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# Studying the default mode and its mindfulness-induced changes using EEG functional connectivity

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**The default mode network (DMN) has been largely studied by imaging, but not yet by neurodynamics, using electroencephalography (EEG) functional connectivity (FC). mindfulness meditation (MM), a receptive, non-elaborative training is theorized to lower DMN activity. We explored: (i) the usefulness of EEG-FC for investigating the DMN and (ii) the MM-induced EEG-FC effects. To this end, three MM groups were compared with controls, employing EEG-FC (–MPC, mean phase coherence). Our results show that: (i) DMN activity was identified as reduced overall inter-hemispheric gamma MPC during the transition from resting state to a time production task and (ii) MM-induced a state increase in alpha MPC as well as a trait decrease in EEG-FC. The MM-induced EEG-FC decrease was irrespective of expertise or band. Specifically, there was a relative reduction in right theta MPC, and left alpha and gamma MPC. The left gamma MPC was negatively correlated with MM expertise, possibly related to lower internal verbalization. The trait lower gamma MPC supports the notion of MM-induced reduction in DMN activity, related with self-reference and mind-wandering. This report emphasizes the possibility of studying the DMN using EEG-FC as well as the importance of studying meditation in relation to it.**

**Keywords:** default mode network; mindfulness meditation; functional connectivity; mean phase coherence; electroencephalography

## INTRODUCTION

This article focuses on two inter-related topics. The first is the identification of the electroencephalographic functional connectivity (EEG-FC) signature of the default mode network (DMN). The DMN, mostly studied by functional magnetic resonance imaging (fMRI), is a task-inhibited network active during resting state and largely related with mind-wandering (Gusnard *et al.*, 2001; Raichle *et al.*, 2001; Buckner *et al.*, 2008;) and self-referential activity (Northoff *et al.*, 2006), which includes the medial prefrontal cortex (mPFC), posterior cingulate cortex (PCC), inferior parietal lobule (IPL), medial temporal lobe (MTL) and lateral temporal cortex (LTC) (Buckner *et al.*, 2008). The second topic of this report is the study of EEG-FC alterations following mindfulness meditation (MM) practice and their possible relation with the DMN. MM, as practiced in the West and as studied in research paradigms, is a technique of remaining aware and noticing the salient features of present experience while refraining from evaluative processes, conceptual elaboration and mind wandering (Kabat-Zinn, 2003). Previous research has indicated that MM may engage mechanism for vigilance, monitoring and cognitive control (Lutz *et al.*, 2008; Zeidan *et al.*, 2010; Hölzel *et al.*, 2011b). Thus, it was expected and indeed found that it would result in decreases of activity in areas of DMN, specifically in mPFC, which has been linked to self-referential narrative thinking and valuation.

In this report we build on a recent publication on DMN activation during MM, in which we reported two major findings (Berkovich-Ohana *et al.*, 2012). The first was the identification of DMN activity as a reduction in gamma power within frontal-midline regions during a time-production (TP) task compared with resting state. The choice of the TP task to index a reduction in DMN activity was based on previous work showing that timing systematically activates several cortical regions, including: (i) attentional regions, such as the right parietal and dorsolateral prefrontal cortex (DLPFC) (reviewed by Walsh, 2003; Oliveri *et al.*, 2009; Wittmann, 2009), consistent with a great body of behavioral studies showing that attention is mandatory for accurate timing (reviewed by Brown, 1997); (ii) the supplementary motor area (SMA) (Coull and Nobre, 1998; Ferrandez *et al.*, 2003; Coull, 2004; Macar *et al.*, 2004) and (iii) the anterior insular cortex (Craig, 2002, 2009; Wittmann *et al.*, 2010). The right parietal and SMA regions are part of the dorsal attention network (Corbetta *et al.*, 2008), comprising a task-activated network, also named the ‘extrinsic system’, suggested to be antagonistic to the task-inactivated DMN (Fox *et al.*, 2005; Golland *et al.*, 2007; Tian *et al.*, 2007) and the DLPFC and anterior insular cortex are part of the frontoparietal control system, interposed between the ‘intrinsic’ and ‘extrinsic’ systems (Vincent *et al.*, 2008) and possibly adjudicating between these two potentially competing brain systems (Vincent *et al.*, 2008; Spreng *et al.*, 2010; Smallwood *et al.*, 2012). To conclude, the TP task is related with the task-activated network and the frontoparietal control system, hence with DMN deactivation. The second finding was that MM practitioners exhibited reduced frontal gamma power, related to DMN activity, as a trait (long term) effect. Nolfe (2011) called attention to the need to expand this study to include functional connectivity, which is precisely the aim of this work.

There is a growing effort to establish the relationship between the DMN-related blood oxygenated level dependent (BOLD) fMRI signal and electrophysiology (Broyd *et al.*, 2009). Most DMN-EEG studies investigated either spectral power (Chen *et al.*, 2008; Berkovich-Ohana *et al.*, 2012) or its correlation with the fMRI BOLD signal (Laufs *et al.*, 2003; Mantini *et al.*, 2007; Meltzer *et al.*, 2007; Scheeringa *et al.*, 2008). Accumulating evidence suggests that while DMN activity is generally negatively correlated with frontal and midline theta (4–8 Hz) power (Meltzer et al., 2007; Scheeringa *et al.*, 2008), the activity in the prefrontal area of the DMN, which is strongly related to self-reference, is manifested in the gamma (25–45 Hz) power band (Mantini *et al.*, 2007; Chen *et al.*, 2008; Berkovich-Ohana *et al.*, 2012). Additionally, the

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posterior regions of the DMN, including parietal-occipital midline cortex, were found to be related positively with alpha (8–13 Hz) power (Knyazev *et al.*, 2011). The manifestation of DMN in EEG-FC has not been reported yet, excluding one conference paper (Chen, 2007), relating DMN activity with higher theta and alpha coherence in the frontal area.

Various meditation techniques were shown to induce changes in EEG-FC (summarized by Cahn and Polich, 2006; Ivanovski and Malhi, 2007). Several meditation studies reported increased FC as both state and trait effects (Cahn and Polich, 2006), the majority being Transcendental Meditation (TM) studies reporting increased state coherence in the theta–alpha range, along two axes: bilateral frontal (Dillbeck and Bronson, 1981; Farrow and Hebert, 1982; Travis and Wallace, 1999; Travis, 2001; Hebert *et al.*, 2005) and frontal-posterior (Aftanas and Golocheikine, 2001, 2002). Similar trait effects were found in TM practitioners during rest or cognitive tasks (Orme-Johnson and Haynes, 1981; Dillbeck and Vesely, 1986; Travis, 1991). Very few meditation studies investigated FC in other forms of meditation. These include reports of state increased coherence in the bilateral frontal theta–alpha range during Zen practice (Murata *et al.*, 2004), and increased frontal and frontal-posterior theta FC during Sahaja Yoga meditation (Aftanas and Golosheykin, 2001). Several studies also reported gamma FC alterations. Lutz *et al.* (2004) studied loving–kindness–compassion meditation in proficient Tibetan practitioners, and reported increased state and trait synchrony. In contrast, Faber *et al.* (2004) found in a Zen practitioner, a state reduction in gamma coherence. In contrast to the generally increased EEG-FC in various meditation forms and in line with Faber *et al.* (2004), Lehmann *et al.* (2012) recently reported reduced state FC for five meditation traditions (Tibetan Buddhists, QiGong, Sahaja Yoga, Ananda Marga Yoga and Zen), for all frequency bands (delta to gamma). This short review reveals ambiguity in the EEG-FC effect of meditation in general as well as a complete lack of studies reporting FC during or following MM practice.

Here, we employ our unique sample of MM practitioners, including three levels of expertise and a suitable control group (Berkovich-Ohana *et al.*, 2012) to explore: (i) the usefulness of EEG-FC for the investigation of a subtle shift in DMN activity; (ii) what the MM-induced trait and state EEG-FC effects are as a function of MM expertise and whether they reflect DMN activity changes. Based on the reports relating DMN activity to EEG as well as on the meditation literature, we focused our analyses on the theta, alpha and gamma bands. Similar to our previous work, DMN activity was identified as a change in FC in a TP task compared to resting state, and hemispheric asymmetry was further considered. In relation to the two questions raised, we tested the following hypotheses based on our previous report and the surveyed literature: (i) EEG –FC would be useful in the study of the DMN, possibly seen as decreased frontal-midline gamma FC and increased frontal theta–alpha FC and (ii) MM practitioners would exhibit lower activity in DMN-related EEG-FC as a trait.

## METHODS

### Participants and procedure

Participants were 36 MM practitioners (all practice within the Theravada tradition), divided into three groups: short, intermediate and long-term (ST, IT and LT, respectively, $n = 12$ each), with varying expertise (mean of ~900, ~2570 and ~7500 h, respectively) and 12 age-matched controls, all right-handed. The research was approved by the institutional ethical committee and informed consent was obtained from participants.

EEG was recorded for 5 min during resting state (RS), a TP task, and a meditation (MED) session of 15 min, all conditions eyes-closed (additional tasks were excluded from this report). For a detailed exposition of the TP task and its analysis, see Glicksohn and Hadad (2012). Briefly, the participants produced target durations (4, 8, 16 and 32 s) by pressing a button. Participants were not supervised as to their strategy and counting was used in >95%. The TP analyses and results have been reported elsewhere (Berkovich-Ohana *et al.*, 2011, 2012).

At the end of the recording session, participants were questioned as to their experiences during the different tasks, by a semi-structured interview. Specifically, the meditation questionnaire comprised several questions, including: (i) did you fall asleep during the meditation session; (ii) what was the meditation depth, compared to your averaged ordinary meditative experience (1, very low; 10, very high) and (iii) what was the percentage of 'free-from-thought' time during the session.

### EEG analysis

EEG was recorded with a 65-channel geodesic sensor net (EGI), sampled at 500 Hz and referenced to the vertex (Cz), with analog 0.1–200 Hz band-pass filtering. Alternating current line noise was removed by a 50 Hz digital notch filter. Impedance was usually kept under 40 kΩ, well below the 200 kΩ limit for accurate signal acquisition with this system (Ferree *et al.*, 2001). The data were referenced offline to average reference and then visually screened for artifacts. Whenever electrodes were affected in a widespread distribution by artifacts, data were excluded. Whenever several channels exhibited a noisy recording due to local high impedance (>40 kΩ, mean of three electrodes per epoch, in ~10% of the epochs), the corrected values were off-line calculated using spherical spline interpolation (Perrin *et al.*, 1989).

For each condition, the first 16 non-overlapping, artifact-free epochs of 2.048 s were extracted for further analysis. For MED, epochs were extracted from the middle (between 5 and 10 min from the start) to enable 'settling' in the condition. From the TP task, all epochs were taken from the period prior to pressing the button, thus excluding the possibility of a motor artifact.

Cortically induced gamma activity is known to be at possible risk of contamination with electromyographic (EMG) muscular activity (Whitham *et al.*, 2007), or saccade-related spike potentials (SP) due to eye movements (Yuval-Greenberg and Deouell, 2009). To minimize this risk, we used four steps for caution: (i) our entire report deals with eyes-closed conditions, whereas the SP is elicited at the onset of small saccades which occur during eyes-open fixation (Martinez-Conde *et al.*, 2004); (ii) given that the EMG peaks at 70–80 Hz (Cacioppo *et al.*, 1990), we used much lower frequencies (25–45 Hz); (iii) we excluded all the circumference electrodes, closest to eyes, neck and face muscles (Figure 1) and (iv) we assessed the reliability for all electrodes included in this study using the coefficient of variation (CV) of log gamma power, which can be viewed as a measure of pattern stability (Fingelkurts *et al.*, 2006). This analysis revealed high internal consistency reliability during RS, MED and TP (detailed in Berkovich-Ohana *et al.*, 2012).

There are different ways of assessing phase synchronization between a pair of EEG signals (for a review, see Pereda *et al.*, 2005). We used the mean phase coherence (MPC) index (Mormann *et al.*, 2000). MPC is a measure of how the relative phase is distributed over the unit circle. If two signals are phase synchronized, the relative phase will occupy a small portion of the circle and MPC is high and vice versa (Pereda *et al.*, 2005). Thus, MPC is close to 0 for uncorrelated signals, whereas it approaches 1 if there is strong phase synchronization. For further mathematical details about the method, see Bhattacharya and Petsche (2001, 2005), Pereda *et al.* (2005) and Reiterer *et al.* (2009). The

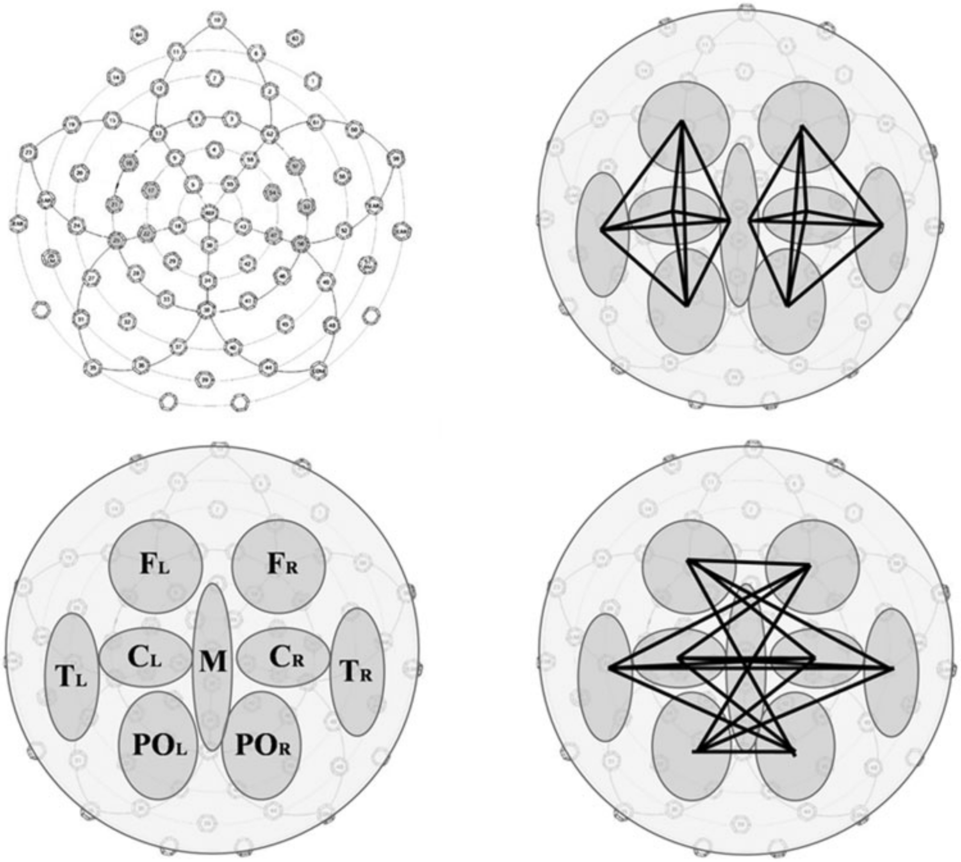

**Fig. 1** Electrode net configuration and ROIs used for MPC calculations (right) as well as intra- (top left) and inter- (bottom left) hemispheric long-range connections used.

application of MPC analysis is not a common practice, therefore, we provide more explanatory comments as well as a comparison of our results with the well-known coherence analysis showing a very high consistency between the two methods (see Supplementary Data).

As MPC is independent of frequency, the raw EEG signal was filtered into the different frequency bands prior to the calculation of MPC values for each electrode pair [i.e. $(65 \times 64) / 2 = 2080$ MPC values for each epoch]. The MPC cannot be supposed to be normally distributed as its values are bounded within the interval [0, 1], hence, we used the Fisher *z*-transformation for statistical comparisons. In order to reduce the dimensionality of the data, nine regions of interest (ROIs) were defined (10 intra-hemisphere connections and 16 inter-hemisphere connections; Figure 1): left and right frontal (F), central (C), temporal (T), parietal-occipital (PO) and midline (M). The mean MPC between different ROIs was calculated as the mean *z*-transformed MPC value of all the possible pairwise connections between the two ROIs.

### Statistical analyses

Analyses of variance (ANOVAs) were performed on the ROI mean *z*-transformed MPC values. The first two were designed to answer the question of DMN-related changes in MPC, testing the inter-hemisphere (inter-HEM) and intra-hemisphere (intra-HEM) connections, respectively, with one grouping factor (C, ST-MM, IT-MM and LT-MM) and with repeated measures on condition (RS and TP), band (theta, alpha and gamma), hemisphere (used only in the intra-HEM ANOVA) and connections (16 inter-HEM or 10 intra-HEM), applying the Greenhouse–Geisser corrected *P*-values.

To answer the question of the trait effect of MM expertise level on MPC, we used two additional ANOVAs, with inter-and intra-HEM connections, respectively. These ANOVAs were conducted only on RS, with a grouping factor and repeated measures on band (used only in the intra-HEM ANOVA), hemisphere and connections (as above).

Finally, to answer the question of state effects in the MM groups, we compared only the MPC values of the MM groups. We did not include any 'meditation' state for the control group, to avoid any procedure that would not be a just comparison with MM. Thus, two ANOVAs were conducted with one grouping factor (three MM groups) and repeated measures on condition (RS and MED), band, hemisphere (as above) and connections (as above).

Although statistically significant results were reported for ROIs only, we added topographic distributions of pairwise electrode MPC values (Figures 2B and 3B) to visualize the more precise distribution of FC on the scalp. For *post hoc* hypotheses we used *t*-tests (asterisk in the figures indicating respective *P*-values, adopting a minimal value of $P < 0.01$ due to multiple tests) as well as Pearson correlations.

## RESULTS

### First-person reports

None of the participants reported sleeping during the meditation session. The reported meditation depth was generally above the average score (of 5), indicating a relatively deep meditative state and was similar for the three MM groups: 5.7 ± 1.7, 6.4 ± 1.8 and 6.9 ± 2.2, for the ST, IT and LT-MM, respectively [$F(2,35) = 1.11$; MSE (mean square error) = 3.7, $P = \text{ns}$]. The percentage of 'free-from-thought' time during the session was significantly different for the three MM groups, rising with expertise: 57.8 ± 22.9, 67.7 ± 29.8 and 86.2 ± 18.3, for the ST, IT and LT-MM, respectively [$F(2,35) = 3.91$; MSE = 568,

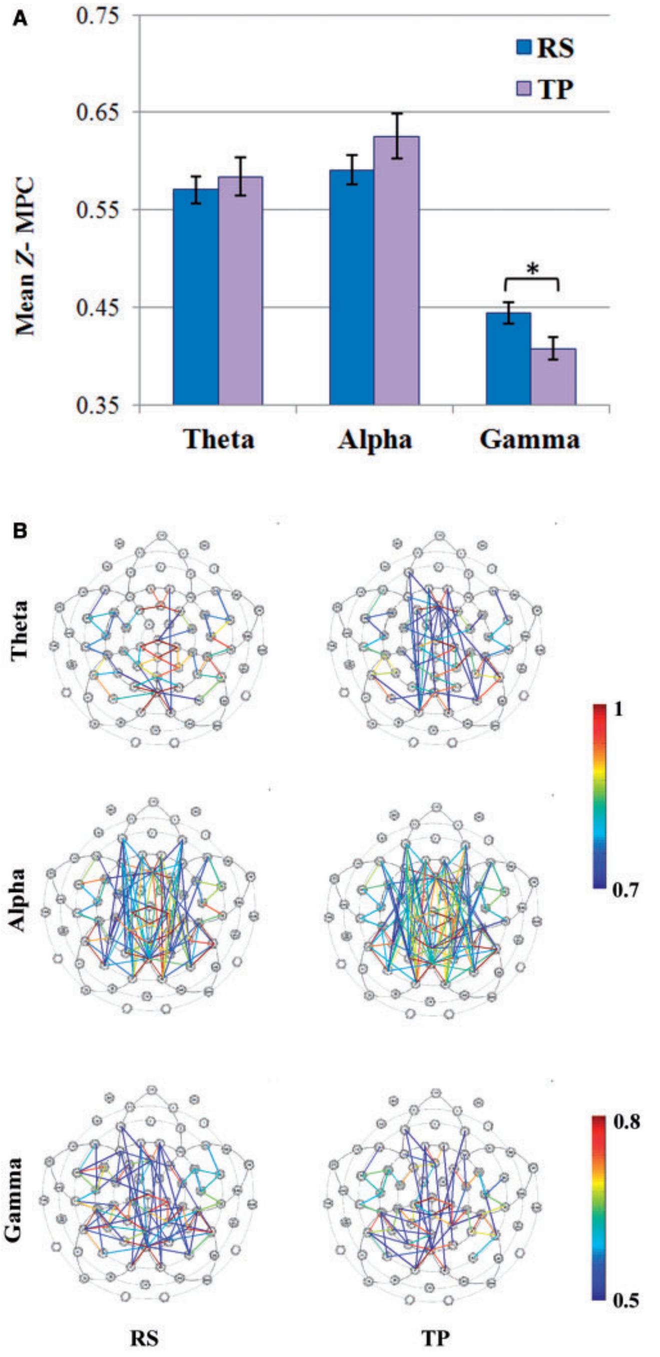

**Fig. 2** (**A**) Mean z-MPC within the intra-HEM connections in the three bands during resting state (RS; left) and the time production (TP; right) task. $^*P < 0.01$. (**B**) Topographic distribution of mean z-MPC values over all subjects ($n = 48$) for individual intra-HEM connections, within the three bands, theta (top), alpha (middle) and gamma (bottom).

$P < 0.05$]. There was no significant correlation between meditation depth and 'free-from-thought' percentages. This could be expected, as meditative depth is scaled compared with the ordinary meditation experience, which varies between participants markedly, and shares no common scale between participants. In contrast, percentages of time shares a common time scale. Additionally, there was no significant correlation between 'free-from-thought' percentages and MPC, which survived the correction for multiple comparisons. These results provide an independent evaluation of relatively deep and 'free-from-thought' laboratory-induced meditative experiences.

### DMN-related MPC changes

In the first ANOVA testing inter-HEM MPC changes in the transition from RS to TP, neither main effect for condition nor any of its interactions were uncovered. Turning to the second ANOVA testing intra-HEM FC, we found a significant condition × band interaction [$F(2,68) = 3.19$; $\mathrm{MSE} = 0.131$, $P < 0.05$], whereas gamma MPC decreased during TP compared to RS, alpha MPC somewhat increased (Figure 2). *Post hoc t*-tests indicated only a significant decrease in gamma MPC during the TP compared with RS [$t = -2.88$, $df = 44$, $P < 0.01$]. This suggests that DMN-related MPC could be generally seen within the gamma band. In addition, we noted three other interactions of interest: The first was a significant band × hemisphere interaction [$F(2,68) = 4.11$; $\mathrm{MSE} = 0.026$, $P < 0.05$], with alpha MPC being generally higher and gamma MPC slightly lower in the right hemisphere (relative to the left). The second was a significant band × connections interaction [$F(18,612) = 9.32$; $\mathrm{MSE} = 0.012$, $P < 0.001$]: the connections between the frontal and other ROIs (F-T, F-PO and F-M) showed highest alpha and lowest gamma MPC, whereas the C-T connections showed highest theta and gamma MPC and lowest alpha MPC. The third was a hemisphere × connections interaction [$F(9,306) = 2.78$; $\mathrm{MSE} = 0.015$, $P < 0.05$] stemming from lower MPC between the Temporal ROI and others (T-C, T-PO and T-M) in the left hemisphere. As to the question of group differences, we found a significant group × hemisphere × connections interaction [$F(27,306) = 1.94$; $\mathrm{MSE} = 0.015$, $P < 0.05$] stemming from: (i) higher MPC in the left hemisphere between the F-M and T-PO connections in the C and ST-MM groups compared to the IT-MM and LT-MM groups and (ii) higher MPC in the right hemisphere between the F-PO and PO-M connections in the C and ST-MM groups compared with the IT-MM and LT-MM groups. The group interaction did not include condition, hence we conclude that there are no group differences related to the way the DMN deactivates during the transition from RS to a TP task, which was the main question tested here.

### MM trait effects in MPC

In the third ANOVA testing the trait effect of MM expertise within inter-HEM MPC during RS, we found, as before, no interesting effects. In contrast, looking at intra-HEM trait differences between the C and the various MM groups (fourth ANOVA), we uncovered two main effects: (i) band [$F(2,68) = 38.76$; $\mathrm{MSE} = 0.108$, $P < 0.001$], with alpha MPC values being the highest and gamma MPC the lowest, as before; (ii) connections [$F(9,306) = 14.15$; $\mathrm{MSE} = 0.024$, $P < 0.001$], with PO-M exhibiting the highest value and F-C and T-M the lowest values.

We further uncovered three significant two-way interactions. The first was a band × hemisphere interaction [$F(2,68) = 3.77$; $\mathrm{MSE} = 0.019$, $P < 0.05$]: as before, whereas alpha MPC was generally higher in the right, gamma MPC was higher in the left hemisphere. The second was a band × connections interaction [$F(18,612) = 3.36$; $\mathrm{MSE} = 0.012$, $P < 0.001$], whereas alpha MPC was generally higher compared to theta MPC, this situation is reversed for C-T. The third was a hemisphere × connections interaction [$F(9,306) = 2.63$; $\mathrm{MSE} = 0.011$, $P < 0.05$]: MPC values for the connections C-T, T-M and C-PO were highest in the right and C-M MPC was highest in the left hemisphere.

More importantly, there was a significant group × band × hemisphere interaction [$F(6,68) = 2.73$; $\mathrm{MSE} = 0.019$, $P < 0.05$] (Figure 3). It should be emphasized that the exact profile of the decrease in MPC over groups is different, as we did not find a group main effect. Thus, we discuss each band and hemisphere separately. In the theta band, we see right greater than left MPC in the control group compared with the MM practitioners, irrespective of expertise. In the alpha band, the MM practitioners exhibit a gradient of

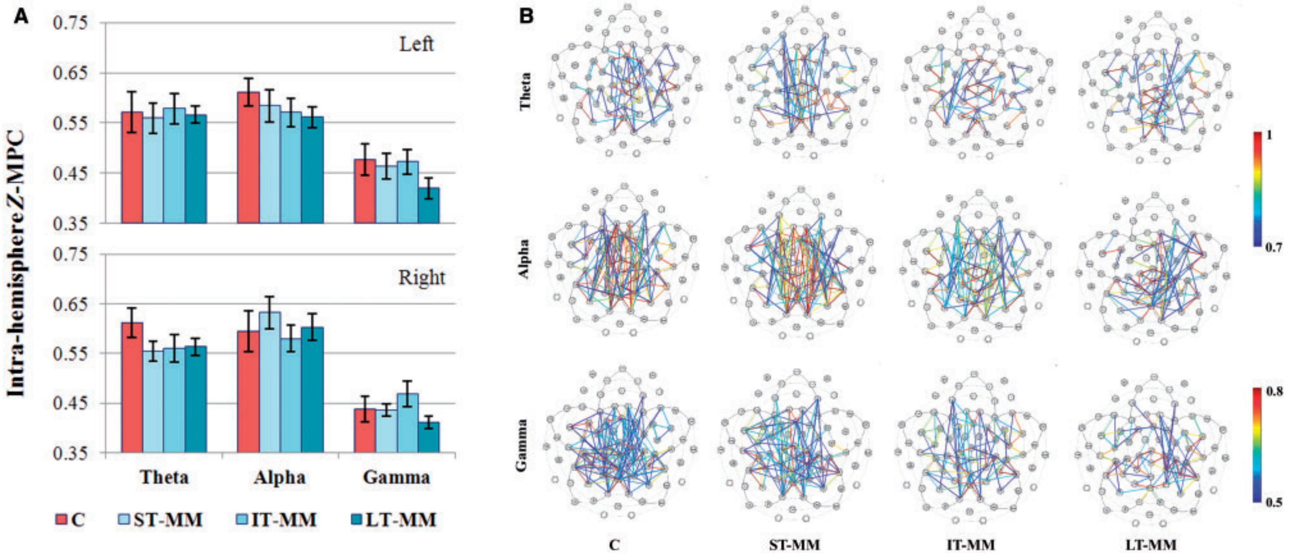

**Fig. 3** (**A**) Mean z-MPC group differences during the resting state: the group · band · hemisphere interaction. (**B**) Topographic distribution of mean *z*-MPC values over the different groups for individual intra-HEM electrode connections within the three bands, theta (top), alpha (middle) and gamma (bottom).

lower MPC values compared to controls seen in the left hemisphere, whereas their right hemisphere values generally exceed those of the control group. A *post hoc* ANOVA designed to compare alpha MPC asymmetry scores (mean left minus right alpha MPC) between the MM and C groups yielded a significant increase in asymmetry toward right hemisphere in the MM [$F(1,47) = 6.113$; MSE = 0.004, $P = 0.01$]. In the gamma band, we see a lower MPC value only in the LT-MM compared with controls, especially in the left hemisphere. A *post hoc* Pearson correlation between mean left gamma MPC and expertise (years) yielded a significant negative correlation [$r = -0.462$, $P < 0.005$, $n = 36$].

### MM state effects in MPC

In the fifth ANOVA testing the state effect of MM within intra-HEM MPC, we uncovered a significant condition × band × hem interaction [$F(2,50) = 3.26$; MSE = 0.021 , $P < 0.05$], depicted in Figure 4. As can be clearly seen, gamma and theta MPC were largely unchanged. Although alpha MPC was high and of equal magnitude in both the left and right hemispheres during MED, it was only during RS that we see MPC R > L asymmetry. We also observed significant band × connections ($P < 0.01$) and condition × band ($P < 0.05$) interactions as well as connections and band main effects (both at $P < 0.001$). For the inter-HEM (sixth ANOVA) we found a significant band × connections interaction as well as connections and band main effects (all at $P < 0.001$), but no interaction or main effect of condition. Interestingly, we did not find a main effect, or any interaction with group, or any correlation between left alpha MPC during MED with expertise level, thus there were no group differences or expertise effects as a state effect.

## DISCUSSION

### Studying the DMN by means of EEG-FC

Our findings reveal that DMN deactivation during the TP compared with RS was manifested by a significantly lower intra-HEM gamma MPC, irrespective of group. Additionally, there was a significant condition × band interaction wherein alpha MPC increased during TP (Figure 2), which might be related to an increase in executive control function, manifested in alpha FC (Sauseng *et al*., 2005).

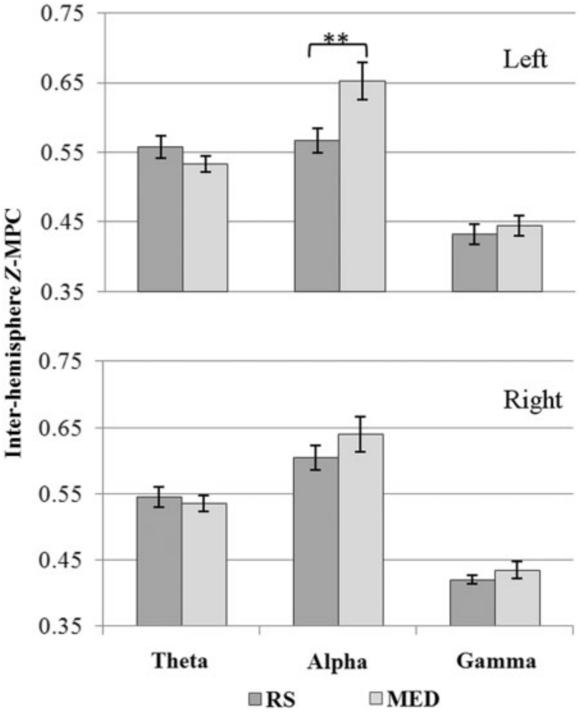

**Fig. 4** Mean z-MPC differences between RS and MED for MM. The Condition · Band interaction for the left-HEM connections (top) and right-HEM connections (bottom). $^{**}P < 0.005$.

Importantly, the reduction in gamma MPC resembles the previously reported decrease in gamma power in the same paradigm and groups (Berkovich-Ohana *et al*., 2012). This is in line with our hypothesis, based on several studies reporting power and FC to co-vary in various cognitive domains, such as sleep (Dumermuth and Lehmann, 1981), language processing (Bastiaansen and Hagoort, 2006) and meditation (Travis, 2001; Travis *et al*., 2002). It is also worth mentioning here that the fact that we report a reduction during the attentionally demanding TP task, and not an increase in gamma FC, strengthens our claim that our results represent cognitive processes, rather than muscular artifacts (see 'Methods' section for discussion of gamma band artifacts).

The decreased gamma and increased alpha FC during the transition from RS to TP could be due to the reorganization of resources in frontal areas associated with the TP task. Particularly, it may index the transition of the control/executive system from coupling with the task-deactivated DMN, possibly reflected within the gamma band, toward coupling with the task-activated network, possibly reflected within the alpha band. This proposition is based on a recent hypothesis, suggesting that the control system could work in conjunction with both perceptual information from the task-activated network and autobiographical information provided by the DMN to selectively reinforce either internal or external trains of thought (Smallwood *et al.*, 2012). Hence, the following could be a plausible scenario: During the RS, the DLPFC, a region systematically related with timing (Walsh, 2003; Oliveri *et al.*, 2009; Wittmann, 2009), which is also a component of the control system (Vincent *et al.*, 2008), was coupled with the DMN, as previously reported (Christoff *et al.*, 2009). However, during the transition to TP, the DLPFC decoupled from the DMN and coupled with the right parietal and SMA regions, which are part of the dorsal attention network (Corbetta *et al.*, 2008) comprising the task-activated network and are also systematically reported to be involved in timing processes (Coull and Nobre, 1998; Ferrandez *et al.*, 2003; Coull, 2004; Macar *et al.*, 2004). Obviously, further work which includes localization would be necessary in order to investigate such a proposition. However, it is detailed here to emphasize how the reorganization of resources in frontal areas might explain the reported results during the transition from RS to TP.

Our results are, however, in disagreement with the only report thus far of DMN-related FC (Chen, 2007), relating DMN activity with higher theta and alpha coherence in the frontal area. A possible explanation for the discrepancy with our results could be the difference in paradigm. Chen (2007) considered the transition from an eyes-closed to an eyes-open condition as a DMN-deactivation task. However, as extrinsic and extrinsic activities are thought to be antagonistic (Fox *et al.*, 2005, Golland *et al.*, 2007), DMN deactivates the more the 'extrinsic' task is demanding (Soddu *et al.*, 2009). Merely opening the eyes will undoubtedly lower alpha activity, as they indeed reported, but could still count as a resting state condition. In fact, an eyes-open resting state condition is customarily tested against external demanding tasks in DMN imaging studies (e.g. Golland *et al.*, 2007; Preminger *et al.*, 2010). Our study bypasses this obstacle by engaging the participant in an attention-demanding task (TP).

The fingerprint of DMN activity in gamma FC shown here is also in accord with recent studies exploring the electrophysiological correlates of the DMN with intracerebral EEG (Jerbi *et al.*, 2010; Ossandón *et al.*, 2011). These studies showed that DMN areas displayed transient suppressions of gamma power during demanding task performance. Our results emphasize the usefulness of non-invasive EEG measures, specifically gamma activity, for the study of the DMN.

### Trait and state MPC changes following MM practice

In this study we report an MM-related trait decrease in FC, irrespective of expertise or band, as seen in the significant group × band × hemisphere interaction (Figure 3). Additionally, we report a state-related increase in alpha MPC (Figure 4). Following is a discussion of each frequency band separately.

Generally, the reported results show large heterogeneity. It should be noted here that establishing a reliable signature of a specific meditation technique is notoriously difficult. Not only are techniques different form each other (even within the Theravada tradition) and have different stages both of the overall progress and of an individual session, but also individual participants develop over the course of their practice their own strategies of getting to desired meditation states. The heterogeneity of results here seems to point to this.

#### *Theta band*

We did not find a state effect in the theta band. Moreover, our results indicate that following MM practice, irrespective of proficiency, there is a decrease in right theta MPC compared with the control group. This is in contrast with other studies investigating various forms of meditation (summarized by Cahn and Polich, 2006; Ivanovski and Malhi, 2007), including Sahaj Samadhi (SS) state effects (Aftanas and Golocheikine, 2001; Baijal and Srinivasan, 2010) and TM state (Gaylord *et al.*, 1989) and trait effects (Orme-Johnson and Haynes, 1981; Dillbeck and Vesely, 1986; Travis, 1991). Yet, it is in some agreement with two other studies reporting meditation-induced state decreased theta in five different techniques (Baijal and Srinivasan, 2010; Lehmann *et al.*, 2012). The explanation for this discrepancy may lie in the meditative practice employed, as different techniques are known to show different characteristics (Dunn *et al.*, 1999; Lutz *et al.*, 2008; Travis and Shear, 2010).

A plausible explanation for the decrease in right theta MPC in MM practitioners compared with controls might be a different right-lateralized proportion of gray to white matter between groups. In the control group, RS theta FC is higher in the right hemisphere (Figure 3), as reported in the literature (Swenson and Tucker, 1983), and attributed to a greater proportion of white matter in the right hemisphere, rendering its organization more diffuse in general and leading to a greater interconnectedness among regions. Thus, the MM-related trait reduction in right theta MPC could indicate a higher proportion of gray to white matter in the right hemisphere. Indeed, MM practitioners were shown to exhibit higher gray matter volume in the right insula and hippocampus, regions related to interoceptive awareness and emotion regulation, respectively (e.g. Hölzel *et al.*, 2007, 2011a; 2011b; Luders *et al.*, 2012).

#### *Alpha band*

As a state effect, we found an increase in left hemisphere alpha MPC (Figure 4). This result is in accord with previous research, both on TM and Sahaj Samadhi (Farrow and Hebert, 1982; Travis and Wallace, 1999; Travis, 2001; Hebert *et al.*, 2005) as well as Zen meditation (Murata *et al.*, 2004).

Interestingly, the MM groups exhibited in the left hemisphere a trait decrease in MPC, while their right hemisphere values generally exceeded those of the control group, rendering their alpha MPC significantly asymmetric toward stronger right hemisphere connectivity compared with controls (Figure 3). This result is in contrast with the literature, where increases in trait alpha coherence are commonly found following meditation (reviewed by Cahn and Polich, 2006). Yet, given that the majority of these are TM studies (Orme-Johnson & Haynes, 1981; Dillbeck and Vesely, 1986; Travis, 1991), they are categorically different from MM (Lutz *et al.*, 2008).

Although an increase in the right lateralization of alpha coherence was previously related to increased anxiety (Swenson and Tucker, 1983), this interpretation for the asymmetrical alpha MPC in the MM practitioners has low plausibility, as MM has been shown to reduce anxiety (reviewed by Chambers *et al.*, 2009; Rubia, 2009).

The significant right asymmetry in MM practitioners compared with controls might be related to heightened creativity, as the left hemisphere was found to present lower synchrony than the right in artists, compared with non-artists (Bhattacharya and Petsche, 2002, 2005). This asymmetry was interpreted as supporting the 'significance of the right hemisphere for metaphors, imagination, expressiveness and emotional memories' (Bhattacharya and Petsche, 2002). Our results support the suggestion that meditation induces a transition toward a more symbolic and creative mode of cognition, as a trait effect (Glicksohn, 1998; Horan, 2009).

### Gamma band

We did not find a gamma state effect, in contrast to the ground-breaking study of Lutz *et al.* (2004), reporting increased state-related gamma FC. The discrepancy with this report might stem from the expertise (experts in the other study *vs* non-experts in this report) or difference in technique (compassion meditation *vs* MM). Following this argument, a more comparable meditation technique would be Zen, another open monitoring technique (Lutz *et al.*, 2008). Faber *et al.* (2004) studied one Zen practitioner (expertise not specified) and reported state-related decrease in gamma coherence. Obviously, further research is warranted, as the current literature on state gamma FC is scarce and ambiguous.

Turning to the gamma FC trait effects, we found a decrease compared with controls in the LT-MM, especially in the left hemisphere (Figure 3). As gamma MPC has been found to reflect DMN activity in this study (previous section), we interpret this finding as lower DMN activity during RS, thus a trait, for the MM practitioners compared with controls, possibly indicative of lower self-reference (Northoff *et al.*, 2006) and mind-wandering (Smallwood and Smith, 2006; Smallwood *et al.*, 2007; Christoff *et al.*, 2009), as hypothesized. This result is in accord with accumulating evidence from fMRI studies, showing reduced DMN activity during meditation. Specifically, mindfulness-induced reduction in activity was found in anterior and posterior midline DMN regions, including the mPFC, PCC and precuneus (Farb *et al.*, 2007; Pagnoni *et al.*, 2008; Brewer *et al.*, 2011; Ives-Deliperi *et al.*, 2011), which are particularly linked with spontaneous self-generated mental activity, i.e. streams of thoughts, episodic memory, mind wandering and self-related processing (Gusnard *et al.*, 2001; Northoff *et al.*, 2006; Smallwood and Schooler, 2006; Mason *et al.*, 2007; Sajonz *et al.*, 2010; Kim, 2012) as well as the lateral temporal cortices, including the angular gyrus (Pagnoni *et al.*, 2008), particularly linked with semantic and conceptual processing (Binder *et al.*, 1999; Buckner *et al.*, 2008). However, while some studies indicate that meditation training may reduce the DMN activity, others show an opposite effect, of meditation-induced increased activity within the DMN, both within the frontal region of mPFC (Hölzel *et al.*, 2007) as well as in posterior regions, including right PCC and precuneus (Tang *et al.*, 2009). Additionally, increased resting state functional connectivity within the DMN was reported (Jang *et al.*, 2011; Taylor *et al.*, 2013) as well as between DMN regions and attention (Hasenkamp and Barsalou, 2012), control (Brewer *et al.*, 2011) and sensory (Kilpatrick *et al.*, 2011) networks. Finally, anatomical studies reported increased gray matter concentration in the PCC (Hölzel *et al.*, 2011b). Taken together, studies indicate that meditation training alters the DMN activity, connectivity and anatomy, but the directions of change vary between studies (Tang and Posner, 2013).

Additionally, our results indicate a negative correlation between MM expertise and left gamma FC, in accord with previous studies where meditation expertise positively correlated with task performance (Chan and Woollacott, 2007; Cahn and Polich, 2009). The left lateralization of the MM-induced lower gamma MPC gives support to the suggestion that 'most systems of meditation alter consciousness by inhibiting cognitive functions associated with the dominant or left cortical hemisphere' (Earle, 1984). We further suggest that it might be related to lower internal verbalization and conceptual processing, reduced with increasing expertise, based on the following arguments: (i) various techniques of meditation are designed purposely to avoid logical and verbal reactions (Bishop *et al.*, 2004; Scola and David, 2011); (ii) there is ample evidence on the relation between the left hemisphere, verbalization and concept formation, accumulating from split-brain (Gazzaniga, 1989, 2000), structural (Fine *et al.*, 2009) and EEG (Davidson *et al.*, 1990) studies and (iii) neuronal synchronization in the gamma frequency is related to manipulation of semantic information when found within the left hemisphere in general (Bastiaansen and Hagoort, 2006) and in left DMN regions in particular (Binder *et al.*, 1999).

## CONCLUSIONS

We summarize this study with two conclusions: (i) EEG-FC could indeed be useful to study DMN activity and (ii) MM-induced EEG-FC effects show reduced trait DMN activity. We also report lateralized effects, which suggest lower internal verbalization and heightened creativity. This report emphasizes the possibility of studying the DMN using EEG as well as highlighting the importance of studying meditation in relation to it (Nolfe, 2011).

## SUPPLEMENTARY DATA

Supplementary data are available at *SCAN* online.

### Conflict of Interest

None declared.

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