, are bound to have some manifestation in cortical electrical activity. In this connection, it should be noted that most of the EEG and EEG-fMRI DMN studies investigated only the resting state. However, most inferences about presumable DMN functions were made from comparisons of its activity in different states. Therefore, an investigation of EEG correlates of psychological processes that are ascribed to DMN is clearly needed. It should be also noted that most of the EEG and EEG-fMRI studies investigated either cortical EEG spectral power distribution (e.g., Chen et al., 2008) or its correlation with the BOLD signal (Laufs et al., 2003b; Mantini et al., 2007; Scheeringa et al., 2008). However, fMRI studies have employed a number of specific analytic techniques for a more purposeful analysis of DMN functions. Two of these techniques, region-of-interest (ROI) seed-based correlation approaches and independent component analysis (ICA), are most commonly employed in the literature. Seed-based approaches use regression or
correlation analyses to examine activity in selected voxels or ROI (Uddin et al., 2008). In contrast, ICA is a model-free approach, which, unlike ROI seed-based analysis, is not bounded by a priori predictions. ICA decomposes data into maximally (temporally or spatially) independent components, representing the characteristic time and spatial signatures of the sources underlying the recorded mixed signals (McKeown et al., 1998). While there are theoretical advantages/disadvantages of each method—a direct comparison reveals comparable results (Greicius et al., 2004).

In this study we aimed to investigate EEG correlates of DMN activity both in “rest” and in two experimental tasks. In our choice of the experimental tasks we proceeded from a necessity for them to share the same kind of stimuli but presented in different contexts. Specifically, we were guided by the above presented evidence linking DMN with social cognition. Therefore, in the target task we wanted to model social interactions with virtual “persons.” Pictures of these persons were presented at the screen and the participants had to establish virtual relations with these “persons.” In the control task, participants were presented with the same pictures, but their task in this case was just to evaluate a degree of hostility-friendliness of presented faces. It is clear that the second task does not exclude a possibility of self-referential processing, because pictures of human faces may unpredictably trigger self-referential thoughts (for example, if the presented face resembles someone familiar to the participant). However, we might be reasonably confident that these processes should be more pronounced in the former than in the latter task.

In all cases we sought to determine a degree of “task-relatedness” of spatial patterns identified in the traditional EEG frequency bands. To do this, we employed the ICA approach in a fashion that is most commonly used in relevant fMRI studies. Contrary to PET/fMRI data, which allow localizing brain activity in a 3D brain volume, EEG data give only a 2D representation. To overcome this limitation, different source reconstruction techniques have been devised. In this study, sLORETA (Pascual-Marqui, 2002) was applied to the data to determine the cortical sources measured on the skull surface electrical activity. We aimed to answer the following research questions: (1) to test whether blind separation methods like ICA applied to 3D-reconstructed EEG data allow reproducing major DMN features outlined in fMRI research; (2) to evaluate a degree of “task-relatedness” of spatial patterns obtained in the traditional EEG frequency bands; (3) to examine separately evoked and induced oscillatory responses in experimental tasks with stimuli presentation.

2. Results

Behavioral results, channel-level analysis, and sLORETA whole brain results are presented in Supplementary data.

2.1 Identification of default mode network activity

3D current source density data were analyzed using combined group ICA and statistical parametric mapping techniques. Group ICA was performed for each condition and each frequency band separately. Besides, in the explicit judgment and social game tasks, separate analyses were performed for induced and evoked oscillations. In total, these analyses generated thirty sets of results (each set comprising 20 independent components). For each set of results, we performed spatial sorting of the components using the GIFT software. The component that (spatially) correlated most significantly with the DMN template (see Section 5) was selected as the default mode component. For all conditions and frequency bands, the respective components demonstrated moderate correlations to the DMN template (Pearson’s $r$ range=0.55 to 0.68). One-sample T-test in SPM5 was used to assess the statistical significance of each identified DMN pattern. For a particular pattern, each subject’s respective independent component image (z score spatial map) was entered into a second-level random-effects analysis and assessed statistically using a threshold of $P_{FDR}<0.05$ (whole-brain corrected) and minimum cluster size of 8 contiguous voxels (Harrison et al., 2008). All ICs that showed highest correlations to the DMN template proved to be statistically significant across subjects.

2.2 Functional comparison of identified networks

2.2.1 Resting condition

After the initial spatial identification of networks in each frequency band, a degree of their “task-relatedness” for each experimental condition was evaluated. For resting condition, the degree of “task-relatedness” was evaluated in the between-subject domain. For each component, a correlation between this component scores and SRTS scores was calculated. Bonferroni correction was applied to correct for multiple comparisons. There were no significant correlations in the eyes open condition. In the eyes closed condition, one alpha band component showed significant correlation with SRTS scores ($r=0.44, P=0.0019$). This component also showed highest (among the 20 alpha band components) spatial correlation to the DMN template ($r=0.56$). Spatial correlations with FH and PH templates were additionally calculated. The DMN alpha band component showed highest (among the 20 alpha band components) spatial correlation to the PH template ($r=0.49$), but low spatial correlation to the FH template ($r=0.04$). Component’s anatomy mostly included the precuneus (BA7) (Fig. 1).

2.2.2 Induced oscillations

For induced oscillations data, which comprised a succession of reference and test intervals, the degree of “task-relatedness” was assessed by means of temporal sorting analysis using the GIFT software. For each set of ICA results, the associated time course for all ICs was correlated with an idealized reference function (see Section 5 for details) of the respective experiment. The component that (temporally) correlated most significantly with the reference function was selected as the most task-related. For the social game task, the highest temporal correlation to the respective reference function ($r=0.87$) was again found in the alpha band of frequencies and was also associated with the IC that showed the highest spatial correlation to the DMN template ($r=0.64$). For other frequency bands, the identified default mode network
patterns did not demonstrate the highest correlation to the respective reference function and generally these correlations were lower than for alpha band. The DMN alpha band component showed highest (among the 20 alpha band components) spatial correlation to the PH template (r=0.58), but no spatial correlation to the FH template (r=0). Component’s anatomy again mostly included the precuneus (BA7 and BA19). Fig. 2 shows the default mode network pattern and its associated time course that was identified for alpha frequency band in the social game experiment.

Note that each pair of consecutive points at the IC activation plot represents a trial of the social game task, which consists of the reference (marked with vertical grid lines) and the test interval. The observed saw-edged pattern with ups corresponding to the reference and downs corresponding to the test interval signifies that DMN alpha oscillations tend to desynchronize during the face presentation period relative to the inter-trial interval. This pattern was positively and most robustly correlated with the idealized (i.e., associated with the activity in the most task-related voxel) reference function relative to other estimated ICs.

For the explicit judgment task, none of the components, that showed the highest temporal correlation to the respective reference function, was associated with the DMN pattern. Their spatial correlations with the DMN template ranged from 0.08 to 0.35. Thus, task-related DMN patterns were observed only in the alpha band of frequencies and only in the resting condition with eyes closed and in the social game task.

Fig. 3 shows most task-related clusters of alpha band activity for the eyes closed resting condition, the social game task, and the explicit judgment task.

For each condition, the topography of two most task-related ICs is presented. For the resting condition with eyes closed (Fig. 3A), the DMN pattern is shown in blue color. Primary clusters of activity are located in the precuneus (BA7, MNI coordinates: x=11, y=-62, z=47), the middle temporal gyrus (BA21, MNI coordinates: x=66, y=-47, z=-3), and the inferior parietal lobule (BA40, MNI coordinates: x=55, y=-27, z=27). Red color shows the topography of a component that just failed to reach Bonferroni-corrected significance level for its correlation with SRTS scores (r=0.37, P=0.008). Primary clusters of activity for this component are located in the precuneus (BA7, MNI coordinates: x=-9, y=-67, z=32), the supramarginal gyrus (BA40, MNI coordinates: x=-34, y=-52, z=27), and the cingulate gyrus (BA31, MNI coordinates: x=16, y=-12, z=37). In fact, in the spatial sorting analysis this
component showed the second largest correlation to the DMN template ($r = 0.46$).

For the social game task (Fig. 3B), the DMN pattern is again shown in blue color. Primary clusters of activity are located in the precuneus (BA7, MNI coordinates: $x = -11, y = -67, z = 42$) and the cingulate gyrus (BA31, MNI coordinates: $x = -9, y = -52, z = 42$). Red color shows the topography of a component that showed the second largest temporal correlation to the respective reference function ($r = 0.87$). This component also showed the third largest correlation to the DMN template ($r = 0.28$). Primary clusters of activity for this component are located in the paracentral lobule (BA3, MNI coordinates: $x = 16, y = -42, z = 57$) and the precuneus (BA7, MNI coordinates: $x = -4, y = -52, z = 52$).

For the explicit judgment task (Fig. 3C), the most task-related component is shown in blue color. Primary clusters of activity are located in the precentral gyrus (BA4, MNI coordinates: $x = -44, y = -12, z = 42$), the insula (BA13, MNI coordinates: $x = -34, y = -7, z = 17$), and the cingulate gyrus (BA24, MNI coordinates: $x = -19, y = -17, z = 42$). Red color shows the topography of a component that showed the second largest temporal correlation to the respective

Fig. 2 – Spatial pattern and its associated time course of the alpha band DMN component that was identified for the induced alpha band responses during the social game task and showed the highest temporal correlation with respective reference function. Each pair of consecutive points at the time course represents a trial of the social game task (only first 18 trials are shown), which consists of the reference (marked with vertical grid lines) and the test interval. The observed pattern shows that this component’s alpha oscillations desynchronize during the test interval relative to the reference interval. Both the color scale at the bottom part of the figure and the $y$ axis at the time course plot are in $z$-scores.

Fig. 3 – Two most task-related components in the alpha band of frequencies overlaid on one another for the rest with eyes closed condition (A), the social game task (B), and the explicit judgment task (C). The scales are in $z$-scores.
reference function \((r=0.52)\). Primary clusters of activity for this component are located in the precuneus (BA7, MNI coordinates: \(x=-14, y=-47, z=52\)), the precenral gyrus (BA4, MNI coordinates: \(x=-29, y=-32, z=52\)), and the superior temporal gyrus (BA22, MNI coordinates: \(x=41, y=-32, z=7\)). Both components showed low spatial correlations with the DMN template \((r=0.10\) and 0.31, respectively).

Finally, we evaluated the degree of correspondence between alpha band DMN-related spatial patterns in the eyes closed resting condition and in the social game task. Spatial correlation between respective patterns was calculated using the GIFT software. The eyes closed rest DMN pattern showed high spatial correlation with the social game task DMN pattern \((r=0.81)\).

### 2.2.3. Evoked oscillations

In both experiments and in all frequency bands, most task-related components showed moderate correlations with the respective reference functions (ranging from 0.47 to 0.66). In both experiments, low frequency oscillations (delta and theta bands) showed highest, whereas high frequency oscillations (gamma band) showed lowest correlations with respective reference functions. None of the most task-related components showed highest (among respective 20 components) spatial correlation with the DMN template. In the social game task, the most task-related alpha band component showed the third largest correlation \((r=0.38)\) to the DMN template. This component also showed the third largest correlation \((r=0.32)\) to the PH template and no correlation \((r=0)\) to the FH template.

All task-related components in other frequency bands (as well as the most task-related alpha band component in the explicit judgment task) showed rather low correlations with the DMN template. Fig. 4 shows most task-related clusters of evoked alpha band activity during the social game task (Fig. 4A) and the explicit judgment task (Fig. 4B).

In the social game task, the primary cluster of evoked alpha band activity was located in the posterior cingulate gyrus (BA31, MNI coordinates: \(x=11, y=-42, z=37\)). For the explicit judgment task, primary clusters of evoked alpha band activity were located in the middle frontal gyrus (BA6, MNI coordinates: \(x=-26, y=2, z=48\)), the inferior parietal lobule (BA40, MNI coordinates: \(x=-49, y=-32, z=47\)), the insula (BA13, MNI coordinates: \(x=-34, y=-2, z=18\)), and the middle temporal gyrus (BA22, MNI coordinates: \(x=56, y=-42, z=2\)).

### 3. Discussion

In all traditional EEG frequency bands both in a resting state and during the studied experimental conditions group ICA of 3D current source density data produced statistically significant across subjects ICs that showed moderate and similar in size spatial correlations with the DMN template comparable with those reported in relevant fMRI studies (see e.g., Harrison et al., 2008). However, only in alpha band of frequencies and only in two experimental contexts (rest with closed eyes and the social game task) did these components simultaneously show the highest (with respect to other estimated ICs) correlations with respective functional outcomes. Remarkably, these two experimental contexts are arguably most favorable for self-referential processes. This result seems somewhat surprising giving reported low correlations of alpha power with DMN BOLD signal. One would rather expect to see theta and beta oscillations as a correlate of DMN activity (see e.g., Laufs et al., 2003b; Meltzer et al., 2007; Scheeringa et al., 2008). However, low correlation between BOLD signal and EEG spectral power does not mean both of them may not moderately correlate with the same psychological process. From a functional point of view alpha oscillations appear to be a promising candidate to consider as a correlate of DMN-related processes. Indeed, the terms “activation” and “deactivation,” that are used to describe DMN functions, have also been frequently used to describe functional correlates of EEG alpha activity. Starting from Berger's (1929) pioneering

![Fig. 4 – Most task-related components of evoked alpha band activity during the social game task (A) and the explicit judgment task (B). The scale is in z-scores.](image-url)
works, many studies have noted a task-related decrease in alpha power. This finding was so pervasive that alpha power has come to be considered as correlate of “idling” and a reverse measure of activation (Adrian and Matthews, 1934). Later, the idling hypothesis has been largely overtaken by a framework where the amplitude of alpha oscillations reflects a level of cortical inhibition (Klimesch, 1996; Klimesch et al., 2007; Pfurtscheller, 2003). From such point of view, deactivation should be associated with an increase of alpha power, whereas activation should be associated with a decrease of alpha power. Indeed, in some studies the BOLD signal has been shown to correlate negatively with EEG power in the alpha band (Goldman et al., 2002; Moosmann et al., 2003, but see Laufs et al., 2003b; Mantini et al., 2007). Accordingly, it is suggested that DMN alpha blocking should be more pronounced in tasks requiring self-referential thought and social cognition (Panksepp and Northoff, 2009). Indeed, this study data show that at least in one part of the DMN, namely in its posterior hub including precuneus and posterior cingulate, the dynamics of alpha band blocking during virtual social interactions shows the best (with respect to other spatial patterns) correspondence to an idealized reference function. This evidence appears to suggest that self-referential processes are accompanied with alpha blocking in the posterior DMN hub. This reasoning absolutely fails however if we try to apply it to the rest with eyes closed data where self-referential thought appears to be associated with alpha power increase in the same brain regions (note that spatial correlation between the two spatial patterns is 0.81). Contradictory as these findings may seem, they are in line with many published observations.

Indeed, in spite of pervasive findings of task-related decrease in alpha power, there have been observations of task-related increase in alpha power. Noteworthy, most of these observations were made in such states as mental imagery, imagination, or internal attention (e.g. Cooper et al., 2003; 2006; Klinger et al., 1973; Ray and Cole, 1985a; b). Klimesch et al. (2007) suggested that alpha synchronization may reflect top-down control processes, whereas alpha desynchronization reflects bottom-up release of this inhibitory control. These data posit a direct and active role for alpha oscillations in the mechanisms of attention and consciousness (Palva and Palva, 2007). On the whole, it could be summarized that internal mental processes are frequently associated with an increase of alpha power. This increase is paralleled by an inhibition of sensory perception and decreased attention. Contrariwise, states of increased attention and sensory perception are associated with a decrease in alpha power (and, naturally, with a disruption of internal mental processes). Thus, alpha power appears to correlate positively with internal mental processes and negatively with attention to the external world and processing of sensory information. However, as Palva and Palva (2007) rightly note, alpha phase relationships with the stimulus and with other oscillations should be taken into account when considering their possible functional significance. The above description relates only to spontaneous and the so-called induced (not stimulus phase-locked) alpha activity. Quite different picture arises when we consider evidence related to the so-called evoked (stimulus phase-locked) alpha responses, which correlate positively with specific sensory processes (Basar, 1998; 1999; Dinse et al., 1997; Silva et al., 1991). If one takes into account that, according to the most currently popular view (e.g., Jansen et al., 2003; Klimesch et al., 2004; Makeig et al., 2002), evoked oscillations arise due to partial phase locking of ongoing oscillations (i.e. resetting of the alpha phases after stimulation), the whole picture seems to correspond to the following pattern. In states associated with internal mental processes alpha activity is increased. This alpha power increase has arguably functional significance, i.e., participates in the integration of relevant cortical areas and simultaneously inhibits irrelevant ones (i.e., those areas that may supply an input which is apt to interrupt the ongoing mental process) (Klimesch et al., 2007). This explains as to why enhanced background alpha oscillations correlate positively with memory (Klimesch et al., 2003), but negatively with visual discrimination (Hanslmayr et al., 2005) performance. Recently, Jensen et al. observed that visual discriminability of a threshold stimulus decreased with an increase in prestimulus occipito-parietal alpha band power (van Dijk et al., 2008). Likewise, they reported that in a go-no-go task false alarms were preceded by higher levels of alpha band power in the occipital cortex and bilateral somatosensory cortices as compared to correct withholds on no-go trials (Mazaheri et al., 2009). All these data could be easily accounted for by admitting alpha power as a correlate of the stream of thoughts. Appearance of a sensory event disrupts this stream along with ongoing alpha oscillations in relevant cortical areas (i.e., in cortical areas that are involved in the adequate processing of this particular event), but also causes their partial phase locking to the sensory event. Presumably, these phase-locked alpha responses also have functional significance, i.e., integrate neural populations participating in the event processing.

Such interpretation implies that synchronization of internal mental processes, as opposed to the processing of exteroceptive stimuli, might be considered as the primary function of alpha oscillations. No wonder then that they dominate EEGs of human beings (Basar and Gunetekin, 2009; Kniazhev and Slobozskaya, 2003) whose internal life is presumably much richer than that of lower mammals. In such capacity alpha oscillations are bound to be related to activity of the DMN, which mostly operates in absence of external stimuli. Last but not least, most DMN researchers emphasize its intimate link with memory. Alpha oscillations are also associated with memory (Klimesch, 1996; Klimesch et al., 2004). Klimesch et al. (2008) suggest that associated with alpha oscillations ‘operating system’ may operate under direct top-down control or in an ‘automated’, ‘default’-like mode.

During the eyes closed resting condition, DMN-related self-referential thought and social cognition are preferentially associated with (enhanced) alpha oscillations. Appearance of relevant to the DMN’s function stimuli (face stimuli in context of the social game task) disrupts ongoing alpha oscillations. The observed spatio-temporal pattern of this alpha blocking implies that repeated transitions from resting mode to stimuli processing within the posterior DMN hub constitute the most prominent feature characteristic of oscillatory responses to this experimental situation. It is not the case in the other experimental situation, namely, the explicit judgment task. In this case other temporally correlated networks appear to play
the leading part. In particular, brain networks associated with conscious recognition of visual patterns (the ventral visual stream, Goodale and Milner, 2008) and the left hemisphere areas involved in classification of visual stimuli in terms of verbal representations appear to be most task-relevant (Knyazev et al., 2009). The blocking of ongoing alpha oscillations upon appearance of relevant to the DMN’s function stimuli is paralleled by (actually is preceded with, see Fig. 2S) a phase-locked to the stimulus response. This presumably means the stimulus resets phase of a (minor) part of alpha oscillators in such a way that they start to oscillate in coherence with each other and the stimulus mode. At the same time the stimulus disrupts synchrony of other oscillators so that they start to oscillate in asynchrony with each other and the stimulus mode. Although the most task-related spatial pattern of evoked alpha responses did not show the highest correlation to the DMN template, it substantially overlaps with its posterior hub. Indeed, the posterior cingulate cortex constituting its major part is the “heart” of the DMN (Fransson and Marrelec, 2008). Although mostly speculative, the interpretation linking alpha oscillations with the DMN has recently received a support in a study by Jann et al. (2009) who have shown that the BOLD correlates of global alpha band synchronization in a resting state are located in brain areas involved in the DMN.

Finally, some limitations and dim points need to be discussed. The most considerable limitation relates to the fact that EEG source localization and ICA were performed on the basis of a somewhat sparse 32 electrodes array. Numerous studies show that localization accuracy improves with increasing number of recording electrodes (e.g., Krings et al., 1999; Laarne et al., 2000; Lantz et al., 2003). ICA decomposition methods generally also require sufficient number of electrodes for reliable and valid component extraction. One could argue however that 32 electrodes are sufficient, so long as there is approximately homogenous scalp coverage as is the case in this study (see Fig. 4S). Thus, Congedo (2006) has shown by point spread function simulations that using an approximate head model sLORETA is capable of exact localization of single dipoles with as few as six electrodes (given the spatial sampling of the scalp is appropriate). Simulation data show that using 32 electrodes instead of 19 improves the localization by 2.7 mm on average, while using 63 instead of 32 electrodes leads to improvements of less than 1 mm (Yvert et al., 1997). Therefore, 32 electrodes array could be considered a tradeoff between acceptable localization accuracy and reasonable price. Indeed, although high density electrode arrays are increasingly becoming available, many recently published studies using source localization and ICA (separately or in combination with each other) still use 32 or less electrodes arrays (e.g., Congedo et al., 2010; Marco-Pallares et al., 2005; Musso et al., 2010; Travis et al., 2010 and many others). Importantly, increasing the number of electrodes increases the spatial resolution, that is, the ability to resolve two closely-spaced dipoles, not the localization ability (Congedo, 2006). It could be argued that high spatial resolution is not necessary for the localization of such widespread network as DMN. Moreover, localization error which might arise due to sparse electrode array is random by nature and should average out in a large-sample group analysis (as is the case in this study), especially when using the group ICA, because it directly estimates components that are consistently expressed in the population and ignores idiosyncratic and random features (Calhoun et al., 2001; Schmithorst and Holland, 2004). Finally, in a reasonably large sample, a random error may decrease the signal-to-noise ratio, which would result in decreasing the probability to find a statistically significant effect. That means that negative results reported in this study (i.e., absence of significant associations related to delta, theta, beta, and gamma bands and to the anterior DMN hub) should be treated with caution and need to be confirmed in further studies using denser electrode arrays. However, positive findings related to alpha band could hardly be attributed to errors arising due to inaccurate localization in the 3D space. Besides, spatial localization of significant correlations of e.g. SRTS scores with alpha power is similar at all analysis levels, i.e., in raw channel data before application of sLORETA and ICA (Fig. 1S), in sLORETA 3D data (Fig. 3S), and in ICs derived from 3D matrices (Fig. 1).

Second limitation relates to the fact that the data from 32 channels are cleaned with ICA in EEGLAB, projected into a much higher-dimensional space, and then submitted for independent component analysis. This procedure may potentially artificially stretch the content of the data and lead to appearance of spurious components. To diminish such possibility, we always retained at least 20 components during artifact rejection and extracted no more than 20 components in the GIFT analysis. Moreover, all components that showed highest spatial correlation to the DMN template were statistically significant across subjects. Basing on this we could be reasonably confident that our results are not just an artifact. Besides, it seems highly improbable that spurious artifactual components may simultaneously show high correlations to both spatial and functional criteria both of which are taken from completely different areas of research (i.e., fMRI and PET studies). Nevertheless, in order to cross-validate our results we have conducted another analysis which may not be reported here in detail due to space limitation. In this analysis we tried to overcome potential pitfalls associated with the step of performing ICA on 3D inverse LORETA solution. In this case temporal group ICA was performed on filtered in the five frequency bands 2D EEG using Group ICA of EEG toolbox (EEGIFT, Version 1.0c; http://icatb.sourceforge.net/). Extracted ICs were then submitted for sLORETA and their spatial 3D images were imported into the Group spatial ICA for fMRI toolbox for the analysis identical to the one described in this paper. These ICs showed generally lower correlations with the DMN template than the ICs derived from 3D data. However, in spite of some minor deviations, the general pattern of results was similar to the one reported here. Thus, only in the alpha band of frequencies were found components that simultaneously showed high spatial correlation to the DMN template and high “task-relatedness.” Moreover, these components also showed high correlation to the PH template and low correlations to the FH template.

Thirdly, in spite of the fact that spatial correlations of obtained ICs with the DMN template are comparable in size with those reported in relevant fMRI studies, the spatial distribution of these ICs differs from the typical fMRI-DMN pattern. The main difference is the complete lack of structures...
belonging to the frontal DMN hub. Whether these discrepancies arise because the physiology and mechanics of EEG and fMRI measurements are fundamentally different such that each method locally emphasizes or underestimates the same patterns of activity in a different way, or these discrepancies appear due to above discussed methodological limitations remains as yet unclear.

Fourthly, the interpretation of the results may not be as straightforward as it appears from the above discussion. Particularly, it would be wrong to conclude that self-referential thought and social cognition are the main correlates of alpha activity. They might be but one among other kinds of internal mental processes that correlate with enhanced alpha oscillations. Moreover, DMN activity is clearly not limited to alpha oscillations. In this study, statistically significant components showing moderate spatial correlation with the DMN template were found in all frequencies, but they did not show highest, relative to other components, correlations with selected reference functions. It should be taken into account however that selected functional correlates of DMN activity reflect only few from described in the literature presumptive DMN functions. Thus, self-referential thought was measured by just three items and social interactions were modeled by a specific social game that is not identical to experimental manipulations used in most relevant PET and fMRI studies. The social game task requires dynamic decisions and behavioral responses, which are absent in such tasks as the moral dilemma task (Harrison et al., 2008), or passive watching of videos (Krämer et al., 2010). Moreover, the explicit judgment task, which we used for comparison, is not attentionally or cognitively demanding, which is a prerequisite for causing DMN deactivation (McKiernan et al., 2006; Singh and Fawcett, 2008). Further research is required to test whether regularities observed in this study hold on across other relevant experimental contexts. It is quite possible that some other experimental conditions relevant to presumptive DMN functions would allow unrevealing the contribution of other frequency bands to DMN activity. Particularly theta and beta seem most likely candidates (Laufs et al., 2003b; Scheeringa et al., 2008), or broadband EEG signatures (Mantini et al., 2007). Furthermore, further research should not be limited to the analysis of oscillation amplitudes. Investigation of phase relationships in different frequency bands within putative DMN regions seems very promising (see Palva and Palva, 2007).

### 4. Conclusion

In this study, we deliberately chose analytical approaches that are routinely used in fMRI research and applied them to the analysis of EEG data. In this endeavor, we were motivated by a desire to try to reproduce major DMN-related findings in EEG domain. In particular, we were interested to test whether blind decomposition methods like ICA are able to identify in 3D-reconstructed EEG data spatial patterns resembling the DMN as it is described in PET and fMRI studies. Further we intended to test a degree of task-relatedness of spatial patterns identified in the traditional EEG frequency bands. In spite of evident inherent to EEG data limitations, such as low spatial resolution and low signal to noise ratio, the applied analytical approaches allowed us to reproduce at least some of DMN spatial features and reveal functional correlates that are broadly compatible with those described in relevant PET and fMRI studies. It appears that, comparative to other frequency bands, alpha oscillations are most robustly associated with DMN-related functional outcomes. The whole pattern of results fits to a hypothesis that spontaneous ("default") self-referential mental processes are associated with enhanced within the posterior DMN hub alpha activity, whereas processing of DMN function-related external stimuli disrupts synchrony of these spontaneous oscillations but simultaneously causes their partial phase-locking to the external events.

### 5. Experimental procedures

#### 5.1. Subjects

Resting state and the social game data were collected in a sample of 48 subjects (26 men and 22 women, age range 18 to 30 years). In the explicit emotion judgment task the sample included 40 participants (19 men and 21 women; age range 17 to 32 years). Both samples consisted of healthy, right-handed volunteers with normal or corrected to normal vision who received a sum equivalent to about 5% of the monthly living wage for participation. All applicable subject protection guidelines and regulations were followed in the conduct of the research in accordance with the Declaration of Helsinki. All participants gave informed consent to the study. The study has been approved by the Institute of Physiology ethical committee.

#### 5.2. Instruments and procedures

During the experiment the subjects sat in a soundproof and dimly illuminated room. The spontaneous EEG registration lasted about 6 min and included alternating 2 min intervals with eyes open and eyes closed. Just after the spontaneous EEG registration participants were asked to fill out a brief questionnaire describing their state and thoughts during the preceding period. Three items from this questionnaire were selected to measure individual variation in the degree of self-referential thought and social cognition. “During the procedure I (1) recollected pleasant episodes of relationships with my boy/girl-friend; (2) thought of something pleasant that I expect in the near future; (3) recollected episodes from my own life.” All items were measured on a five-point Likert scale. The self-referential thought scale (SRTS) showed high internal consistency reliability (Cronbach’s alpha = 0.85).

In both experimental tasks we used as stimulation an ensemble of the photographs presented by Ekman and Friesen (1976). We selected 30 photographs, specifically, 5 different females and 5 different males with 3 different facial expressions (angry, happy, and neutral). The pictures were presented black and white (17×17 cm) and displayed on a screen at a distance of 120 cm from the subjects. In both experiments, first, a fixation cross appeared at the center of the screen for 1 s. Then a face picture was presented. Angry, happy, and neutral
faces were delivered randomly, and inter-stimulus-interval randomly varied between 4 and 7 s. The number of face stimulations was 150 for each subject, including 50 faces of each category. In the explicit judgment task, participants were instructed to evaluate emotional expression of each presented face on an analog scale ranging from −100 (very hostile) to 100 (very friendly). The face picture was present at the screen for 4 s, and was followed by presentation of the evaluative scale.

In the social game task, participants were asked to imagine that faces, which they will see at the screen, are living persons whom they have to interact with. They had to choose one out of three options: “attack,” “avoid,” or “make friends” (pressing “1,” “2,” or “3” button, respectively). “Vis-à-vis” reaction might be different depending on his/her “character.” As a result, the participant gained or lost points which afterwards were added or, respectively, subtracted from his/her fee. In reality, all avoidances received neither reward nor punishment (zero points), whereas aggressive and friendly choices were randomly rewarded or punished with a fixed number of points. After the button press, a feedback announcement appeared at the screen for 1 s, such as “0 points,” “+20 points,” or “−20 points.” After both experiments the subjects filled out a set of psychometric questionnaires and were debriefed.

5.3. EEG recording

Thirty-two EEG electrodes were placed on the subject’s scalp. The electrodes were mounted in an elastic cap on the positions of the international 10–20 system which ensured homogenous scalp coverage (Fig. 45). A mid-frontal electrode was the ground. The electrode resistance was maintained below 5 kΩ. The signals were amplified with a multichannel biosignal amplifier with bandpass 0.05–70 Hz, −6 dB/octave and continuously digitized at 300 Hz. The electrodes were referred to linked-mastoids. The horizontal and vertical EOGs were registered simultaneously. EEG data were artifact-corrected using Independent Components Analysis via EEGLAB toolbox (http://www.sccn.ucsd.edu/eeglab/) retaining minimally 20 out of 32 components and recompute to average reference.

5.4. sLORETA

For eyes open and eyes closed resting condition artifact-free epochs of 1.7 s duration were supplied for cross-spectrum calculation in sLORETA. For analysis of induced oscillations, for each single-trial experimental data, cross-spectra were calculated separately for reference (750 to –100 ms prior to fixation cross presentation) and test (100–750 ms after the face stimulus presentation) intervals. For analysis of evoked oscillations, EEG data were averaged across trials and submitted for cross-spectrum calculation in sLORETA. Subsequently current source densities of delta (2–4 Hz), theta (4–8 Hz), alpha (8–12 Hz), beta (12–30 Hz), and gamma (30–45 Hz) oscillations were estimated in sLORETA. For more details of sLORETA analysis see Supplementary data.

5.5. Independent component analysis

Blind source separation techniques are increasingly becoming popular in EEG research. The scalp EEG samples a volume-conducted, spatially degraded version of the electrical activity, where the potential at any location and latency can be considered a mixture of multiple independent time-courses that stem from large-scale synchronous field potentials (Makeig et al., 2004a; Onton et al., 2006). Temporal unmixing of the EEG by means of ICA potentially allows studying the process of interest buried in the spread of other, unrelated sources. In EEG research, ICA is usually applied to the raw EEG signal of each subject. Obtained independent components (ICs) are said to represent temporally independent signal sources and have scalp maps that nearly perfectly match the projection of a single equivalent brain dipole (Delorme and Makeig, 2004). Such approach is perfectly suited for studying relatively local (spatially and temporally) processes (e.g., related to a single ERP component), but are less suitable for studying widely spatially distributed networks, such as the DMN. Besides, following ICA, there is no natural and easy way to identify a component from one subject with a component from another subject. Thus, the problem of identifying equivalent components across subjects (which is necessary for making population inferences) is non-trivial (Makeig et al., 2004b). Unlike univariate methods such as the general linear model, ICA is not naturally suited to generalize results from a group of subjects. There are two strategies to allow for matching of independent components across individuals: one is to combine individual ICs across subjects with clustering techniques (Esposito et al., 2005; Onton et al., 2006). This implemented in EEGLAB toolbox approach makes it possible to summarize results of ICA-based analysis across more than one condition from a large number of subjects. However, it may hardly solve the problem of identifying DMN-related spatial patterns across subjects. Another approach is to create aggregate data containing observations from all subjects, estimate a single set of ICs and then back-reconstruct these in the individual data (Calhoun et al., 2001; Schmither and Holland, 2004). We adopted the latter strategy for the group EEG temporal ICA analysis, because it directly estimates components that are consistently expressed in the population, involves the least amount of user interaction and is straightforward to compare with the existing framework for group ICA of fMRI data (Calhoun et al., 2001). Therefore, adopted in this study strategy was to (1) calculate using sLORETA current source density of the five EEG frequency bands for each of 6430 brain voxels and (2) to apply group ICA to obtained 3D data in a fashion that is routinely used in fMRI research.

For the analysis of induced oscillations, for each condition of each subject a set of first 50 trials was selected. This implied selection of 50 test and 50 respective reference interval data. For resting condition 50 successive epochs were selected. A more complex approach had to be applied for the analysis of evoked oscillations, because they have low amplitude in comparison with the background EEG activity and in consequence, they are hardly visualized in the single-trials. To constrain the single trial EEGs to the time-frequency features relevant for the evoked activity, each subject’s 100 first single-trials were first wavelet-denoised using EP_den v2 software package developed by Quian Quiroga (Quiroga and Garcia, 2003) (http://www.vis.caltech.edu/~rodri) and subsequently submitted for sLORETA cross-spectra calculation.
After sLORETA transformation, for each experimental task and each frequency band, each subject’s and each trial’s sLORETA images were converted into the Neuroimaging Informatics Technology Initiative (NIFTI) format using modified by the first author LOR2SPM function by Sergey Pakhomov (http://www.ihb.spb.ru/~pet_lab/L2S/L2SMain.htm). Subsequently, in the case of induced oscillations, for each frequency band and each subject, an array of 100 files was constructed by consecutive concatenation of respective reference and test interval images (this stage was skipped for resting and evoked EEG data). In this study, ICA was performed using the Group spatial ICA for fMRI toolbox (GIFT, Version 1.3b; http://icatb.sourceforge.net/), using methods and algorithms described in recent studies (Calhoun et al., 2001, 2004). Briefly, for each experimental condition and each frequency band, a single Group ICA was performed at the group level after subject-wise data concatenations, and back reconstruction of single-subject time courses and spatial maps from the raw data matrix (Calhoun et al., 2001). The number of extracted components was estimated from the data using the minimum description lengths (MDL) criteria. For different datasets this number varied from 20 to 28, so in all cases we decided to extract 20 components. ICASSO toolbox (http://www.cis.hut.fi/projects/ica/icasso/) was used in GIFT to determine the reliability of ICA algorithm. ICA algorithm was run 10 times on Infomax algorithm to determine the algorithmic reliability or stability. In total, thirty sets of results (6 sets of data × 5 frequency bands) were generated that were investigated further with statistical comparisons. For each set of results, we identified a statistically significant spatial pattern of temporally correlated activity (an independent component) that reproduced the major anatomical features of the DMN. To reduce observer bias in the selection of independent component patterns, we performed a spatial sorting analysis in GIFT. For each respective set of Group ICA results, independent components were spatially correlated with an anatomically defined default mode template and were ranked according to a “highest correlation” criterion (Pearson’s r) with this anatomy (for a similar approach see Garrity et al., 2007; Greicius et al., 2004; Harrison et al., 2008). In this study, we used a DMN template that was created by GIFT developers and is supplied with the GIFT package (the ref_default_mode.nii file). This template has been used in a published research (Garrity et al., 2007) and was generated by WFU Pickatlas developed at Wake Forest Pharmaceuticals University (http://www.fmr.i.wfubmc.edu/). According to the description, it contains the posterior parietal cortex (Brodmann’s area 7), the frontal pole (Brodmann’s area 10), and the occipito-parietal junction (Brodmann’s area 39), as well as the posterior cingulate and precuneus (Garrity et al., 2007). This template was smoothed with a 3-mm³ Gaussian kernel. We created two additional templates using the Wake Forest Pick atlas toolbox. These templates were created to allow separate measurements for the two major DMN hubs—the frontal and the posterior hub. The frontal hub (FH) template included the superior frontal gyrus (BAs 8/9/10) and the anterior cingulate cortex (BAs 11/32). The posterior hub (PH) template included the posterior parietal cortex (Brodmann’s area 7), the occipito-parietal junction (Brodmann’s area 39), the posterior cingulate, and the precuneus.

The similarity indices with a template were computed based on positive (after Z-transformation) loads. One-sample (within condition) T-tests in SPM5 were used to assess the statistical significance of each identified default mode network pattern. For a particular pattern, each subject’s respective independent component image (z score spatial map) was entered into a second-level random-effects analysis and assessed statistically using a threshold of P_{FDR}=0.05 (whole-brain corrected) and minimum cluster size of 8 contiguous voxels.

After the initial spatial identification of networks, a temporal sorting analysis was performed in GIFT to determine the degree of “task-relatedness” of the default mode network patterns in the five frequency bands. For each set of ICA results, the associated time course for all ICs was correlated with an idealized reference function (task waveform) of the five frequency bands. For induced responses the reference functions were constructed for each subject and each frequency band separately by calculating the time courses, that is, arrays of 100 values (one for each of the alternating reference and test interval epochs) of the current source density in a voxel showing maximal T value in a respective sLORETA test vs. reference interval contrast. These reference functions allowed to evaluate in a within-subject manner the degree of “task-relatedness” of each of respective 20 components.

Such approach was not possible for resting condition where only a between-subject measure of “task-relatedness” (a subjective evaluation by each subject of his/her preoccupation with presumably DMN function-related thoughts during EEG registration, that is, SRTS scores) was available. In this case, first, for each of 20 ICs generated for each frequency band of the eyes open and eyes closed resting condition, a voxel showing maximal T value in the respective one-sample-T-test analysis was identified. Next, for each IC, this voxel’s value in a respective independent component image was identified for each subject. Third, a correlation between these values and SRTS scores was calculated across subjects. For each frequency band within each condition this produced 20 correlations. Therefore, Bonferroni correction (0.05/20 = 0.0025) was applied to correct for multiple comparisons.

For evoked oscillations data, for each denoised trial of each subject, in the time interval between 100 and 500 ms post stimulus presentation onset, amplitudes of maximal positive and negative peaks in each channel data were summed. For each subject this procedure produced a matrix of values whose dimensions were equal to the number of trials × number of channels. These matrices were further used as a reference function for temporal sorting analysis using the GIFT software.

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