Integrating Different Aspects of Resting Brain Activity: A Review of Electroencephalographic Signatures in Resting State Networks Derived from Functional Magnetic Resonance Imaging

Keiichiro Nishida a  Nadja Razavi b  Kay Jann c  Masafumi Yoshimura a  
Thomas Dierks b  Toshihiko Kinoshita a  Thomas Koenig b

a Department of Neuropsychiatry, Kansai Medical University, Moriguchi-City, Japan; b Department of Psychiatric Neurophysiology, University Hospital of Psychiatry, University of Bern, Bern, Switzerland; c Ahmanson-Lovelace Brain Mapping Center, Department of Neurology, University of California, Los Angeles, Calif., USA

RSNs. This review article leads to the conclusion that spatially delimited θ and whole/local α may be the most promising measures, but the time domain methods add important additional information.

Introduction

Ninety years ago, Hans Berger, the inventor of the electroencephalogram (EEG), suggested that the brain is not only active during stimulation but also during rest [1]. Positron emission computerized-tomography (PET) and later functional magnetic resonance imaging (fMRI) – especially the blood oxygenation level-dependent (BOLD) contrast-enhanced studies – also described common dynamics of metabolic measures across spatially distant regions in the resting brain. These networks of interconnected brain regions were termed resting state networks (RSNs). Among these RSNs, the default mode network (DMN) [2] has received particular attention, since it is typically more active during rest than under task load. Apart from the DMN, around 10–20 other, mainly task-positive RSNs [3, 4], such as the dorsal and ventral frontoparietal networks (FPNs) [5], the salience network (SN)
Since both EEG and fMRI measure resting state brain activity, simultaneous EEG and fMRI studies are being conducted. Some of the earliest studies combining EEG and fMRI simultaneously were published by Ives et al. [10], Lemieux et al. [11], Krakow et al. [12], Goldman et al. [13] and Laufs et al. [14], and numerous other studies followed.

Why do we need to combine EEG-fMRI data at all? The extracranial EEG has a limited spatial but a very high time resolution, which is in the range of milliseconds. On the other hand, fMRI based on the BOLD signal has a very high spatial and a moderate time resolution. Since these methods measure quite different aspects of neuronal activity, the usage of a single imaging modality yields only limited perspectives for understanding the brain’s state or function. However, to improve understanding seems to be crucial to elucidate pathophysiological mechanisms and to develop novel treatment options [15, 16]. Since these methods measure quite different aspects of neuronal activity, the usage of a single imaging modality yields only limited perspectives for understanding the brain’s state or function. However, to improve understanding seems to be crucial to elucidate pathophysiological mechanisms and to develop novel treatment options [15, 16].

Facilitated by the rapid development of equipment and technology, nowadays, we can find many informative papers which combined quantitative EEG (qEEG) and fMRI. Many of these studies focused on methods how to combine qEEG and fMRI, how to eliminate artifacts and how to correct differences in neuronal response times, for example, since especially the BOLD signals are delayed compared to the electrophysiological changes. In terms of application, the most successful usage of combined EEG-fMRI has been in the domain of epilepsy: EEG is a reliable and well-established method for the diagnosis of epilepsy, and fMRI is good at delineating the epilepsy-producing region in the brain based on its good spatial resolution. It is thus reasonable to combine EEG and fMRI to find the origin of the epileptic seizure [10, 18–21]. Combined EEG-fMRI measurements are nowadays regularly employed in the routine workup of epilepsy [22].

Under normal conditions, the link between qEEG and fMRI (or fMRI-RSN) has also been investigated, but the overall picture is less clear, because there is a considerable variance in the methods used to quantify the EEG. There are many different analysis methods of qEEG; most of them have the advantage to separate functionally different brain rhythms, and/or allow to make statements about synchrony and/or subsecond temporal dynamics of changes in the brain’s state. However, each of these features is not equally well represented by each method, and the precise rationales for their computation vary. Thus, based on theoretical considerations alone, it is difficult to select EEG features that correspond well to (and might be taken as) an index of fMRI-RSN activity.

The aim of this paper was thus to address this question based on a review of the existing literature. The first part of this article briefly reviews the different qEEG analysis methods employed and primarily studied fMRI-RSNs so far. In the second part, we present and evaluate a systematic overview of how these features have been found to be associated to a subset of well-known fMRI-RSNs that are particularly interesting in the context of psychiatric disorders. Finally, we will talk about what we can speculate from those previous papers.

Review of the Currently Employed qEEG Parameters

Global Power Spectrum

The EEG power spectrum (synonymous with spectral analysis or frequency analysis) is probably the most frequently used resting state EEG parameter, and usually computed through the fast Fourier transformation. For the computation of the global power spectrum, the EEG spectral power is averaged within typical EEG frequency bands and time windows, and across all channels, yielding a single number per time window and frequency band. Typical frequency bands were δ (1.5–3.5 or 1.5–6.0 Hz in Kubicki’s band [23]), θ (3.5–7.5 or 6.5–8.0 Hz in Kubicki’s band), α (7.5–12.5 Hz), β (12.5–20 to 30 Hz) [24] and γ (20–35 to 40–80 Hz). The spontaneous fluctuations in these global power spectra across the analysis have then been correlated with the time courses of the BOLD signal in the RSNs [14, 25]. Recently, some studies demonstrated that the association of different EEG frequency bands to fMRI was consistent across subjects within a given type of RSN, but varied systematically between different fMRI-RSNs [26]. The global power spectrum is, therefore, an interesting parameter that additionally avoids problems of multiple testing or a priori selection of electrodes. However, by averaging within frequency bands and across all channels, the topographical constellation of the EEG-RSN correlates is lost. Local averages, local derivatives and covariance mapping, which are presented below, are different ways to address this problem.

Local Averages and Spatial Derivatives

The EEG varies considerably across the scalp, and spatially delimited changes in EEG have been related to local changes in brain functional states [27]. Therefore, it is also reasonable to search for fMRI correlates of more local EEG changes. One simple approach is to use averages across...
(scalp) regions of interest, e.g. electrodes above the occipital cortex (e.g. Laufs et al. [28] in 2006). The spatial selectivity can be further enhanced by using so-called local derivatives, such as current source density, that represent the EEG activity of a given electrode as deviation from the activity of neighboring electrodes (e.g. Mo et al. [29] in 2013). Finally, one may use factor analysis strategies to compute weighted averages of EEG signals, where the weights are obtained using an objective algorithm with a precisely defined rationale (e.g. Scheeringa et al. [30] in 2008).

Covariance Mapping

Covariance mapping is a method that has been first described by Koenig et al. [31] (where the computational details are given). This method was designed to investigate spatially extended scalp field distributions and their correlation to some continuous external variable. The principle of this method assumes that there is a linear relationship of an EEG signal with an a priori unknown spatial distribution to the external variable. It has been successfully applied to combine multichannel EEG parameters and fMRI-RSN dynamics [32]. Thus, compared to global spectral power, covariance mapping yields topographical and therefore local information about individual EEG-RSN associations. The communality of these associations across subjects and eventual differences between subject groups can then be further tested for significance using randomization tests [33, 34].

Global Field Synchronization

Global field synchronization (GFS) has been proposed by Koenig et al. [35] and applied by Jann et al. [36] for combining with fMRI. GFS quantifies the amount of the total variance of the EEG at a given frequency that can be explained by a set of brain electric sources that oscillate with a common phase. There is thus an intrinsic relation of GFS to functional connectivity and network binding processes [37]. Technically, GFS is computed based on an eigen vector decomposition of the complex output of the fast Fourier transformation. For technical details about the computation of GFS, see Koenig et al. [35]. Importantly, GFS is mathematically independent of the global power spectrum. In the domain of combined EEG-fMRI, Jann et al. [36] found very interesting correlations between GFS in the α band and BOLD signals.

Microstate Maps

EEG electric field data display subsecond periods (60–120 ms) of stable brain states that repeat across time and individuals [35, 38]; these quasi-stable periods are called microstates [39, 40]. Microstate analysis is applied both to resting state and event-related potential data [41] and associated with the specific mental operations during spontaneous thought and under cognitive task conditions [42, 43]. Microstates are identified using spatial pattern recognition algorithms [44, 45]. Koenig et al. [46] identified 4 normative microstate maps based on a sample of about 500 normal subjects. The meaning of each microstate map is still not precisely resolved, but certain classes, for example a microstate class labelled D, have been shown to be shortened in schizophrenia patients, especially during hallucinations [38, 47–51], and the duration of another microstate class labelled A was shorter in patients suffering from panic disorder than in healthy controls [52]. Recently, some interesting studies reported a relationship of microstate maps and RSNs. Britz et al. [53] revealed the relationship of qEEG and RSNs by using spatial processing and general linear model analysis, and concluded that microstate maps A, B, C and D were related with BOLD signals in temporal, occipital, fronto-insular and frontoparietal areas, respectively. Similarly, Yuan et al. [54] correlated the time course of microstates (obtained by independent component analysis) and RSN fluctuations. They showed that each RSN has an association with one or several microstate maps (table 1).

Review of RSNs

Over the past decade, research has shown an increasing interest in RSNs in fMRI. RSNs represent a number of distinct functional networks that show temporally synchronized low-frequency BOLD signal fluctuations. Two main computational approaches are used to identify such RSNs, the seed-based approach and independent component analysis. While both approaches have advances and pitfalls, especially when it comes to avoiding artifacts and selecting the most interesting regions, both are equally valid to identify RSNs. For a detailed comparison of these approaches, see Fox and Raichle [3], Joel et al. [55] and Cole et al. [56]. Several distinct RSNs have been consistently found irrespective of the approaches used, such as the DMN, dorsal and ventral FPNs [executive control, attentional network and right and left working memory (or language) networks], SN, somatosensory and motor cortex network, auditory associated network, as well as primary, ventral and dorsal visual networks. Generally, researchers classify these RSNs as substrate of either higher cerebral functions or primary sensory functions. In this review, we are especially interested in DMN, FPNs and...
Table 1. Summary of the relationship between qEEG and RSNs

<table>
<thead>
<tr>
<th>Investigators</th>
<th>Subjects</th>
<th>qEEG</th>
<th>Frequency</th>
<th>Time</th>
<th>Electrodes</th>
<th>Global EEG</th>
<th>Local EEG</th>
<th>BIRI measure</th>
<th>Eyes bands</th>
<th>RSNs</th>
<th>task-negative network</th>
<th>task-positive network</th>
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<tbody>
<tr>
<td>subjects</td>
<td></td>
<td></td>
<td>domain</td>
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<tr>
<td>Laufs et al. [20]</td>
<td>NC (11)</td>
<td>power</td>
<td>whole</td>
<td>×</td>
<td>whole</td>
<td>O1–O2</td>
<td>1 + 2 EC</td>
<td>δ (1–4)</td>
<td>α (6–8)</td>
<td>β (13–30)</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Mantini et al. [26]</td>
<td>NC (15)</td>
<td>power</td>
<td>whole-collapsed across channels</td>
<td>×</td>
<td>×</td>
<td>whole, collapsed across channels</td>
<td>3</td>
<td>EC</td>
<td>multiple bands</td>
<td>α (6-15)</td>
<td>β (13–30)</td>
<td>±</td>
</tr>
<tr>
<td>Scheeringa et al. [30]</td>
<td>NC (20)</td>
<td>power and dipole</td>
<td>whole, weighted based on ICA</td>
<td>×</td>
<td>2</td>
<td>EO</td>
<td>δ (2-9)</td>
<td>±</td>
<td>± in frontal area</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Jann et al. [36]</td>
<td>NC (14)</td>
<td>GPS PWR</td>
<td>×</td>
<td>whole</td>
<td>×</td>
<td>2 + 3 EC</td>
<td>α1 (8.5-10)</td>
<td>α2 (10.5-12.5)</td>
<td>±</td>
<td>±</td>
<td>±</td>
<td>±</td>
</tr>
<tr>
<td>Musso et al. [84]</td>
<td>NC (11)</td>
<td>LORETA and microstate</td>
<td>×</td>
<td>whole</td>
<td>×</td>
<td>2 + 3 EC</td>
<td>10 microstate maps/subject</td>
<td>±</td>
<td>±</td>
<td>±</td>
<td>±</td>
<td>±</td>
</tr>
<tr>
<td>Britz et al. [53]</td>
<td>NC (8)</td>
<td>microstate</td>
<td>×</td>
<td>whole</td>
<td>×</td>
<td>3 + 2 EC</td>
<td>microstate map 1-4 (typical maps)</td>
<td>±</td>
<td>±</td>
<td>±</td>
<td>map 4 (D)</td>
<td>±</td>
</tr>
<tr>
<td>Hlinka et al. [77]</td>
<td>NC (20)</td>
<td>power</td>
<td>×</td>
<td>whole, collapsed across channels</td>
<td>×</td>
<td>3</td>
<td>EC</td>
<td>absolute and relative δ (1–4)</td>
<td>±</td>
<td>±</td>
<td>±</td>
<td>±</td>
</tr>
<tr>
<td>Jann et al. [32]</td>
<td>NC (20)</td>
<td>CovMap</td>
<td>×</td>
<td>whole, local info retained</td>
<td>×</td>
<td>3</td>
<td>EC</td>
<td>δ (1.0-3.5)</td>
<td>β1 (3.5-6.25)</td>
<td>α1 in central parieto-occipital</td>
<td>±</td>
<td>±</td>
</tr>
<tr>
<td>Yuan et al. [54]</td>
<td>NC (9)</td>
<td>microstate</td>
<td>×</td>
<td>whole</td>
<td>×</td>
<td>2 + 3 EC</td>
<td>microstate map 1–13</td>
<td>±</td>
<td>±</td>
<td>±</td>
<td>±</td>
<td>±</td>
</tr>
</tbody>
</table>
### Table 1. (continued)

<table>
<thead>
<tr>
<th>Investigators</th>
<th>Subjects (n)</th>
<th>qEEG</th>
<th>Frequency domain</th>
<th>Time domain</th>
<th>Electrodes</th>
<th>Global EEG</th>
<th>Local EEG</th>
<th>BRI measure</th>
<th>Eyes bands or maps (Hz)</th>
<th>RSNs</th>
<th>task-negative network</th>
<th>task-positive network</th>
</tr>
</thead>
<tbody>
<tr>
<td>Meyer et al. <a href="2013">93</a></td>
<td>NC (12)</td>
<td>power: electrophysiological correlation pattern</td>
<td>×</td>
<td>×</td>
<td>whole, collapsed across electrodes</td>
<td>×</td>
<td>3</td>
<td>EO</td>
<td>δ (2–4) θ (4–7) α (6–12) β (12–30)</td>
<td>δd αe βd δ (right FPN) α+β δ (right FPN)</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Mo et al. <a href="2013">29</a></td>
<td>NC (14)</td>
<td>power and CSD</td>
<td>×</td>
<td>O1, O2, Oz</td>
<td>×</td>
<td>2</td>
<td>EC EO</td>
<td>α (6–12)</td>
<td>EC ± EO: α power and CSD in posterior DMN nodes</td>
<td>–</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>Chang et al. <a href="2013">74</a></td>
<td>NC (10)</td>
<td>power</td>
<td>×</td>
<td>×</td>
<td>whole, average of a subset of electrodes</td>
<td>×</td>
<td>1</td>
<td>EC</td>
<td>α (individual peak ± 1 Hz) θ (4–7)</td>
<td>decreased α (increased θ) indicated increased correlation between DMN-DAN</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Razavi et al. <a href="2013">34</a></td>
<td>schizophrenia (11)</td>
<td>CovMap</td>
<td>×</td>
<td>×</td>
<td>whole, full local info</td>
<td>×</td>
<td>3</td>
<td>EC</td>
<td>δ (1.0–3.5) θ1 (3.5–6.25) θ2 (6.25–8.2) α1 (8.2–10.5) α2 (10.5–14.0) α3 (14.0–18.75) β1 (18.75–21.88) β2 (21.88–30.0)</td>
<td>the coupling of EEG frequency bands in DMN and left WMN, respectively, shifted toward lower EEG frequency in patients suffering from schizophrenia (CovMaps for the DMN of healthy controls in β1 were similar to those of patients in θ1 and α2; additionally, CovMaps for left WMN of healthy controls in α1, α2, and β1 were similar to those of patients in θ1 and θ2.)</td>
<td>–</td>
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</table>

DAN = Dorsal attentional network; WMN = working memory network; PWR = global spectral power; LORETA = low-resolution brain electromagnetic tomography; CovMap = covariance mapping; CSD = current source density; ± = no difference, – = untested; EC = eyes closed, EO = eyes open, ICA = independent component analysis, ROI = region of interest, NC = normal control, FC = functional connectivity. Musso et al. [84] tested DMN, executive function network and the dorsal and ventral pathways, and found single subject correlations.

1. Microstate maps 7–12 are of the same pattern: mainly sensory and motor networks in the general linear model (voxel wise).
2. Large variations between subjects leading to nonsignificant correlations at group level.
3. FC in DMN: FC of the average in 6 ROI associated with DMN.
4. One of 16 participants in toto.
5. Two of 16 participants in toto.
6. The approach used in this paper did not separate the dorsal FPN (DAN) from the ventral FPN (WMN).
7. One subject showed that both right and left FPNs had inverse relationships with α-band activity; in addition, the other subject showed only a negative correlation of the right FPN with activity.
the SN, which are attributed to higher cognitive brain functions [4, 7, 8, 32]. Another type of categorization of RSNs distinguishes networks that increase in BOLD intensity during task execution, the so-called task-positive networks, from task-negative networks. Typical task-positive networks are the FPNs and the SN [4, 6], whereas the DMN [2] is the major task-negative network.

Task-Negative Network: the DMN

The DMN is typically activated during the resting state while showing consistent deactivation during a wide range of cognitive tasks [2, 4, 57], which is a behavior typical for task-negative networks. In a meta-analysis of PET studies, Raichle et al. [2] observed that subjects in the awake resting state showed increased glucose metabolism in the posterior cingulate, in the inferior parietal lobule and the dorsal medial prefrontal cortex compared with the other brain regions. This network has become the most extensively investigated RSN in the field of fMRI- RSNs and is regarded to be associated with intrinsic brain activity, such as internal reasoning, mind-wandering and self-referential processes. The DMN further showed dysfunction in patients suffering with psychiatric and neurodegenerative disorders [58, 59], especially Alzheimer’s disease [60–62], and has been expected to be a predictor of diagnosis and/or a state marker for these diseases.

Task-Positive Networks: Dorsal and Ventral FPNs

Task-positive networks comprise brain areas that increase BOLD signals when examinees engage in attention-demanding cognitive processes [5, 63]. These task-positive networks usually comprise frontal and parietal brain areas, we will thus refer to these networks as FPNs. These networks could be separated into dorsal and ventral attention networks [64, 65]. The dorsal attention network, including the medial intraparietal sulcus, superior parietal lobule, supplementary motor area and precuneus, is associated with top-down attention-oriented control. The ventral attention network includes the (mainly right) temporoparietal junction and the ventral frontal cortex (and sometimes also supramarginal, superior temporal and inferior temporal gyri, but this may make a separation from the dorsal attention network difficult) and has been correlated with attention to the spatial locations of unexpected stimuli. Besides these attention systems described by Fox et al. [65], there are other RSNs that show a distinct but also task-positive pattern of frontal and parietal brain activation. Amongst them are the left and right executive control network [66] comprising dorsolateral prefrontal cortex, parietal lobe, middle temporal gyrus as well as the anterior cingulate, and language- and working memory-related networks involving associated brain areas like inferior frontal and middle temporal gyrus [8]. These networks often show separations into left and right hemispheric networks. What is to be noted is that the DMN and FPNs exhibit overall anticorrelations especially in the resting state [3, 4, 57]. This relationship suggested that the brain may switch or transfer resources between states of the more outward-oriented attentional focus and self-referential, inward-oriented cognitive processes. Accordingly, research has been interested in both normal and psychiatric patients. Specifically schizophrenia patients that show cognitive impairments in working memory [34, 67–69] and language [67, 70] as well as present symptoms such as hallucinations indicate that the respective networks might show pathophysiological alterations not just during task execution but also during the resting state.

Task-Positive Networks: the SN

More recently, not only frontal and parietal brain areas, but also the insular cortex have been found to be critical for spatial and verbal working memory in a number of studies in task-positive networks. Seeley et al. [6] identified an RSN associated with anxiety; this network was defined by co-activations of the dorsal anterior cingulate cortex and anterior insular cortices and termed SN. Seeley et al. [6] and Menon [71] further suggested that this SN supports an important function for switching between DMN and other task-positive networks such as the executive control networks [71, 72]. In line with his proposal, Palaniyappan et al. [73] proposed the concept of SN dysfunction in schizophrenia, since volume reduction in the anterior cingulate cortex and anterior insulae correlated with positive symptoms such as hallucinations and delusions.

Literature Review

We searched MEDLINE for all publications available up to August 2013 studying the association between EEG and fMRI-RSNs with the keywords: EEG, fMRI and resting state. We only included studies with adult human subjects and those employing a simultaneous EEG and fMRI design under a no-task resting state condition. We were interested in three prominent RSNs that are particularly interesting in a psychiatric context, namely the DMN, FPNs (including the working memory, executive control or dorsal attention networks) and the SN. These three networks are considered as neurocognitive systems...
central for higher brain processes that are the biological substrate for self-relevant, attentional and task-switching functions [32, 72, 74, 75].

Studies on epilepsy, seizures, encephalitis, ischemia, vegetative state, sleep disorder and amnesia patients were excluded, as well as studies measuring adolescents, children or elderly subjects in order to investigate development, autism, attention deficit hyperactivity disorder and dementia. In addition, the scope was limited to undisturbed, spontaneous resting states, such that studies including tasks, sleep, meditation and neuromodulating interventions such as transcranial magnetic stimulation or anesthesia were not considered. Studies with a primary focus on technical issues were also excluded. After adapting these inclusion and exclusion criteria, twelve papers were available (and one additional paper with schizophrenia patients).

Each of these papers was summarized under the following aspects:
- Sample size
- Methods used to quantify the EEG (following the scheme outlined above): we particularly distinguished time domain from frequency domain results, and within the frequency domain studies distinguished the different frequency bands
- Accounting for the spatial information of the EEG, namely if the data were collapsed across the entire scalp or across selected regions, or whether some spatial derivatives were employed
- Methods used to identify BOLD signal correlates of EEG dynamics
- Peculiarities of the study design (e.g. eyes open/closed)
- Results, in terms of RSNs showing a correlation with the specific EEG parameters

Table 1 shows a summary of the contents of each study. Based on this information, we attempted to answer the question if there are particular EEG features that, across the evidence given by the papers included, can be used as indicators of the activation or deactivation of particular fMRI-RSNs. This would extend the empirical basis for a discussion of the broad body of knowledge about EEG resting state abnormalities in psychiatric patients. The feasibility of this endeavor is discussed in the remainder of the article.

### Discussion

**EEG Frequency Domain**

#### α-Band Correlates of fMRI-RSNs

Table 1 shows that the majority of the studies reported on frequency domain EEG correlates of fMRI activation patterns and that the majority of these correlates were found in the α band and to a somewhat lesser extent in the β band. α-Band activity is currently seen as an interplay within thalamocortical networks that are important for sensory gating processes, and the control and allocation of vigilance and attention [76]. Because α-band activity is most pronounced over posterior scalp regions, there is a hypothesis about positive correlations between α-band activity and the DMN. This is indeed what most studies combining EEG and fMRI showed, either using global power spectra [26, 77], current source density in occipital electrodes [29] or covariance mapping [32], positive DMN covariance over parieto-occipital regions in the upper α band. A study by Jann et al. [36] showed that not only α-band power but also α-band synchronization correlated with DMN activation, assigning an additional, previously suggested role to α-band activity as a network-binding mechanism [76]. Interestingly, the same authors could also relate individual α-band features to structural connectivity measures in regions that interconnect the different nodes of RSNs, including the DMN [78].

However, fMRI correlates of α-band spectral power were not limited to the DMN. Laufs et al. [25] demonstrated the relationship between α power and (ventral) FPN in fMRI for the first time. Gonçalves et al. [79] confirmed the result by reporting that 3 of 7 participants showed a relationship between frontoparietal lobes and α-band activity. These studies suggest that α-band activity was inversely correlated to FPN activation. Since the DMN is both positively correlated to α-band activity and inversely correlated to FPN activation (see Review of RSNs), these findings are mutually compatible and can be integrated under the view of task-related allocation and de-allocation of attentional resources.

Importantly, a series of papers by Jann et al. [32, 36] suggests that the upper and lower α GFS, or global and local power, have very different fMRI counterparts. The upper and lower α band may thus also represent quite different functional aspects and it may be important to separate the α band to correctly investigate brain functional networks.

#### β-Band Correlates of fMRI-RSNs

Apart from the above-mentioned α-band findings, there is a series of β-band correlates with higher cognitive RSNs. Apparently, despite the classical functional separation of α- and β-band EEG activity, the correlation pattern of β EEG with fMRI-RSN during the resting state often resembles that encountered in the α band: a study by Mantini et al. [26] showed that higher values of both β and α power correlated positively with the DMN and neg-

<table>
<thead>
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<th>Summary of the contents of each study.</th>
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<tbody>
<tr>
<td>Sample size</td>
<td>Methods used to quantify the EEG (following the scheme outlined above): we particularly distinguished time domain from frequency domain results, and within the frequency domain studies distinguished the different frequency bands.</td>
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<tr>
<td>Accounting for the spatial information of the EEG, namely if the data were collapsed across the entire scalp or across selected regions, or whether some spatial derivatives were employed.</td>
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<tr>
<td>Methods used to identify BOLD signal correlates of EEG dynamics.</td>
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<tr>
<td>Peculiarities of the study design (e.g. eyes open/closed).</td>
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<tr>
<td>Results, in terms of RSNs showing a correlation with the specific EEG parameters.</td>
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**DOI:** 10.1159/000363342
atively with the FPN, and that these rather common patterns for α and β power contrasted with the correlation patter for δ, θ- and γ-band power. Hlinka et al. [77] reported that both absolute and relative β power increases correlated with DMN activation, similarly as relative EEG α activity.

However, important distinctions exist between the two frequency bands, too: in the data presented by Jann et al. [32], α and β band separated naturally, based on a classification of their correlation patterns with RSN networks, indicating that there are systematic differences. A paper by Laufs et al. [14], while not correlating the EEG to previously determined fMRI-RSNs, showed that β2 (17–23 Hz) power was positively correlated with posterior cingulate and dorsal medial prefrontal areas, while the α (8–12 Hz) power was negatively correlated with prefrontal and parietal areas. These results indicated that the relation of EEG β activity and RSNs are still an open question.

Slow-Frequency-Band Correlates of fMRI-RSNs
Some of the studies reported in table 1 also included correlates of the DMN to slow frequencies such as θ and δ. Increases in frontal θ were previously attributed to task engagement [80, for review see ref. 81, 82]. In contrast, increases in general θ and δ power have often been related to wake-sleep transitions or reduced vigilance [83]. The general consensus on simultaneous EEG/fMRI studies is, however, that an increase in θ power, particularly in the frontal regions, may be an index for decreased DMN activity. Thus, θ may have an inhibitory function on the task-negative DMN [30, 32]. This hypothesis is supported by the finding that increased θ tended to be associated with an increased correlation between the DMN and FPNs (dorsal attentional network) as well as other networks (i.e. SN) [74]. Similarly, increased δ power was negatively correlated with functional connectivity within the DMN [77]. Dysfunctional coupling of dominant resting EEG frequencies and RSNs may thus lead to severe information processing failures due to an insufficient suppression of normally anticorrelated RSNs as well as pathologically altered alertness states. In that sense, a recent study in psychiatric patients demonstrated a shift toward slow-wave-frequency coupling to the DMN and FPN (left working memory network) in patients with schizophrenia spectrum disorders [34]. These findings indicate that there may be no direct correlation between the frequency of qEEG and RSNs. In other words, the relationship between neurophysiological activity and the effect of BOLD might indicate alterable endophenotypes of mental diseases.

EEE Time Domain
Three studies have investigated fMRI-RSNs and conducted EEG microstate analysis. Musso et al. [84] combined microstate and low-resolution brain electromagnetic tomography as qEEG. They showed spatial and functional similarities between fMRI and qEEG in each subject. Each microstate factor in each participant was correlated with some RSN, although there was no association between the three main networks (DMN, FPNs and SN) and the results of microstate and low-resolution brain electromagnetic tomography at the group level. Britz et al. [53] confirmed the relationship between typical microstate maps, which have been defined in previous studies and fMRI-RSNs. Of note, the SN was positively correlated with map C, and the FPN was negatively correlated with map D. These results offer new perspectives about the similarity of fMRI and EEG microstate maps [53, 85, 86]. On the other hand, Yuan et al. [54] verified the communality between fMRI-RSNs and EEG microstates using independent component analysis. The result is more combinational than that of Britz et al. [53], although it is also notable for considering the relationships on the basis of functional brain networks. Taken together, the relationship between fMRI-RSNs and EEG microstates remains controversial. However, we showed an interesting correlation, as the microstate map indicated alterations in patients with frontotemporal dementia [51], and this result matches with the result of Britz et al. [53] on the correlation of map 3 with the SN and the fMRI study showing dysfunction of SN in patients with frontotemporal dementia.

Conclusion

Across many of the studies reviewed here, global α-band power appeared to be an interesting parameter, representing a functionally relevant overall assessment of the brain functional state. Most studies of EEG global α power showed widespread and often inverse correlations with BOLD data. In addition, the interaction between the DMN and FPNs seems to be suppressed during periods of high α power. These results suggest that α-band activity may be important to understand brain connectivity at a system level, as it affects the interactions between different RSNs [74].

When taking the local information contained in the spectral EEG into account, frontal θ and occipital α seem to be interesting counterparts to RSN dynamics [32, 74]. Nevertheless, the spatial resolution of EEGs is consider-
ably inferior to that of other methods. In the context of psychiatric diseases, α- and θ-band activity is important for the understanding of depression [87–89] and schizophrenia [49, 90–92]. It seems natural to conclude to dedicate more scientific attention to these large-scale and/or local α and spatial θ processes (see also the review by Klimesch [81]).

Time domain approaches such as microstates open another interesting avenue, because they were also shown to be correlated to RSNs [53], seem to be rather independent of spectral parameters [46] and show systematic links to psychopathology [51]. Given the relevance and independence of frequency and time domain analyses, and their link to psychiatrically relevant functions, an integration of the different methods seems to be particularly promising and attractive.

**Limitations**

One of the difficulties of the combination of fMRI and EEG studies is interindividual variance, as some studies have demonstrated. For example, Gonçalves et al. [79] confirmed that 3 of 7 subjects showed a correlation with the frontal-parietal-occipital lobes, but other subjects had different patterns. The studies by Musso et al. [84] and Meyer et al. [93] also presented variation within individuals. Meyer et al. [93] investigated the relationship between electrophysiological correlation patterns and fMRI-RSNs with eyes opened and a long scanning time. Their outcome showed large variations in each subject and revealed temporary changes in RSNs. It is thus important to study the fundamental mechanisms of EEG-fMRI associations in further detail and further extend the repertoire of methods.

Another important limitation is that both fMRI and EEG are neuronal mass events that may represent different, and possibly intermixed, functions, including excitatory and inhibitory activity, top-down and bottom-up processing or content representation as opposed to neuromodulation [76, 94]. Despite these limitations, it is critical to note that combined RSNs-qEEG studies yield valuable information. For example, in psychiatry, the conclusions about resting state abnormalities that can be drawn based on EEG or fMRI alone are still quite primitive. The paper by Razavi et al. [34] might provide first evidence that RSNs and qEEG show common alterations in patients suffering from schizophrenia compared to healthy controls. Schizophrenia patients had the spatial EEG signatures of RSN activity consistently shifted from higher- to lower-frequency bands. It is possible that the link between abnormalities of no-task resting state brain activity may be a key concept to the understanding of psychopathology.

**References**


14 Neuropsychobiology 2015;71:6–16
DOI: 10.1159/000363342

Nishida/Razavi/Jann/Yoshimura/Dierks/Kinoshita/Koenig


