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Mindfulness-induced changes in gamma band activity – Implications for the default mode network, self-reference and attention

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H I G H L I G H T S

- EEG gamma power over frontal and midline areas reflects default mode network (DMN) activity.
- Mindfulness Meditation (MM) practitioners show lower frontal gamma activity, related to DMN and narrative self-reference.
- MM practitioners produce longer time durations, these being negatively correlated with frontal gamma activity.

A B S T R A C T

Objective: There is a growing scientific interest in mindfulness meditation (MM), yet its underlying neurophysiological mechanism is still uncertain. We investigated whether MM affects self-referential processing, associated with default mode network (DMN), either as short (state) – or long-term (trait) effects.
Methods: Three levels of MM expertise were compared with controls (n = 12 each) by electroencephalography (EEG).
Results: DMN deactivation was identified during the transition from resting state to a time production task, as lower gamma (25–45 Hz) power over frontal and midline regions. MM practitioners exhibited a trait lower frontal gamma activity, related to narrative self-reference and DMN activity, as well as producing longer durations, these being negatively correlated with frontal gamma activity. Additionally, we found state increases in posterior gamma power, suggesting increased attention and sensory awareness. MM proficiency did not affect the results.
Conclusions: Gamma power over frontal midline areas reflects DMN activity. MM practitioners exhibit lower trait frontal gamma activity, as well as a state and trait increases in posterior gamma power, irrespective of practice proficiency.
Significance: First, the DMN can be studied non-invasively by EEG. Second, MM induces from the early stages of practice neuroplasticity in self-referential and attentional networks.

1. Introduction

In recent years there has been a growing scientific interest in the neurophysiological bases of meditation (Barinaga, 2003; Knight, 2004), reflecting the exploding interest in neuroplasticity, namely experience-induced changes in the brain (Lutz et al., 2007). Meditation is a body-and-mind self-regulating practice that focuses on training attention in order to bring mental processes under greater voluntary control. Accumulating evidence shows meditation-related changes either as state (short-term) or trait (longer-term, resting state changes) (reviewed by Cahn and Polich, 2006). Meditation was shown to induce neuroplasticity in brain function (Davidson and Lutz, 2008) as well as structure (Hölzel et al., 2011).

One form of meditation which has been largely related to well-being is mindfulness meditation (MM) (reviewed by Rubia, 2009). MM aims at cultivating a non-judgmental awareness of the internal and external stimuli present in each moment (Hart,

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1987; Kabat-Zinn, 2003). MM, among other Buddhist practices, could be expected to affect self-referential processing, as the major aim of practice is the realization, by direct experience, of the lack of any essential 'self' (Dreyfus and Thompson, 2007).

Self-referential processing has been attributed to a set of regions which were designated the 'Default Mode Network' (DMN). The DMN, which involves the medial prefrontal cortex (mPFC), the medial temporal lobe (including the hippocampus and parahippocampal gyrus), posterior lateral cortices, anterior and posterior cingulated cortex (ACC, PCC) and precuneus, was shown to be active when individuals are engaged in internal processing, and to deactivate when attention shifts towards external stimuli (Raichle et al., 2001).

Accumulating evidence of several recent functional magnetic resonance imaging (fMRI) studies supports the idea that various types of meditation training alter DMN activity. Farb et al. (2007) showed that in MM trained participants, meditation resulted in a reduction in the mPFC activity, and increased engagement of a right lateralized network, comprising the lateral PFC and viscerosomatic areas such as the insula, secondary somatosensory cortex and inferior parietal lobule. They also reported lower functional connectivity in practitioners compared to controls of the habitual coupling between the mPFC regions, supporting cognitive–affective representations of the self, and more posterior lateral viscerosomatic areas, representing neural images of body state. Pagnoni et al. (2008) tested Zen practitioners using fMRI during meditation interspersed with a lexical decision task. The neural correlates of conceptual processing were identified in left regions of the DMN. While there were no behavioral performance differences between the practitioners and the controls, the practitioners displayed a reduced duration of the neural response linked to conceptual processing in left regions of the DMN, suggesting voluntary regulation of the flow of spontaneous mentation.

These neuroimaging studies demonstrate that meditative practices can generally decrease activity and lower habitual connectivity patterns within regions of the DMN during meditation. Other fMRI studies showed, on the contrary, meditation-induced increased activity within the DMN. Hölzel et al. (2007) reported increased activity within the mPFC and ACC in MM practitioners compared to controls while comparing meditation to a mental arithmetic task. Jang et al. (2011) reported resting state greater functional connectivity within the DMN in the mPFC area in brain-wave vibration meditation practitioners, a method based on focusing attention on bodily sensations and emotions, compared to controls. In addition, in a single-photon emission computed tomography (SPECT) study, after only five days of integrative body–mind training (IBMT, combined Chinese traditional meditation and MM training) compared to a relaxation training group, there was a resting state activation increase in the ACC and PCC, two nodes of the DMN (Tang et al., 2009). Finally, another recent fMRI study (Kilpatrick et al., 2011) reported that 8 weeks of MM training induced changes in functional connectivity between self-reference networks and sensory (auditory and visual) awareness networks.

Taken together, neuroimaging studies support the idea of meditation-induced DMN plasticity, although the exact changes are inconclusive, probably due to the engagement of various types of meditation and different study designs.

Several studies investigated the relationship between the DMN as measured by fMRI and neuronal oscillatory processes in different electroencephalographic (EEG) frequency bands (summarized by Broyd et al., 2009). Gamma power (25–45 Hz) increase has been related to activity in the prefrontal node of the DMN (Chen et al., 2008; Mantini et al., 2007), which is closely related to self-referential processing (Northoff and Bermpohl, 2004; Northoff et al., 2006). The activity in the rest of the DMN, excluding the prefrontal node, was related to global alpha and beta power increase (8–13 and 13–25 Hz, respectively) (Chen et al., 2008; Laufs et al., 2003; Mantini et al., 2007). Finally, the DMN activity was generally negatively correlated with frontal and midline theta power (4–8 Hz) (Meltzer et al., 2007; Scheeringa et al., 2008), as was the activity in anterior medial cortex (Mizuhara et al., 2004). To sum, activity in the prefrontal node of the DMN, largely related to self-reference, is manifested mostly in the gamma band.

Gamma oscillations are typically related to top-down attentive processes (Herrmann et al., 2010), enhanced arousal and focused attention (e.g. Engel et al., 2001) and to conscious awareness (e.g. Lutz et al., 2002). While meditation was frequently shown to increase activity in the theta and alpha rhythms (reviewed by Cahn and Polich, 2006; Ivanovski and Malhi, 2007; Rubia, 2009), reports on gamma-band changes related to meditation practice are sparser, albeit starting to accumulate. Increased gamma power was recorded over fronto-parietal sites in highly experienced meditators compared with a control group, during compassion meditation as well as during resting state, and this was found to be in positive correlation with the degree of training (Lutz et al., 2004). Another study reported increased gamma power over parieto-occipital sites during MM compared to resting state in expert practitioners. This effect was enhanced with practice proficiency (Cahn et al., 2010).

Lehmann et al. (2001) evaluated one highly experienced meditator using low resolution brain electromagnetic tomography (LORETA) while practicing different forms of meditation. Each meditation type yielded different LORETA functional images of the EEG gamma band: image visualization increased gamma power in the right posterior occipital area, and mantra verbalization increased gamma power in the left central–temporal region, both being consistent with known functional anatomy. Interestingly, during self-dissolution (the meditator concentrated on the experience of dissolution of the self into a boundless unity, or emptiness) and self-reconstitution meditation (the meditator concentrated on experiencing the reconstitution of the self) gamma activity increased in right superior frontal and right temporal-parietal sites, brain regions which have been linked to an altered sense of self (Mathew et al., 1999; Miller et al., 2001) and body schema functions (Cassady et al., 1998), respectively. Another study reported a lack of frontal gamma power in response to emotionally aversive movie clips in long-term Sahaja Yoga meditators compared to controls (Aftanas and Golosheykin, 2005). Finally, Travis et al. (2010) tested Transcendental Meditation (TM) practitioners before and after a 10-week training, and reported a reduction in gamma power over frontal and parietal sites during TM compared to rest. Taken together, there is accumulating evidence for meditative training-induced changes in the gamma rhythm.

In this study, we tested the hypothesis that MM training would result in changes in DMN activity, in a measurable manner within the gamma band EEG, and in a gradual manner with MM proficiency. Specifically, we attempted to answer the following three questions:

(1) Can the reduction in DMN activity associated with the transition from resting state to an attentional task be identified in the gamma band?
(2) Could the expected changes in DMN activity associated with meditation practice be identified in the gamma band as a trait- or as a state-effect?
(3) Are any of these changes related to practice proficiency?

As will be shown, we answer the three questions by: (1) identifying DMN deactivation during the transition from resting state to

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a time production task, as lower gamma power over frontal and midline regions; (2) showing that MM practitioners exhibit a trait lower frontal gamma activity mainly right lateralized, related to self-reference and DMN activity, as well as producing longer durations, these being negatively correlated with frontal gamma activity; and (3) MM proficiency did not affect the results, suggesting neuroplasticity in early stages of practice. Furthermore, we found state, and to a lesser extent trait increases in posterior gamma power, mostly right lateralized, attributed to increased attentional skills and heightened sensory awareness. This effect was again unrelated to practice proficiency.

2. Methods

2.1. Participants

Participants comprised 36 Mindfulness Meditation (MM) practitioners and 12 healthy controls who had no prior meditation experience, but who declared an interest in meditation in a preceding written interview (interest > 5 on a 0–10 scale). The MM practitioners were recruited via word of mouth in local MM organizations. They were divided into three groups ($n = 12$ each) with varying degree of expertise, on the basis of accumulated hours spent in formal meditation during retreats and daily practice (M ± SD, min.–max.): Short-term (ST, 894 ± 450 h, 180–1430 h), Intermediate-term (IT, 2570 ± 471 h, 1740–2860 h), and Long-term practitioners (LT, 7556 ± 5027 h, 3870–23,000 h). The MM groups (mean ages, 41.6 ± 13.3, 37.9 ± 10.4, 45.6 ± 10.6, respectively) were age-matched with a control group (mean age, 41 ± 12.5). All participants were right handed and healthy, and were tested at least 3 h after their last meditation session, to control for immediate effects and enable studying long-term, trait effects of practice. The research was approved by the institutional ethical committee, and informed consent was obtained from each participant.

2.2. Design and procedure

The study was conducted using a pre-post design. Spontaneous EEG during resting state was recorded for 5 min (2.5 min eyes open and then 2.5 min eyes closed) prior to a battery of tasks designed to measure temporal and spatial perception, as well as attentional skills. The only task which will be reported here is a time-production task, used to compare resting state with a closed eyes task enabling continuous EEG recording. EEG was then recorded during a meditation session of 15 min, while the control participants were given the instruction to "relax as best as you can without falling asleep". Then, resting state EEG was acquired again as above (5 min), and the task battery was administered once more. Only three eyes-closed conditions will be reported here: the initial resting state (RS), the time production task (TP) and the meditation (MED).

2.3. Time production (TP) task

2.3.1. TP procedure

For an approximate length of 2–3 min, the participants were requested by recorded instructions to produce specified target durations by pressing a finger button when they estimated that the time which passed from the 'beep' sound equaled the specified requested duration. Four time intervals were used: 4, 8, 16 and 32 s, each interval twice, with random order of presentation (Glicksohn et al., 2009). Before the task, a practice of two time intervals (4 and 8 s) was given. The task was performed with closed eyes to reduce ocular artifacts in the EEG, and to facilitate the comparison with RS. The participants were not supervised concerning the time estimation strategy during the task itself (internal counting, or other), and were questioned afterwards concerning the employed strategy.

2.3.2. TP analysis

Produced (P) durations were log-transformed (to base 2), with required durations rendering thereby a linear scale ranging between 2 and 5, with a midpoint value of 3.5. A one-way analysis of variance (ANOVA) was performed on mean log(P) to investigate group differences.

2.4. EEG recording and protocol

EEG was recorded with a 65-channel geodesic sensor net (Electrical Geodesics, Eugene, OR), sampled at 500 Hz and referenced to the vertex (Cz), with analog 0.1–200 Hz band-pass filtering, and a digital notch filter at 50 Hz to remove artifacts caused by alternating current line noise. 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 screened for blinks, horizontal–vertical eye movements, muscle artifacts and possible sleepiness by visual inspection. When any of these artifacts affected electrodes in a widespread distribution, the data did not enter the analysis. In some of the artifact-free epochs chosen for further analysis, several channels exhibited noisy recording due to local high impedance (>40 kΩ, mean of 3 electrodes per epoch, in ~10% of the epochs), in which case the corrected values were off-line calculated by using spherical spline interpolation (Perrin et al., 1989).

For each condition, the first 16 non-overlapping, artifact-free epochs of 1024 sample points (2.048 s duration) were extracted for further analysis. For the meditation, epochs were extracted from the middle (between 5–10 min from the start of meditation) to enable 'settling' in the condition.

The power (measured in μV^2) spectral distribution was calculated by first multitapering the raw data (using a Matlab-based software package – http://chronux.org/), in order to minimize power leakage (Bronez, 1992; Thomson, 1982; van Vugt et al., 2007), then transforming it from the temporal domain to the frequency domain using fast-Fourier transform (0.5 Hz resolution, 1024 point block-size, Hanning window, 0.5–46 Hz). For each electrode, the absolute spectral power was grouped into frequency bands: delta (0.1–3.5 Hz), theta (3.5–7.5 Hz), alpha (7.5–13 Hz), beta (13–25 Hz) and gamma (25–45 Hz), then log transformed and averaged across the 16 epochs. Electrodes were collapsed into nine Regions of Interest (ROIs, see Fig. 1) – left and right frontal (F), central (C), temporal (T), parietal–occipital (PO) and midline

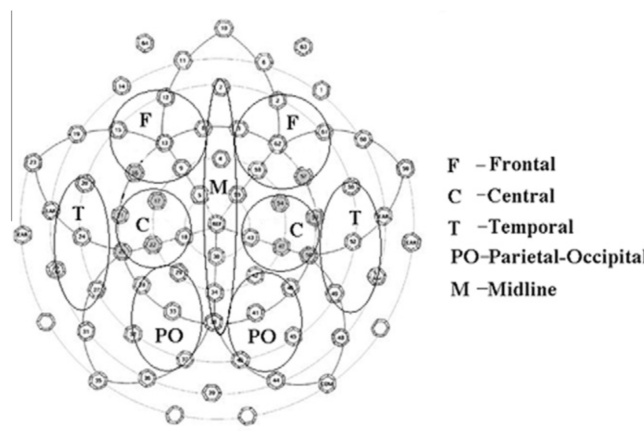

Fig. 1. Defined regions of interest (ROIs).

(M) – and the mean log spectral power was calculated for each ROI separately.

2.5. Gamma band reliability

A possible confounding effect for cortically induced gamma power is electromyographic (EMG) activity from scalp and neck muscles (Whitham et al., 2007), or saccade-related spike potentials (SP) due to eye movements (Yuval-Greenberg and Deouell, 2009). In this study, we used three steps for caution: first, we carefully visually inspected the raw data, manually extracting artifact-free epochs. Second, as the EMG peaks at 70–80 Hz (Cacioppo et al., 1990), we used much lower frequencies, in the 25–45 Hz. And third, we excluded from statistical analyses all the circumference electrodes, closest to eyes, neck and face muscles (see Fig. 1).

In addition to these three cautious steps, we also assessed the reliability of the data using the coefficient of variation (CV) of log gamma power, defined as the standard-deviation/mean. The CV can be viewed as a measure of pattern stability, in which CV $\sim$ 1 indicates a nearly random process and CV $\ll$ 1 reflects very high stability (Fingelkurts et al., 2006). CV was computed for the electrodes included in this study for 8 odd epochs and 8 even epochs (2.048 s each, total of $\sim$32 s). The analysis of CV revealed within-subject stability: the individual CVs were quite low ($M \pm SD$) for RS, TP and MED being 0.37 ± 0.45; 0.17 ± 0.37; 0.19 ± 0.55, respectively, indicating that the electrophysiological measures of gamma power indeed show high internal-consistency reliability. The mean CV values of the odd and the even epochs showed significant correlation across participants (r = .47, p < .05, n = 48).

To sum, we think that our results could be considered clean from artifacts for two reasons: first, our entire report deals with closed-eyes conditions, while the SP is elicited at the onset of small saccades which occur during eyes-open fixation (Martinez-Conde et al., 2004). Second, our data shows high within-subject consistency. All this suggests that our results represent cognitive processes, rather than muscular artifacts.

2.6. Statistical analyses

We focus in this report on the gamma band. Three analyses of variance (ANOVAs) were performed on the log power gamma values. The first was designed to answer the first question: Can the reduction in DMN activity associated with the transition from resting state to an attentional task be identified in the gamma band? This ANOVA had one Grouping factor (MM and C), and repeated measures on two within-participant factors: Condition (RS and TP), and ROI (left and right F, C, T, PO and M), adopting the Greenhouse-Geisser p-value for each and every effect. The same ANOVA also answered the first part of the second question, concerning trait effects in DMN activity associated with meditation practice.

A second ANOVA, designed to answer the third question – whether the effects revealed by the first ANOVA were related to practice proficiency, had one Grouping factor (ST-MM, IT-MM and LT-MM), and repeated measures on the two within-participant factors above: Condition (RS and TP) and ROI.

The third ANOVA was conducted to test for any state differences between resting state and meditation, testing also their relation to expertise level, and was thus designed to answer the second part of the second question, as well as the third question. This ANOVA was designed like the previous, with one Grouping factor (ST-MM, IT-MM and LT-MM), and with repeated measures on the two within-participant factors above: Condition and ROI, but with different conditions (RS and MED).

While statistically significant results were reported for ROIs only, we added topographic distributions of pair-wise electrode t-tests (Figs. 2, 3 and 5). These figures are to be taken as illustrative

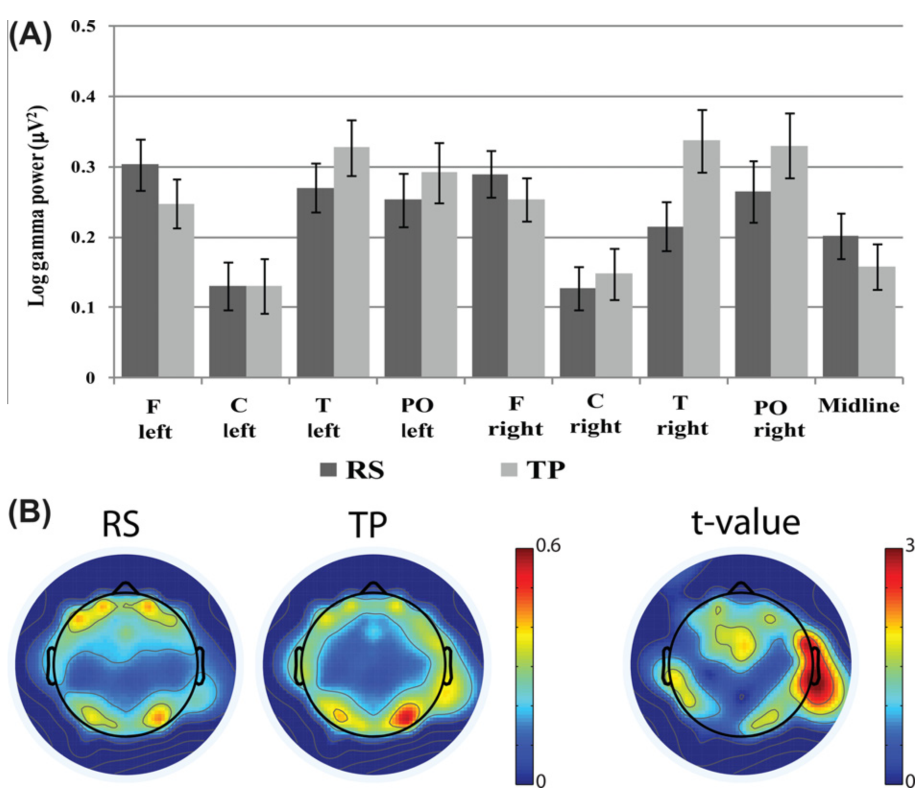

Fig. 2. (A) Log gamma power (M ± SEM), for the ROI × condition interaction seen for the MM and C groups together (n = 48); (B) topographic distribution (left and middle) of the mean log-gamma power during RS and TP for all participants together (n = 48), and t-values (right) of electrode-wise t-test (two-tailed) of RS vs. TP.

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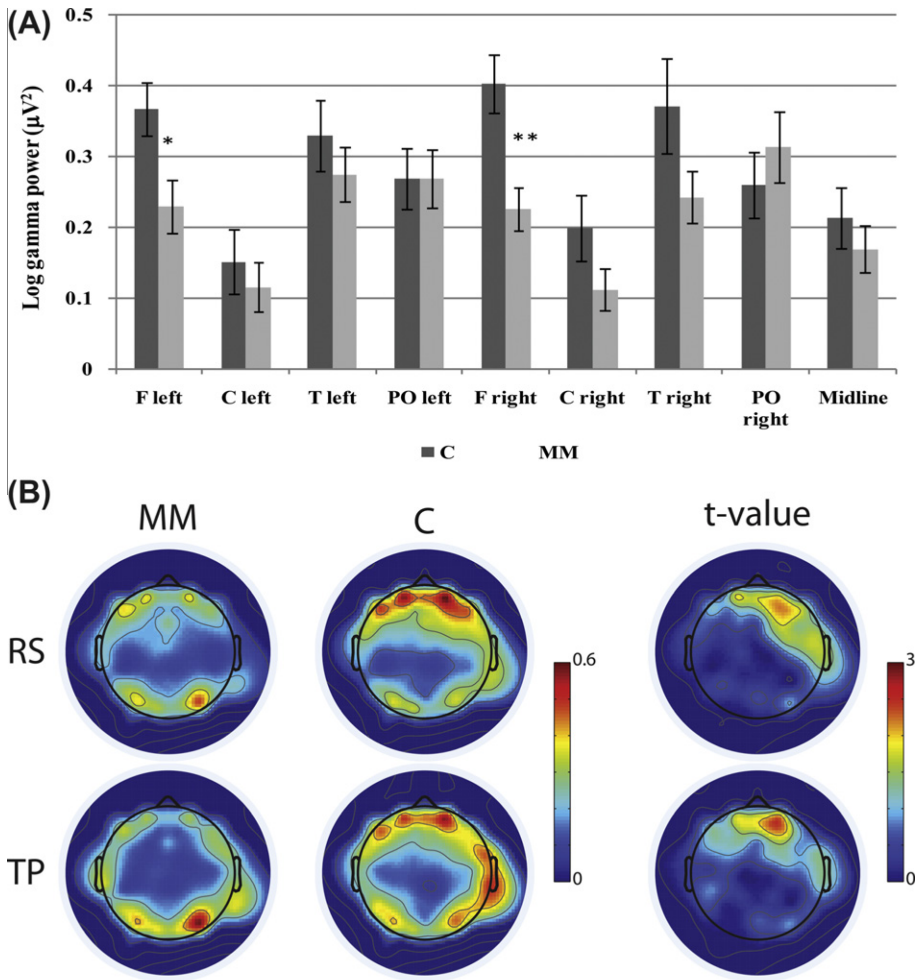

Fig. 3. (A) Log gamma power ($M \pm$ SEM), for the ROI × group interaction (mean of the RS and TP conditions). $^{*}p < .05$; $^{**}p < .005$; (B) topographic distribution (left and middle columns) of the mean log-gamma power for the 3MM and C groups, during RS and TP, and the *t*-values (right column) of the electrode-wise *t*-test (two-tailed) of the 3MM groups vs. C, over the RS and TP conditions.

in nature, albeit assisting in visualizing the more precise distribution of differences on the scalp compared to the gross ROIs.

3. Results

3.1. Subjective reports

The subjective reports from the meditators revealed that they were able to successfully perform meditation in the laboratory, with meditative depth (on a 1–10 scale, where 5 indicates 'success in the lab meditation as much as in one's regular practice') of 5.50 ± 2.64, 7.14 ± 1.77 and 6.92 ± 1.73 for the short-term (ST), intermediate-term (IT) and long-term (LT) groups, respectively [$F(2, 35) = 1.05$, $MSE = 3.34$, *ns*]. During the TP task, the percentages of participants who reported mental counting were 100% for C, ST-MM and IT-MM groups, and 83% for the LT-MM. The rest (17%) of the LT-MM reported 'unverbal sensing' the passage of time rather than counting.

3.2. Gamma power

The first ANOVA testing gamma-band changes in the transition from RS to TP revealed a main effect for ROI [$F(8, 360) = 10.53$, $MSE = .034$, $p < .0001$] stemming from lower gamma power over C and M ROIs. More importantly for the issue of DMN deactivation in the transition to an attentional task, we found a significant ROI × Condition interaction [$F(8, 360) = 4.87$, $MSE = .012$, $p < .001$] (Fig. 2): While values were generally lowest during the RS compared to the TP condition for most ROIs, it was reversed for the F and M ROIs. This effect indicates that DMN activity in the gamma band could be seen over the bilateral F and M ROIs.

Of importance to the question of trait effects following MM practice, the ROI × Group interaction was significant [$F(8, 360) = 2.75$, $MSE = .034$, $p < .05$]: whereas gamma power was generally larger in the C compared to the MM group, especially over the right F, this situation was inverted over the right PO (Fig. 3). The group's mean log gamma power results are given in Table 1 (an example of individual gamma power distributions is given in Fig. 4).

The second ANOVA, designed to differentiate trait differences between the three MM groups, revealed as before a significant ROI × Condition interaction [$F(8, 256) = 10.24$, $MSE = .006$, $p < .0001$], indicating a shift away from DMN activity (Fig. 2B). There were no group related main effects or interactions.

Finally, the third ANOVA tested for state effects by comparing MED to RS within the three MM groups. We found a main effect for Condition [$F(1,34) = 17.00$, $MSE = .054$, $p < .0001$], with gamma power being generally higher during MED compared to RS, and a main effect of ROI [$F(8,272) = 8.10$, $MSE = .039$, $p < .0001$] stemming again from lower gamma power over C and M ROIs. More

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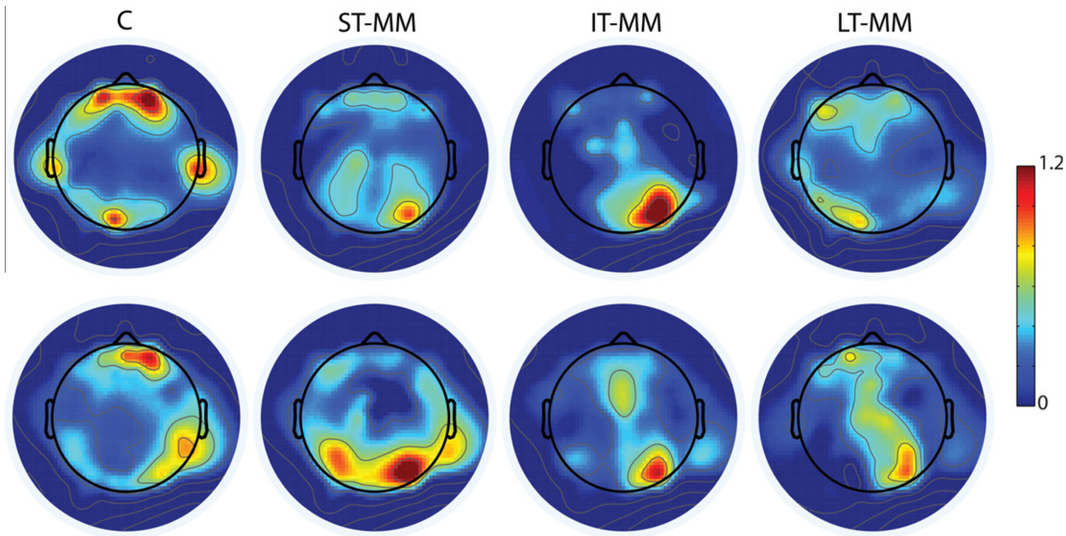

Fig. 4. An example of individual distributions of log gamma power (μV^2) during RS. Two participants from each study group (C, ST-MM, IT-MM and LT-MM) are presented. Notice that the right F values are higher in the control participants compared to the six MM participants, as opposed to the right PO values.

Table 1
Log gamma power (Mean ± SEM), for the C (n = 12) and MM (n = 36) groups, during the three experimental conditions RS, TP and MED.

ROI	RS		TP		MED	
	C	MM	C	MM	C	MM
F left	0.38 ± 0.07	0.28 ± 0.04	0.35 ± 0.08	0.21 ± 0.04	0.41 ± 0.08	0.31 ± 0.04
C left	0.14 ± 0.09	0.13 ± 0.03	0.17 ± 0.11	0.12 ± 0.04	0.22 ± 0.12	0.17 ± 0.04
T left	0.30 ± 0.07	0.26 ± 0.04	0.36 ± 0.09	0.32 ± 0.04	0.44 ± 0.12	0.37 ± 0.04
PO left	0.24 ± 0.09	0.26 ± 0.04	0.29 ± 0.11	0.29 ± 0.04	0.30 ± 0.12	0.34 ± 0.05
F right	0.43 ± 0.07	0.24 ± 0.03	0.37 ± 0.08	0.21 ± 0.03	0.44 ± 0.09	0.29 ± 0.03
C right	0.20 ± 0.09	0.10 ± 0.03	0.20 ± 0.11	0.13 ± 0.03	0.20 ± 0.10	0.17 ± 0.03
T right	0.31 ± 0.09	0.18 ± 0.03	0.43 ± 0.12	0.31 ± 0.04	0.39 ± 0.10	0.33 ± 0.03
PO right	0.23 ± 0.09	0.28 ± 0.05	0.29 ± 0.11	0.34 ± 0.05	0.25 ± 0.11	0.38 ± 0.05
Midline	0.23 ± 0.08	0.19 ± 0.03	0.20 ± 0.10	0.14 ± 0.03	0.28 ± 0.09	0.23 ± 0.04

importantly, we found an ROI × Condition interaction [$F(8, 272) = 3.55$, $MSE = .008$, $p < .001$], with significantly higher gamma power over left T and PO and right C, T and PO ROIs during MED compared to RS (Fig. 5, see also Table 1 for group mean values and Fig. 6 for an example of individual distributions). There were no significant group related differences. When looking at the correlation between hours of MM practice and log gamma power we find an inverted U-shape for the PO ROIs, but this effect did not reach significance. There was no observed correlation with the F or T ROIs.

In addition, we found a positive correlation between the MM subjective reports of meditation depth and frontal gamma power during MED [$r = .417$, $p < .05$, $n = 36$].

3.3. Time production task

The mean log transformed produced (P) duration [mean log(P)] distinguished significantly between the groups, as found by a one-way ANOVA, with MM exhibiting significantly longer mean log(P) compared to C (mean of 3.77 vs. 3.42 for the MM and C groups, respectively) [$F(1,45) = 8.43$, $MSE = .121$, $p < .01$]. However, there were no significant differences between the three MM groups (for further details, see Berkovich Ohana et al., 2011).

We also tested for Pearson correlations between mean log(P) and gamma power during the TP task. Interestingly, we found a significant negative correlation with frontal gamma power, both left [$r = -.289$, $p < .05$, $n = 48$], and right [$r = -.351$, $p = .01$, $n = 48$].

4. Discussion

4.1. DMN activity within the gamma band

The transition from resting state (RS), a condition shown to be related to DMN activity and self-processing, to time production (TP), which is a task engaging attention in temporal measurement with a trade-off in attention allocation to other cognitive modules performing nontemporal information processing (Glicksohn, 2001), is accompanied by a decline over the frontal (F) and midline (M) ROIs (Fig. 2). Considering that: (i) a positive correlation between induced gamma oscillations, measured by changes in the signal power in response to sensory stimulation, and the blood oxygen level dependent (BOLD) signal has been established, both in animals (Logothetis et al., 2001) and in humans (Foucher et al., 2003); (ii) gamma power has been related to the frontal node of the DMN, the mPFC (Mantini et al., 2007); and (iii) the DMN essentially involves frontal and midline structures (Buckner et al., 2008; Gusnard et al., 2001), it seems feasible to consider gamma power over the frontal and midline ROIs as a marker of DMN activity. Hence, the expected decline in DMN activity in the transition to the TP task is indicated by the reduction in gamma power over the F and M ROIs. In support of this conclusion, Jerbi et al. (2010) recently provided rare data from depth recordings in humans that show transient neural deactivation within the gamma band range in the mPFC during task-engagement.

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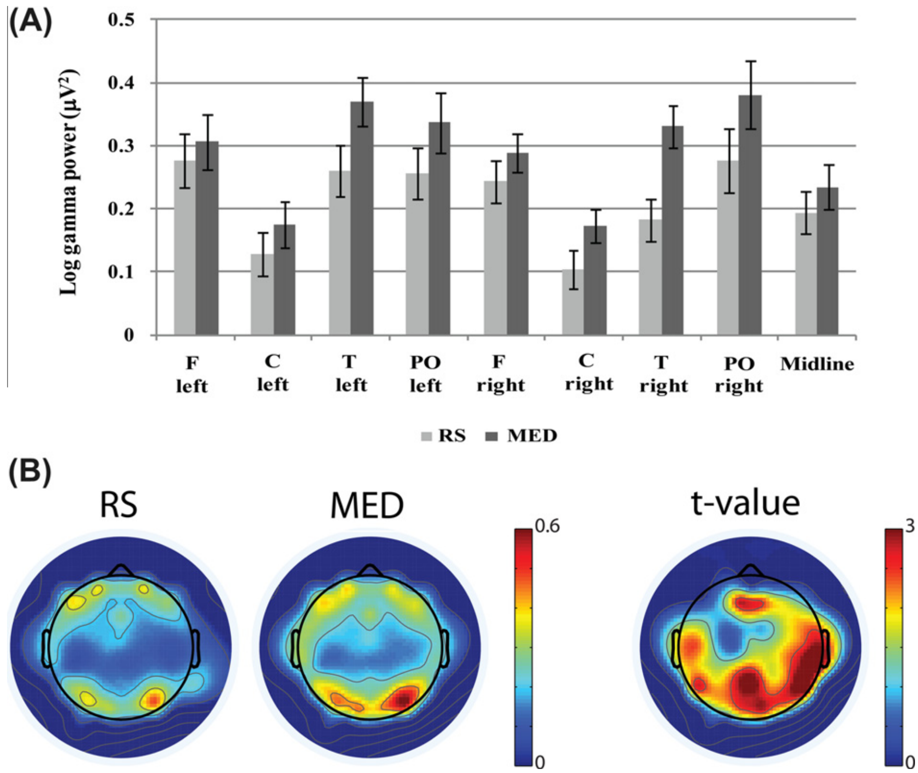

Fig. 5. (A) Log gamma power ($M \pm$ SEM) for the ROI × condition interaction in the MM group ($n = 36$) during RS and MED. $^{*}p < .01$, $^{**}p < .005$, $^{***}p < .001$; (B) topographic distribution (left and middle) of the mean log-gamma power during RS and MED for the 3MM groups ($n = 36$), and t-values (right) of electrode-wise t-test (two-tailed) of MED vs. RS.

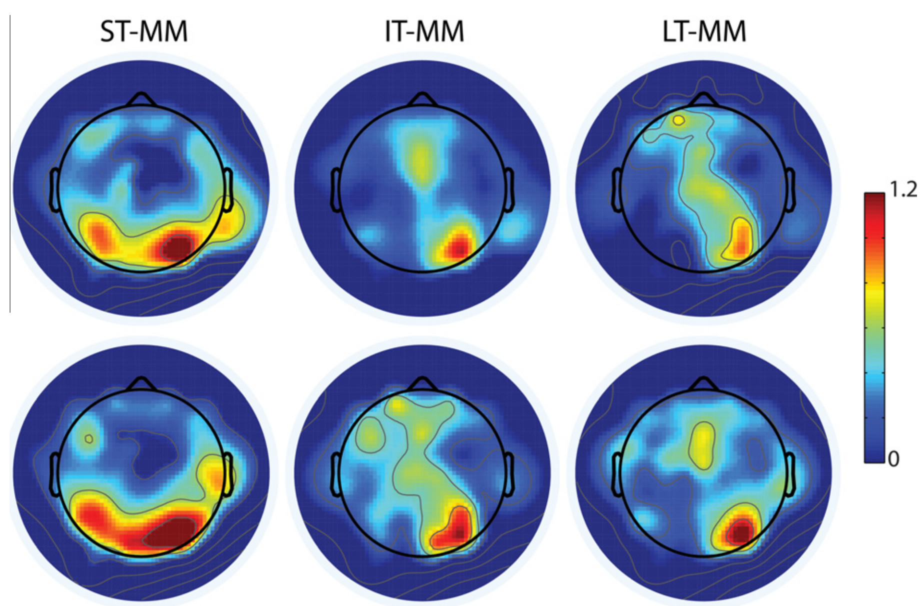

Fig. 6. An example of three individual distributions of log gamma power (μV^2) during RS and MED (one from each MM group: ST, IT and LT). Notice the increase over the right PO.

The increase in gamma power during the TP task over the right, and to a much lesser extent over the left, temporal (T) and parietal-occipital (PO) ROIs (Fig. 2) could be possibly attributed to an increase in anterior insular activity, which has been suggested by several authors as a neurophysiological mechanism for the encoding of duration (Craig, 2009; Wittmann, 2009).

4.2. Meditation induced changes in the gamma band

4.2.1. State effects

We have found increased gamma power over left T and PO, and right central (C), T and PO ROIs during meditation (MED) compared to RS in the MM practitioners (Fig. 5). The only other study that tested EEG state effects of MM practice was Cahn et al. (2010), who found a similar increase in gamma power during MM, more restricted to the PO. A possible interpretation for the posterior gamma power increase is an enhanced momentary sensory awareness, as suggested by Cahn et al. (2010). Indeed, other studies support the notion of heightened sensory awareness following meditation practice (Farb et al., 2007; Lazar et al., 2005; Nielsen and Kaszniak, 2006). For example, in the study of Farb et al. (2007) the state of MM, which they termed 'experiential-focus' as opposed to the DMN activity 'narrative-focus', induced in the practitioners an increase in activity in a right lateralized network, involving viscerosomatic areas such as the insula, secondary somatosensory cortex and inferior parietal lobule.

Another possible interpretation could be an increase in attentional activity, as numerous meditation studies reported increased attentional skills in meditation practitioners (e.g. Brefczynski-Lewis et al., 2007; Lutz et al., 2008, 2009; Tang et al., 2007). Further, the primary oscillatory activity that is modulated by selective attention is the gamma frequency range (Fries et al., 2001; Tiitinen et al., 1993), and the brain region that modulates selective attentional demand is the posterior parietal lobe (Behrmann et al., 2004). MM uses initially two skills which regulate attention, monitoring and disengagement from distracting stimuli (Lutz et al., 2008). In the bipartite attentional-network model of Corbetta and Shulman (2002), these attentional processes are attributed to the ventral system, or the 'bottom-up' system of attention, which includes the ventrolateral PFC and the temporoparietal junction. This system carries out stimulus-driven, exogenous, bottom-up control of attention, and is largely lateralized to the right hemisphere (Corbetta and Shulman, 2002; Fox et al., 2006; Serences et al., 2005). Following this line of interpretation, during the state of MM, practitioners are more engaged in monitoring and disengagement from distracting stimuli, hence PO activity rises, reflected by an increase in local gamma activity. This interpretation also accounts for the increased effect over the right hemisphere, as the ventral system is largely lateralized to the right.

Both interpretations suggested above for the largely right lateralized state temporal-posterior gamma increase reflect the shift away from narrative-focus, self-referential processing, towards experiential-focus heightened external attention and increased momentary sensory awareness.

4.2.2. Trait effects

The only ROI where MM practitioners exhibited higher gamma power compared to controls during the RS was the right PO (Fig. 3). This might be interpreted as a long-term, trait increase in attention allocation towards interoceptive or external sensory awareness, supporting the idea of neural plasticity in these networks in response to meditative training.

We also observed significantly decreased gamma power over the F ROIs compared to controls (Fig. 3), the effect being stronger for the right hemisphere. Converging evidence based on results from lesion and neuroimaging studies relate the right PFC with self-awareness and self-related processing, such as distinguishing stimuli related to one's own self from those that are not relevant to one's own concerns (Keenan et al., 2003). For instance, increased activity in the right PFC has been associated with self-recognition (reviewed by Keenan et al., 2000; Morita et al., 2008), and with increased self-relevance during metacognitive evaluation of trait adjectives (Schmitz et al., 2004). In addition, the right PFC activation has been related to retrieval of episodic memories (Allan et al., 2000; reviewed by Wheeler et al., 1997), and attributed to autonoetic consciousness, defined as the capacity to mentally represent and become aware of subjective experience over time (Markowitsch, 2003; Wheeler et al., 1997). This autonoetic consciousness, introduced by William James as the 'Me' (James, 1890), has been given different names, including "autobiographical self" (Damasio and Meyer, 2009), "narrative self" (Gallagher, 2000) and the "self-reflective self" (Zahavi, 2011). However, one can also be noetically aware about one's self, which means thinking objectively about the world, without involving self-relevance to whatever one experiences (Keenan et al., 2000). This phenomenon was differentiated from the 'Me' by William James as the 'I' (James, 1890), largely characterized by momentary bodily experiencing, and called by others the "core self" (Damasio, 1999; Damasio and Meyer, 2009), the "experiential or prereflective self" (Zahavi, 2011), and the "minimal self": (Gallagher, 2000). The largely right lateralized F ROI gamma reduction seen in the MM practitioners compared to controls, both during RS and TP (Fig. 3), suggests a trait transition from self-reference processing which is narrative in nature, towards experiential self-reference mode.

The results presented here are the first electrophysiological evidence for meditation-induced trait gamma power reduction within the right PFC accompanied by trait increase in right PO gamma, which suggests a trait shift from dwelling mentally within the extended self with its engagement in self-processing experience, towards the minimal, momentary and embodied experiencing self.

4.3. Temporal perception

We found a significant negative correlation between produced duration and gamma power over both F ROIs during the TP task. Further, we found that MM practice alters temporal perception in the direction of longer produced duration. This supports the hypothesis suggested by Glicksohn (2001), based on the cognitive-timer model (Treisman, 1984), that within a TP paradigm, the more focused internally is one's attention (as is during meditation), the slower the rate of functioning of the cognitive timer, coupled with larger subjective time units—hence longer produced duration. Yet, increasing MM proficiency did not have an effect, suggesting that the neuroplasticity in the temporal cognition networks takes place in the early stages of MM practice.

Going back to the issue of self-reference, the 'I' (core-self) and the 'Me' (narrative-self) have a different and complementary existence in the spatio-temporal domain: while the 'Me' places one in individual historical time and place, his or her actual past and possible future, the experiential 'I' is rooted in the here and now, in momentary experience (Damasio, 1999). Our TP results, both the cognitive measure and its negative correlation with frontal gamma power, give further support to our suggestion that MM reduces the narrative, and increases the experiential self-reference processing. Further evidence for this line of argument comes from a recent fMRI study, which revealed that 'time dilation' occurs in conjunction with the activation of several midline structures, such as the anterior cingulate and left precuneus (Van Wassenhove et al., 2011; Wittmann et al., 2010), related to experiential self-referential processing, or core-self (Northoff and Bermpohl, 2004; Northoff et al., 2006).

4.4. Meditation depth

While we could expect a negative correlation between the MM subjective reports of meditation depth and frontal gamma power during MED, we found a positive one. This indicates that subjective experience of 'meditation success' requires enhanced frontal gamma activity, possibly related to narrative self-referential processing. We speculate that lower narrative self-referential processing might be subjectively experienced and judged as lower metacognitive monitoring. Metacognitive monitoring involves the flow of information from the object level to the meta-level. It refers to evaluation (bottom-up) and control (top-down) of one's cognitive processes. The role of the meta-level is to evaluate what is being

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monitored, and based on this evaluation, control object-level processing by a feedback flow of information (Koriat, 2007; Nelson, 1996). However, Brown and Ryan (2004) make a point that mindfulness is not metacognition: "consciousness and cognition are distinct processing modalities. As a cognitive process, metacognition operates within the realm of thought, to monitor and control cognitive activities and to ensure that cognitive goals have been met... Mindfulness differs from such metacognitive processes in that its mode of operation is perceptual, operating upon thought, as well as upon emotion and other contents of consciousness, rather than within them" (p. 243).

4.5. The question of meditation proficiency

In this study we included 36 MM practitioners with great expertise variability, ranging between 180 - 23,000 h, grouped in three groups. Albeit the large expertise range, we did not find any MM expertise-related significant effects in gamma power for the F ROI during RS or TP, suggesting that the trait shift in self-reference mode from narrative-focused to experiential-focused occurs in early stages of MM practice. This conclusion is further supported by Farb et al. (2007), who provided evidence that after MM training of two months there was a state shift in self-reference processing during meditation. Our results indicate that the shift in self-reference mode is: (1) a trait, and not only a state, acquired following a short MM training (in the range of hundreds of formal practice hours); and (2) could be clearly seen noninvasively over the frontal, especially right hemisphere, in the gamma band of the EEG.

In addition, MM expertise did not affect the state (measured during MED) gamma power increase over T and PO ROIs, as well as the trait right PO gamma power (measured during RS or TP), attributed to increased attentional skills and heightened awareness to internal and external sensory stimuli. This disagrees with the results reported by Cahn et al. (2010), who found that meditation-related increases in occipital gamma power significantly covaried with meditational expertise, indexed by total years of daily practice. However, Cahn et al. (2010) compared 10 practitioners with over 10 years of practice with 6 practitioners having less than 5 years of practice. In comparison, our study included a much larger group sample, within the same expertise range (15 participants had > 10 years of practice, 7 had > 5 years, and 14 were in between). Another study which tested the correlation between the total hours of formal meditation and overall gamma power in eight long-term practitioners of Tibetan Buddhism reported a positive correlation coefficient, which did not, however, reach significance (Lutz et al., 2004).

5. Conclusions

In this study we employed EEG to investigate whether the regular practice of mindfulness meditation (MM) affects self-referential processing, either as short-term (state) or as long-term (trait) effect, in relation to practice proficiency. To this end, we first identified the electrophysiological changes associated with the transition from resting state to a simple time production task—lower gamma power over frontal and midline regions. This effect was similar in practitioners and controls. We then continued by comparing our three groups of MM practitioners to matched controls during a resting state, and showed that MM practitioners exhibited lower frontal gamma activity, mainly right-lateralized, related to narrative self-reference and default mode network activity. In addition, we have identified state increases in temporal and parieto-occipital (PO) gamma power, largely lateralized to the right, attributed to an increase in attentional skills and heightened awareness to internal and external sensory stimuli. An increase in right PO gamma power was also found in the MM practitioners, compared to controls, during the resting state, indicating a trait effect. Taken together, these results support the notion that the regular practice of MM induces a shift away from narrative self-referential processing towards an experiential and momentary self-reference processing.

Finally, the state and trait MM-induced changes in gamma activity were found to be irrespective of expertise level, suggesting that: (i) the shift in habitual self-referential processing from narrative to experiential focus, and (ii) the increase in attentional skills and heightened awareness to internal and external sensory stimuli, both occur in the earlier stages of MM practice, within the first 1000 h of practice.

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