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Research report

Effects of mindfulness meditation training on anticipatory alpha modulation in primary somatosensory cortex

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ABSTRACT

During selective attention, ~7–14 Hz alpha rhythms are modulated in early sensory cortices, suggesting a mechanistic role for these dynamics in perception. Here, we investigated whether alpha modulation can be enhanced by “mindfulness” meditation (MM), a program training practitioners in sustained attention to body and breath-related sensations. We hypothesized that participants in the MM group would exhibit enhanced alpha power modulation in a localized representation in the primary somatosensory neocortex in response to a cue, as compared to participants in the control group. Healthy subjects were randomized to 8-weeks of MM training or a control group. Using magnetoencephalographic (MEG) recording of the SI finger representation, we found meditators demonstrated enhanced alpha power modulation in response to a cue. This finding is the first to show enhanced local alpha modulation following sustained attentional training, and implicates this form of enhanced dynamic neural regulation in the behavioral effects of meditative practice.

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1. Introduction

Changes in alpha rhythm properties have recently been associated with enhanced filtering of inputs to primary sensory cortex. In the visual system [52,49], attention cued to a spatial location drives topographically precise alpha power reduction in the attended sub-region and enhancement in disattended locations. Such cue-induced alpha decreases have been correlated with perceptual success [32]. Similarly, cues directing attention to specific body regions induces alpha modulation in those representations in primary somatosensory neocortex (SI) [26].

Based on such findings, modulation of alpha rhythms in primary sensory cortex, once regarded as an epiphenomenal index of over-

all levels of alertness, is now viewed as playing an active role in the process of attentional selection by regulating or ‘gating’ thalamocortical sensory transmission [52,39] [6]. Localized neocortical alpha power increases are thought to decrease throughput of distracting stimuli, while concomitant alpha power decreases enhance throughput of relevant stimuli [52,23,33]. Behaviorally relevant differences in alpha rhythms prior to a visuo-motor task found in elite athletes vs. controls suggest that some functionally specific alpha rhythm properties may be alterable with training [11].

This study examined whether a form of behavioral training called “mindfulness” meditation (MM) would enhance cue-induced alpha modulation. MM is said to train the ability to pay moment-by-moment attention to sensations, feelings and thoughts in order to cultivate present moment awareness. MM training has been reported to improve performance in a spatial attention task [24], similar to that used to test alpha modulation (as in [52]), and elicits functional and structural changes in brain regions related to attention [15,20].

The present study tested whether training in meditation enhanced 7–14 Hz alpha modulation. We further asked whether

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meditators demonstrated enhanced modulation in specific sub-bands of alpha previously linked to specific functions (a lower band [7–8 Hz] associated with arousal; a middle band [9–10 Hz] associated with attention; and an upper band [11–14 Hz] associated with task specific performance in memory tasks) [37,38,35]. Because calculating each individual's peak alpha frequency may help control for variability in alpha seen across different age and patient groups [36,42], we also evaluated alpha modulation by considering alpha power related to each individual participant's individualized peak alpha frequency.

We investigated a standardized and relatively well-studied form of MM [15,14,9] called mindfulness-based-stress-reduction (MBSR). This training has significant effects on distress in chronic pain [41,43] and on quality-of-life in a broad range of illnesses [7]. MBSR is thought to train participants to disengage from habitual negative thoughts [12] by attending to present-moment experience. MBSR training has been correlated with functional changes in the BOLD response in somatosensory cortices [13] and in measures of electrical current over the central sulcus [10]. Techniques used in MBSR include a meditative body scan in which participants are taught to sweep attention across the body, pausing to notice sensations in specific somatotopic representations, (e.g., foot, hand). This training also includes sitting meditation, in which students are asked to attend in a moment-by-moment way to the breath and related somatic sensations. Given the importance of somatic attention training to MBSR, we hypothesized meditators would demonstrate an enhanced differentiation of 7–14 Hz alpha power in response to a cue (cue-“foot” vs. cue-“hand”) in the hand map of SI. To test our hypothesis, we used MEG to record signals from the hand area in right SI, using signals from the SI finger representation. As in previous studies, [26,34,27], we localized the finger representation using the equivalent-current-dipole generated by evoked responses to taps of the 3rd digit fingertip of the left hand.

2. Methods and materials

2.1. Participants

Sixteen participants were recruited with notices on bulletin boards and computer lists. Participants were required to be 18–50 y.o., right-handed healthy English speakers without any active medical (including neurological and rheumatological) or psychiatric disorder, willing to comply with study requirements, including 23 h of instruction and a daily meditation practice. Persons already trained in meditation were excluded. The study was registered with a trials registry (Clinicaltrials.gov) and approved by ethics boards at Massachusetts General Hospital and Harvard Medical School. All participants gave written consent to participate and allow use of their data for research. The average age was 31.6 (s.d. 7.0). Fifteen of sixteen participants were women, with 12 Caucasians, 2 Hispanics and 1 Asian American (1 drop out was unknown). The data reported here are from 12 participants (6 in each group) with 1 in each group lost to drop out and 1 subject's scans in each group lost to MEG artifacts. Scans were acquired at 0, 3 and 8 weeks. Participants were randomly assigned to MBSR or a control group. Control group members were asked not to meditate during the study and were promised free MBSR at the trial's end. MEG scans and analysis were performed by blinded technicians.

2.2. MBSR intervention

Class instruction followed CFM guidelines described in [34].

2.3. MEG scan experimental procedures

The experimental procedures were described previously in Jones et al. 2010 [26]. Here we review these methods.

2.3.1. Tactile stimuli

Throughout the experimental session, the subject's hand and foot rested on plastic frames through which tactile stimuli (single cycle of a 100 Hz sine wave, 10 ms duration) were delivered by fused multi-layer piezoelectric benders (Noliac, Inc., see [27]). Stimuli were applied to distal pads of the 3rd digit of the left hand and 1st digit of the left foot. Matched intensity of stimulation, relative to perceptual threshold, was maintained throughout for each subject using a Parameter Estimation Sequential Testing (PEST) procedure [40,8]. During cued attention runs (Fig. 1), stimulus

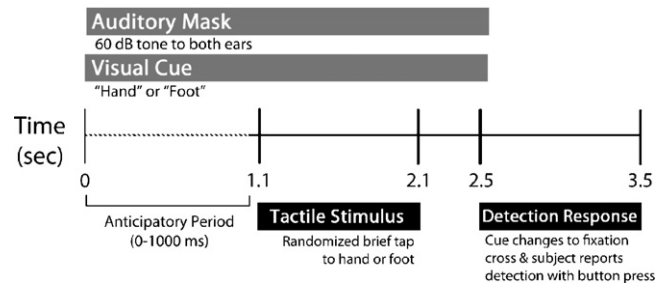


Fig. 1. Schematic illustration of cued attention runs. See Methods.

strength was kept at a 66% detection level with supra-threshold (100% detected) and null-stimuli randomly interleaved for 10% and 20% of the trials (as in [27,28]).

2.3.2. Localization runs

To localize primary equivalent current dipoles (ECDs) in the SI, hand representation, each experiment began with a run of supra-threshold stimuli for 3 min with an ISI of 3 s with 60 trials/run. Separate localization runs were also performed on the foot. However, because dipoles could not be reconstructed from foot data, only hand area activity is presented.

2.3.3. Cued attention-detection runs

Subjects were instructed to fixate on a cross on a projection screen. After an initial PEST psychophysical threshold run lasting 3 min, there were at least 5 cued attention-detection runs, described in Fig. 1. Each cued attention-detection trial lasted for 3.5 s. Each trial began when the fixation-cross changed into a visual word cue on a projection screen facing the subject. The cue directed the participant to attend to the cued location in preparation for completing the detection task of reporting whether he/she detected a light tactile stimulus at the cued body area (e.g., cue-“hand,” cue-“foot,” or cue-“either,” with the present study reporting only on the difference in alpha modulation in the “hand” vs. “foot” runs). Cues were non-informative about where the actual stimulus took place and were only informative in directing the subject to focus on a location in order to report whether a stimulus was felt at that cued location.

The visual cue was accompanied by a 60 dB, 2 kHz auditory tone delivered to both ears to mask the tactile stimulator's audible clicks. Visual and auditory stimuli lasted for 2.5 s. At a randomized time between 1.1 and 2.1 s after the cue, the tactile stimulus, consisting of a brief (10 ms) sine wave cycle, was delivered to the finger or toe.

Psychophysics were standardized across subjects in order to facilitate discovery of differences in prestimulus alpha modulation: stimulus intensity was dynamically maintained at a 66% detection rate using a two-up-three-down staircase PEST algorithm [27]. Each scan session included at least 5 runs with at least 40 stimuli per run for the cue-“foot” and cue-“hand” conditions. Scans were acquired at 0 weeks, 3 weeks and 8 weeks.

2.4. MEG source analysis

Previous publications have described MEG data acquisition, and MEG source analysis [26–28]. We summarize them here.

2.4.1. MEG data acquisition and source analysis

MEG signals were recorded using a 306-channel whole-head planar dc-SQUID Neuromag Vectorview system (Helsinki, Finland). Data were acquired at 601 Hz and filtered from 0.1 to 200 Hz. For details about head position, vertical and horizontal electro-oculogram (EOG) parameters and rejection of eyeblink-contaminated trials, see [27].

The contribution from the left 3rd digit representation in SI to measured fields (an example is displayed in Fig. 2) was estimated using a least-squares fit with a dipole forward solution [45,19]. Averaged data from localization runs were used to find an equivalent current dipole (ECD) (Elekta-Neuromag Software) at the time of peak activity (mean peak activity = 66.8 ms, s.d. = 6.4 ms) in the suprathreshold runs (minimum $n = 50$ trials per subject). Further description of localization methods including goodness of fit and co-registration with MR image can be found in [28]. Localization runs and dipole source fittings were repeated for each scan (weeks 0, 3, and 8) for each subject, with goodness-of-fit values similar to our previous studies [27,28]. However, in 8/36 total scans, localizations from the same subject in a different week were used. All analysis considered the forward solution from the SI source.

2.5. Data analysis

2.5.1. Spectral analysis

We calculated spectral power from SI source activity using a complex wavelet, from which time–frequency representations (TFRs) were determined. TFRs were cal-

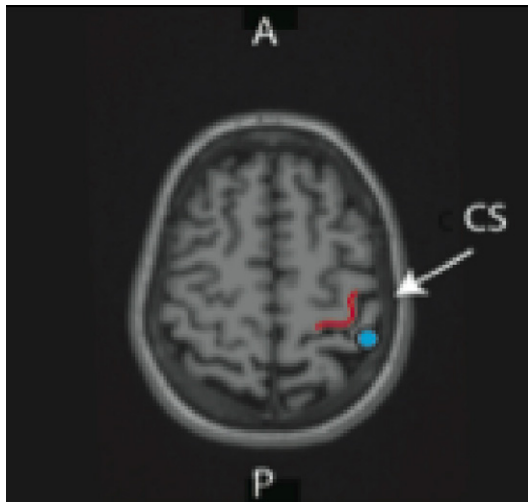


Fig. 2. Localization of SI hand map. An example from one subject's data of the estimated SI ECD derived from the response evoked by a suprathreshold tactile stimulus to the left hand, third digit. The data localized to the SI hand representation in area 3b was confirmed by crosschecking with subjects' anatomical MRI identified with a red line outlining the omega shaped hand area in the central sulcus. Figure reprinted with permission from Jones et al. 2010.

culated from 1 to 40 Hz on the SI ECD timecourses by convolving the signals with a complex Morlet wavelet of the form $w(f, f_0) = A \exp(-t^2/2\sigma_t^2) \exp(2i\pi f_0 t)$, for each frequency of interest f_0 , where $\sigma_t = m/2\pi f_0$, and i is the imaginary unit. The normalization factor was $A = 1/(\sigma_t \sqrt{2\pi})$, and the constant m defining the compromise between time and frequency resolution was 7, as in [28].

Time–frequency representations of power, i.e., spectrograms, were calculated as the squared magnitude of the complex wavelet-transformed data (with power normalized as a percentage of each subject's total alpha power at baseline to control for individual differences), see examples in Fig. 3 (see also Table 1 for individual participant's total alpha power, with baseline as defined in the section, "Measuring Alpha Modulation"). The spectrograms allowed us to visualize the dominant power bands expressed and to eliminate the possibility that non-specific broadband power increase was a possible generator of any effects calculated by averaging over the alpha band.

Table 1
Baseline total alpha power in meditators and control subjects.

Meditation	1.73×10^{-16}
Meditation	3.00×10^{-17}
Meditation	1.22×10^{-16}
Meditation	1.11×10^{-16}
Meditation	3.00×10^{-17}
Meditation	3.17×10^{-17}
Control	8.75×10^{-17}
Control	3.36×10^{-17}
Control	4.24×10^{-17}
Control	5.86×10^{-16}
Control	5.62×10^{-17}
Control	5.40×10^{-16}

In addition to the spectrogram, we calculated average power from 5 to 15 Hz for each subject to display each subject's peak alpha frequency in week 8 (Fig. 4).

2.5.2. Estimation of cue-evoked alpha

To confirm that any effect observed in the postcue period was the result of induced changes in alpha power and not the result of evoked activity time-locked to the visual cue we calculated the maximal alpha power resulting from the time-locked visual-cue evoked response in SI as a percentage of maximal induced alpha power (see typical individual plot of visual-cue evoked response in SI, Supplementary material, Fig. 1) and found that mean maximal cue-evoked response was 2.4% (s.d. = 2.03 with one outlier removed) of the maximal alpha power during the period from -200 ms before the cue to 1100 ms after the cue. This low percentage indicates that the visual cue evoked alpha recorded in SI was nearly 2 orders of magnitude smaller than the measures of alpha power from which alpha modulation was derived, discounting the idea that meditators' enhanced alpha modulation was due to a change in cue-evoked alpha response. Therefore, we did not remove cue-evoked activity as was relevant in prior studies [44,1].

2.5.3. Measuring alpha modulation

We investigated changes in anticipatory alpha power in the hand area. For each condition (**cue-“hand”** and **cue-“foot”**) time evolutions (0–1 s) of postcue **alpha power** (calculated as described above) were normalized as a percent change from baseline, where baseline was defined as the average alpha power 200 ms around the cue (-100 ms to $+100$ ms). Although setting the baseline at -100 to $+100$ ms of cue onset renders the data insensitive to the first 100 ms following the cue, this method allows the baseline to be reliably centered on the cue. The mean number

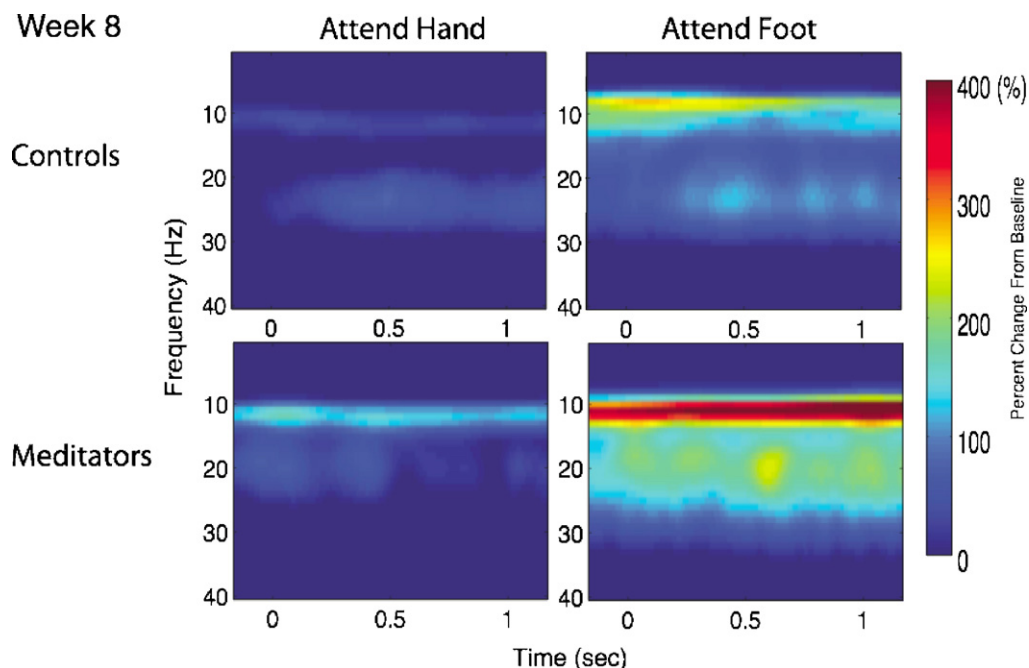


Fig. 3. Spectrogram of control, meditation groups in cue-“foot” and cue-“hand” conditions during postcue period in week 8. To control for individual differences, data is normalized as a percentage of each subject's baseline alpha power. Display shows specificity of alpha power modulation and absence of broad band power changes during the postcue period of interest (600–1000 ms).

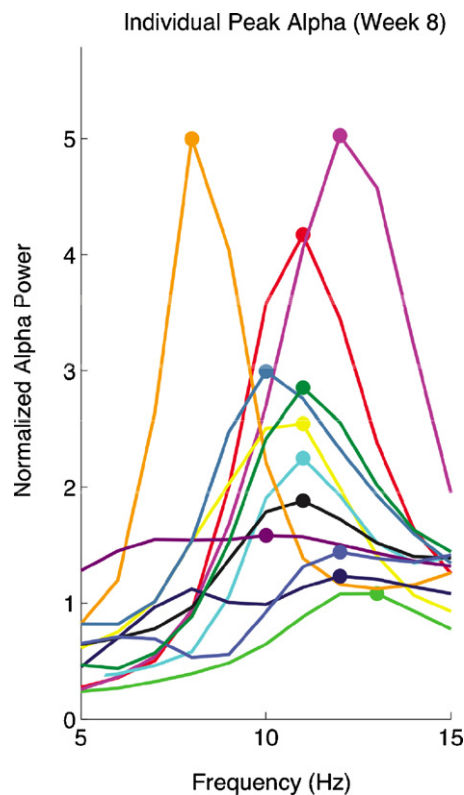


Fig. 4. Average total power from 5 to 15 Hz for each individual participant shows predominance of 10–12 Hz individual alpha frequency.

of trials for each subject was $n=267$, $s.d.=69$ cue-“hand” trials and mean $n=267$, $s.d.=66$ cue-“foot” trials.

We evaluated group differences in alpha modulation using an approach developed in the only prior controlled study to our knowledge confirming the efficacy of an intervention (theanine) on cued-induced alpha modulation [16]. Specifically, we developed an **alpha modulation index**, αMI , as a metric of attentional efficacy in differentiating cue-induced alpha modulation in the cue-“foot” vs. cue-“hand” conditions.

We focused our analysis on the 600–1000 ms period when cue-induced alpha modulation effects are believed to be strongest ([12,19]). Based on our finding that in week 0, prior to training, the early (600–800 ms) vs. late (800–1000 ms) components of the 600–1000 ms post-cue period were significantly different ($p < 0.01$, Wilcoxon signed rank test), we considered the early and late periods as separate variables.

Based on the fact that previous studies found *alpha increases in the disattended location* and *alpha decreases in the attended location*, the αMI was operationalized by subtracting the alpha power in the hand area in SI following the attend-location-cue (cue-“hand”) from alpha power in the hand area in SI following the disattend-location-cue (cue-“foot”). Thus, in each time period (early [600–800 ms] and late [800–1000]), the αMI was calculated as the difference in alpha modulation (defined as a percent change from baseline as above) between cue conditions (e.g., cue-“foot”–cue-“hand,”) averaged across time (Fig. 5). Two cue-induced alpha modulation indices (αMIs) for each subject were calculated (e.g., early and late αMI).

For our primary question, we tested whether the meditation group demonstrated significantly greater differential modulation of alpha rhythms in response to a cue (i.e., meditators demonstrated a significantly higher αMI than controls) using the same (7–14 Hz) alpha band definition used in our previous study [26], similar to that used in [52] (Fig. 5). We also tested whether meditation enhanced alpha modulation in specific alpha sub-bands (alpha low1, 7–8 Hz; alpha low2, 9–10 Hz; upper alpha, 11–14 Hz) and whether meditators showed enhanced modulation compared with controls in their individualized alpha frequency (defined as peak alpha frequency, see Fig. 4, ± 1 Hz) (Fig. 6). Because αMI was distributed non-normally across subjects (evaluated with the Shapiro–Wilk test), analyses were conducted with non-parametric tests. For our primary test comparing meditators with controls, the Mann–Whitney U test was used to evaluate differences between groups in the αMI , in the early and late periods. Any significant difference in any alpha parameter was further evaluated to discover whether the difference survived if participants’ baseline alpha power values were considered as covariates (using ANCOVA on rank-transformed data [48] as a non-parametric test of significance).

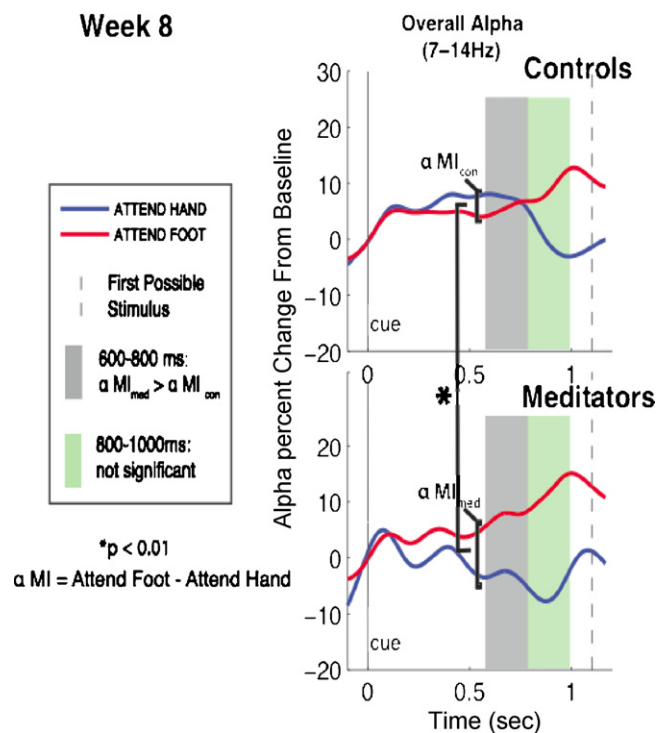


Fig. 5. Temporal evolution of overall (7–14 Hz) alpha power in cue-“foot” and cue-“hand” in meditators vs. controls displays between group comparison of αMI in early (600–800) and late (800–1000) periods. MEG data acquired from SI hand representation in controls (top panel) and in meditators after completion of an 8-week MM training course (bottom panel). The time series displays temporal evolution of 7–14 Hz alpha power during a 0–1000 ms anticipatory period prior to a tactile stimulus, after the onset of a visual cue to attend to “foot” or to “hand.” Alpha power for each cue condition is normalized as a percentage of power at cue onset. The red line represents cue “foot” responses, the blue line “hand” responses. Differences in alpha modulation index (αMI) (calculated as mean cue-“foot”–mean cue-“hand”) between groups are significant in the early component (600–800 ms, indicated by gray shading) of the alpha modulation period, with the meditation group demonstrating a significantly larger αMI than controls ($p < 0.01$, Mann–Whitney U test) indicating a greater ability to modulate alpha in the SI hand map during the 600–800 ms period.

2.5.4. Longitudinal analysis

To analyze the longitudinal effect of training, we classified subjects with $\alpha MI > 0$ in the early or late period as successful modulators and subjects with $\alpha MI < 0$ as unsuccessful modulators (e.g., we coded each αMI as a positive or negative value). A sign-test was then used to compare the number of positive αMI vs. negative αMI within each group at 0 and 8 weeks (Fig. 7). For each statistical test, significance is taken to be $p = 0.05$.

3. Results

3.1. Baseline (week 0) group difference in alpha modulation

To assess the success of randomization in equalizing αMI at the beginning of the trial, we compared the two groups (7–14 Hz) αMI at week 0 using the Mann–Whitney U test and found no significant pre-training differences.

3.2. Time–frequency representations of power (1–40 Hz)

For visualization of peak frequencies of activity that are modulated with attention, Fig. 3 shows time–frequency spectrograms of 1–40 Hz power in each group in attend hand and attend foot conditions in week 8 while Table 1 lists each participant’s total alpha power. Peaks in the spectrogram occur in alpha (7–14 Hz) and beta (15–29 Hz), with clear attentional modulation observed in the alpha band (7–14 Hz), as seen in our prior study [26]. These panels confirm the absence of broad-band power changes during

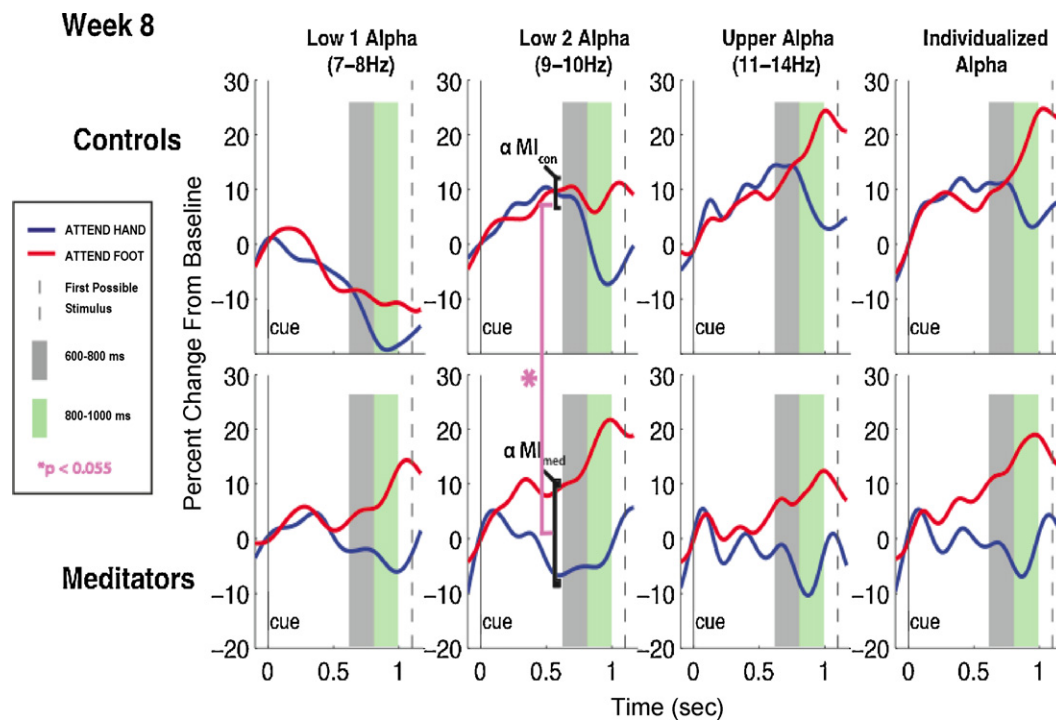


Fig. 6. Temporal evolution of alpha sub bands (low1, low2, upper and individualized alpha frequency). The time series displays temporal evolution of 7–14 Hz alpha power during a 0–1000 ms anticipatory period prior to a tactile stimulus, after the onset of a visual cue to attend to “foot” or to “hand.” Alpha power for each cue condition is normalized as a percentage of power at cue onset. The red line represents cue “foot” responses, the blue cue “hand” responses. A trend showing a significant difference ($p < .055$) between meditators and controls’ α MI in the low2 alpha (9–10 Hz) band previously associated with attentional modulation is indicated with an asterisk (using the Mann Whitney U test).

the postcue period of interest (600–1000 ms). Statistical analyses of these differences across groups are examined below and referred to in Figs. 5 and 6.

3.3. Averaged total power in 5–15 Hz frequency bins in week 8

We calculated total averaged power from 5 to 15 Hz to determine the peak alpha frequency for each participant and found that 10/12 subjects’ peak alpha power was centered over the 10–12 Hz range with only one subject showing peak alpha power in a lower alpha band (<10 Hz) and one subject at 13 Hz.

3.4. Group difference in alpha modulation at 8 weeks in 600–800 and 800–1000 ms postcue period

3.4.1. Overall alpha band (7–14 Hz) modulation

For our primary analysis of the effect of group on alpha modulation at week 8, we compared the α MI across groups in the early and late alpha modulation periods and found a significant difference in the early (600–800 ms) period ($p < 0.01$, Mann–Whitney U test, Fig. 5), such that the α MI was greater in meditators than controls. The difference remained significant when considering participants’ baseline alpha power as a covariate, tested with analysis of covariance (ANCOVA) used as a non-parametric test on rank-transformed α MI and baseline alpha power data ($p > 0.014$, $F = 9.12$, 1.9). There was no significant difference between groups in the late (800–1000 ms) period ($p > .26$, Mann Whitney U test).

3.4.2. Analysis of alpha sub bands and Individualized alpha frequency

When we tested whether meditation enhanced alpha modulation in specific alpha sub-bands and at the alpha peak for each individual subject, we found that in the alpha low1 band (7–8 Hz) previously associated with arousal, a comparison of meditator and

control α MI in the early and late alpha modulation periods showed no significant difference in either period (600–800 ms, $p < 0.52$. 800–1000 ms $p < 0.63$. Mann–Whitney U test, Fig. 6). In the alpha low2 band (9–10 Hz), previously associated with attentional processes, we found that a comparison of meditator and control α MI in the early and late alpha modulation periods showed a significant difference in the early period (600–800 ms, $p < 0.055$). There was no significant difference in the late period (800–1000 ms, $p < 0.42$, Mann–Whitney U test). In the upper alpha band (11–14 Hz) previously associated with specific task performance in working memory and other tasks, we found that a comparison of meditator and control α MI in the early and late alpha modulation periods showed a trend towards enhanced modulation by meditators in the early period (600–800 ms, $p < 0.078$). There was no significant difference in the late period (800–1000 ms, $p < 0.52$, Mann–Whitney U test).

When looking at the individualized Alpha band modulation (defined as each individual’s peak frequency ± 1 Hz), we found that a comparison of meditator and control α MI in the early and late alpha modulation periods showed no significant differences in the early (600–800 ms, $p < 0.26$) or late periods (800–1000 ms, $p < 0.52$ Mann–Whitney U test).

To assess whether the trends showing enhanced α MI in low1 and upper alpha were upheld when considering baseline alpha power as a covariate, we performed an analysis of covariance as a non-parametric test on rank-transformed data and found the trend was upheld in the low2 alpha band (low2 alpha, $p > 0.088$, $F = 3.65$, 1.9) but not in the upper alpha band (upper alpha, $p > 0.39$, $F = 1.05$, 1.9).

3.5. Within group learning effects across weeks in 7–14 Hz alpha modulation

To test for learning effects in either the meditation or control group, we evaluated change from 0 to 8 weeks in overall 7–14 Hz

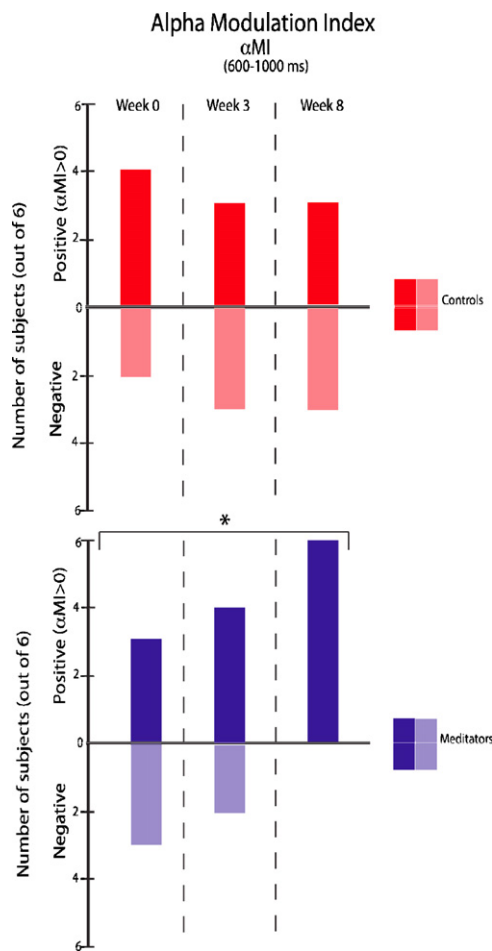


Fig. 7. Longitudinal change in alpha modulation index (α MI) in controls and meditators over the course of the trial (0, 3 and 8 weeks). The number of subjects with positive vs. negative α MI in the 600–800 ms period after the cue for each group, in scans acquired in week 0, week 3 and, week 8. Meditation group's significant improvement from week 0 (3/6 positive α MI) to week 8 (6/6 positive α MI) ($p < 0.03$, sign test) is indicated by asterisk. There was no significant change in the control group.

alpha power modulation in the 600–800 ms and 800–1000 ms period, comparing the sign of group members' α MI at 0 and 8 weeks. In meditators, a significant difference was observed between weeks 0 and 8 in the early (600–800 ms) period with 3/6 meditators with α MI > 0 in week 0 vs. 6/6 meditators in week 8, ($p < 0.031$, sign test, Fig. 7). There was no significant difference between week 0 and week 8 in controls (4/6 controls with α MI > 0 in week 0, vs. 3/6 controls in week 8) in either period.

4. Discussion

When compared with controls, meditators demonstrated enhanced differentiation of 7–14 Hz alpha power in response to an instruction (cue-“foot” vs. cue-“hand”) in the hand map of SI during the 600–800 ms postcue period. Additionally, meditators showed significant enhancement from 0 to 8 weeks in 7–14 Hz alpha modulation in the 600–800 ms postcue period, while no change was observed in controls. Meditators also showed enhanced alpha modulation (when compared with controls) in a specific alpha sub-band. Specifically, we found that the low2 [9–10 Hz] band previously related to attentional modulation was sensitive to enhancement by meditation, reinforcing the view that training of attention targets this dynamic.

Meditators' greater demonstration of α MI may be a correlate of increased attentional control of neural responsiveness in primary

sensory neocortex. This result may explain the specific improved attentional performance on a spatially cued attention task (the orienting component of the Attention Network task) seen in an earlier study of MM training [24].

4.1. Significance of enhanced alpha modulation in meditation

Prestimulus suppression of alpha rhythm power over sensorimotor cortex prior to a predictable pain stimulus predicts increased pain perception [25,2,4]. This finding suggests that an enhanced ability to modulate alpha power depending on the contextual cue could be used to modulate the intensity of perceived pain, in agreement with recent experiments showing mindfulness meditation training decreases pain perception [53]. Working memory performance is also associated with the ability to modulate sensory alpha rhythms in SI [18] and over parietal-occipital cortex [46,23,50,47,30]. Working memory performance is thought to be enhanced by the ability to take irrelevant sensory cortical processing areas off-line while maintaining performance in task relevant areas [22]. Given these reports of sensory cortical alpha modulation as a facilitator of working memory performance, the finding reported here, that MM training enhanced the ability to modulate alpha power in sensory neocortex in response to a cue, may also shed light on cortical mechanisms by which MM may preserve working memory performance under stressful conditions [3].

The alpha modulation observed here may be related to earlier reports of highly experienced meditators demonstrating modified alpha rhythm properties, with the most robust replicated finding being non-localized increases in tonic alpha power when compared with normal subjects (for a review of previous studies, see [5] for an early example of tonic alpha correlation with meditation, see [29]). Especially given the event-driven but relatively widespread expression of alpha observed, for example, with internally-focused tasks such as working memory [23,18,50], the phenomena observed here could relate to prior reports of increased alpha in some meditative states. That said, the relationship of ongoing and more spatially generalized alpha levels to the phasic, event-related and localized alpha modulation observed here remains an open question that merits further study, especially as the few modern studies evaluating relationships between tonic global EEG measures and phasic event-related alpha measures have found them to have distinct properties and characteristics [21,31,17].

4.2. Limitations

There are two important limitations to this study. First, because the study's tactile psychophysics were designed to be maintained at a standardized detection rate across subjects, the study did not evaluate whether meditators showed better behavioral performance in tactile detection. However, although the present study can draw no conclusions about whether neural changes in enhanced alpha modulation gave meditators an advantage in tactile detection, an earlier study by our group using a similar protocol found that pre-stimulus alpha levels predicted successful detection [26]. In addition, in a study of cue-induced alpha modulation in visual cortex, a greater lateralized modulation index was associated with faster reaction time and greater accuracy in detecting visual stimuli [49,32]. Future studies should investigate whether enhanced alpha modulation in meditators is correlated with superior behavioral performance.

Second, although this study is the first to provide evidence that a behavioral intervention can enhance alpha modulation, the study did not use an active control group. That is, because the control group did not actively train a non-sensory form of meditation (for example, a meditative practice that teaches subjects to focus on a repeated word or phrase), the study did not test directly whether it

was the specific somatic attentional focus of the training that led to the enhanced somatosensory alpha modulation. Future controlled studies should compare different meditation training regimens to validate that the specific somatosensory attentional mechanisms proposed here are associated with enhanced alpha modulation.

5. Conclusion

The study found meditators post-cue alpha modulation index in SI was larger than controls during the 600–800 ms component of the anticipatory period, prior to a tactile detection task, such that meditators showed greater differentiation in alpha modulation in response to distinct somatic cues (“foot” vs “hand”, Fig. 5). Meditators also showed enhanced alpha modulation from 0 to 8 weeks (Fig. 7). Differences between meditators and controls appeared to be centered on a lower alpha frequency band (the “low2 9–10 Hz band”) previously associated with attentional processing. This study documenting the effects of mindfulness on alpha modulation is the first to demonstrate that any behavioral intervention is associated with enhanced attentional modulation of alpha in a well-localized early sensory cortical area.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.brainresbull.2011.03.026.

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