Alpha and theta brain oscillations play a complementary role in inducing levels of altered consciousness during meditation practice

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Abstract

Background: Neurobiological changes accompanying meditation training are well-characterised. However, little is known about the neural and physiological basis of altered consciousness induced through meditation, despite such alteration being considered essential for the positive effects of meditation on mental health. The meditation depth questionnaire (MEDEQ) measures alteration of consciousness in five progressive levels of experiential "depth": *hindrances*, *relaxation*, *concentration*, *transpersonal qualities* and *nonduality*.

Methods: Using the MEDEQ, we investigated the brain (EEG) and bodily (pulse and respiration) correlates of meditation depth in two groups: long-term meditators (LTM) and meditation-naïve controls (CTL).

Results: CTLs reported experiencing more *hindrances* than LTMs. Whereas, LTMs reported more *transpersonal qualities* and *nonduality* during practice compared to baseline. In both groups, theta (4–6 Hz) oscillations correlated positively with *hindrances*, and increasingly negatively with progressively deeper experiences. Alpha (7–13 Hz) amplitude followed the exact opposite pattern. Experiential deepening was accompanied by theta deactivation over different regions in the two groups—frontal-midline in LTMs and frontal-lateral in CTLs—which correspond to two different aspects of executive processing, monitoring and regulation respectively. Experiential deepening was also associated with reduced heart-rate in CTLs but not LTMs.

Conclusions: Alpha and theta oscillations have long been reliably associated with meditation. Our study reveals how they relate to different subjective experiences accompanying such

practices. We moreover find that—while critical for overcoming *hindrances*—executive neural processing is downregulated during deep meditation experiences, and that prolonged training enables downregulation of an earlier stage of executive processing. Finally, prolonged meditation training may help reduce interoceptive influences on conscious experience.

Keywords

attention; consciousness; mindfulness; meditation; EEG; psychophysiology

Introduction

The benefits of meditation training on mental health have been demonstrated by numerous studies along with an impact on critical cognitive abilities such as attentional control and emotional regulation (Chiesa and Serretti, 2009; Malinowski, 2013; Leyland *et al.*, 2019). The psychological changes are moreover accompanied by reliable changes in brain structure (Fox *et al.*, 2014), neural signatures of cognitive processing (Cahn and Polich, 2006; Lomas *et al.*, 2015) as well as physiological markers of autonomic activity (Jevning *et al.*, 1992). However, there is another dimension of meditation training that has received less attention. Contemporary and traditional literature posits that changes in cognitive abilities are accompanied by alterations in conscious experience in a manner that is unique to the practice of meditation (e.g., Wallace, 1999; Lutz *et al.*, 2007; Dunne *et al.*, 2019), and even that such altered conscious experience is what essentially supports the positive psychological aspect of such practices (Brown *et al.*, 2007; Lutz *et al.*, 2015). However, little is currently understood about the neurobiology of alteration in conscious experience induced through meditation practice.

One potential reason for the dearth of work on meditation-induced alteration of conscious experience is the long-standing belief about the unreliability of subjective reports (Nisbett and Wilson, 1977; Jack and Roepstorff, 2002). Recently, several methodological remedies have been proposed to overcome the issue of such unreliability (Overgaard *et al.*, 2008; Berkovich-Ohana *et al.*, 2020). Francisco Varela, for example, proposed using a Husserlian-phenomenology-based epoché-and-reduction approach to obtaining generic structures of conscious experience and correlating them with neurobiological

measurements; a paradigm he referred to as *neurophenomenology* (Varela, 1996). Gallagher proposes an alternative "front-loading" approach where prior phenomenological insight about an experimental procedure can be used to obtain experiential self-reports during the procedure, and then correlated with neurobiological measurements (Gallagher and Sørensen, 2006).

Some previous studies have used these approaches to study the neural correlates of altered conscious experiences during meditation. In a series of studies, Berkovich-Ohana and colleagues used magnetoencephalography (MEG) to study the experience of self-dissolution during meditation both using a front-loaded paradigm (Dor-Ziderman *et al.*, 2013) and a neurophenomenological approach (Dor-Ziderman *et al.*, 2016). They found that self-dissolution was related to the deactivation of beta-band (13—25 Hz) activity in parietal cortex. Another study used an experience-sampling approach, periodically probing whether participants were on task or mind-wandering during meditation (Brandmeyer and Delorme, 2016). They found increased alpha and frontal midline theta—the two frequency bands most robustly associated with meditation (Cahn and Polich, 2006; Lomas *et al.*, 2015)—when participants reported being on task compared to mind-wandering. It was unclear however whether there were phenomenological differences in the *way* they were on task (e.g., effortfully or effortlessly), which was investigated by a series of studies by Brewer and colleagues using neurofeedback. They found that when either gamma-band EEG activity (van Lutterveld *et al.*, 2017) or fMRI BOLD activity (Garrison *et al.*, 2013) from posterior cingulate

cortex (PCC) was fed back to participants, it corresponded to the experience of effortless concentration when PCC was deactivated and distraction when it was more active.

While self-dissolution and effortless concentration are two specific types of altered experiences during meditation (Lutz *et al.*, 2015), it is also widely believed that different types of altered conscious experiences occur at different stages of a practitioner's training (Wallace, 1999; Lutz *et al.*, 2008; Dunne *et al.*, 2019; Tang *et al.*, 2019). In that sense, there is a more general classification of altered experiences through meditation where different such experiences can be clustered into different levels of "meditation depth" (Piron, 2001), including among them effortless concentration and self-dissolution. Using a sample of advanced practitioners from a variety of contemplative traditions, Piron (2001) developed the meditation depth questionnaire (MEDEQ) to measure different such experiences in five progressive levels of depth. The first level – *hindrances* – includes challenges associated with meditation practice such as drowsiness, distraction, etc. The second – *relaxation* – captures experiences like calmness, patience etc., which may occur even at early stages of practice. The third – *concentration* – captures experiences such as effortless concentration and mindfulness. The fourth – *transpersonal qualities* – captures interpersonal and affective experiences, such as love, surrender, joy, humility, etc., which onset at a somewhat advanced stage of training. And the fifth – *nonduality* – captures experiences such as cessation of thoughts, unity/infinity of consciousness, self-dissolution, etc., which may take several decades to master (Wallace, 1999). The MEDEQ thus provides an ideal front-loading

phenomenological instrument for investigating neurobiological mechanisms underlying the progressive stages of meditation-induced alteration of conscious experience.

In addition to neural activity, meditation practice also alters autonomic nervous system activity. Two repeatedly observed changes are reduction of respiration-rate (Corby *et al.*, 1978; Zautra *et al.*, 2010; Wielgosz *et al.*, 2016) and increase in heart-rate variability (Lehrer *et al.*, 1999; Sarang and Telles, 2006; Tang *et al.*, 2009; Nesvold *et al.*, 2012). In addition, heart-rate has also been found to reduce with meditation (Delmonte, 1985; Zeidan *et al.*, 2010), though practices engaging the affective system like compassion or loving-kindness have also been found to increase heart-rate following medium to long-term training (Lutz *et al.*, 2009; Lumma *et al.*, 2015). Interoception and bodily signals play a central and constitutive role in theories of conscious experience, especially pertaining to self and affect (Damasio, 1999; Gallagher, 2006; Seth, 2013). Moreover, past work has shown that prolonged meditation training may improve interoceptive accuracy (Fox *et al.*, 2012). It however awaits to be seen if bodily signals associated with meditation are also related to meditation-induced alteration in conscious experience.

In the present study, we investigated the neurobiological basis of meditation depth by measuring neural (EEG) and physiological (pulse and respiration) activity in two samples of participants, long-term meditators (LTM), and a meditation-naïve control group (CTL). We were interested in studying how seven neuro-physiological measures (NPM; 4 neural oscillatory bands: theta, alpha, beta and gamma, and 3 autonomic measures: respiration-rate (RR), heart-rate (HR), and heart-rate variability (HRV)) were related to meditation-depth, and if the relationship between them differed between groups. To sample from a wide-range of potential experiences, participants reported on the MEDEQ four times: after an initial

baseline, after listening to chanting music (to relax and prepare for meditation), and after two different types of meditation practices. CTLs engaged in secular mindfulness of breath and loving-kindness meditation practices widely used in mindfulness-based mental health interventions, while LTMs engaged in their daily practices (see Supplementary Methods). We hypothesised that while alpha, theta, gamma and HRV may be positively correlated with the subjective experience of meditation depth, beta, RR and HR would be correlated negatively.

Methods

Participants

We recruited two groups of participants, LTM (n = 13; 4 females; Mean and SD meditation training: 32.2 ± 9.7 years) and CTL (n = 15; 6 females). The groups were matched for age (Mean and SD: LTM = 56.8 ± 12.3; CTL = 53.5 ± 14.2 years) and years of formal education. Included participants reported no prior psychiatric or neurological diagnosis. Upon arrival, participants provided written informed consent in compliance with the Institutional Review Board of the University of California Davis.

EEG and physiological data acquisition

We used a 32-channel BrainVision ActiChamp system (Brain Products, Germany) to measure continuous EEG activity (sampling frequency 1000 Hz). The active ActiChamp electrodes help improve the signal-to-noise ratio. Each channel was ensured to have an impedance below 16 kΩ prior to data collection. We also measured continuous respiration and pulse

(sampling frequency 128 Hz) using a respiration belt and a photoplethysmogram respectively through the NeXus–10 (Mind Media, Netherlands) device.

Procedure

Each participant underwent the following protocol. The participants first underwent a task measuring self-referential processing published elsewhere (Katyal *et al.*, 2020). This was followed by four blocks, each with the following sequence: 1) A period where the participants kept their eyes closed either listening to a podcast (baseline; BL) or chanting (CH), or engaging in one of two meditation practices (M1, M2), 2) A set of questions from the MEDEQ where they reported their experience during 1) on a computer, and 3) 5 1-minute runs of the binocular rivalry following BL, M1 and M2. The binocular rivalry task is under review as a separate manuscript.

Subjective report about experience

Subjective reports of meditation depth were measured using 14 out of 30 questions from the MEDEQ that captured all five depth levels (Piron, 2001). We label these five depth-levels DL0—DL4 respectively indicating that DL0 or *hindrances* is inversely related to the other depth-levels. Participants were asked to allocate a depth value between 0 and 12 based on

prior experiences. The Likert scale was accompanied by markers at the lowest (*not at all*), middle (*medium*) and highest (*maximum possible*) values.

For detailed Methods about participants, task, data processing, and statistics, see Supplementary Material.

Results

We used linear mixed models (LMM) with the intercept value for each participant as a random effect in all the models for analyses (see Supplementary Materials).

Subjective reports of meditation depth

For CTLs, we expected more *hindrances* than LTMs, and lower (if any) increase in *transpersonal qualities* and *nonduality* from BL to CH, M1, M2. Figure 1 shows ratings for the five depth-levels of the MEDEQ for the two *groups* (LTMs, CTLs) and four *blocks* (BL, CH, M1, M2). For DL0 (*hindrances*), there was no group by block interaction ($\chi^2(3) = 0.43$, $p = 0.94$) but a significant main effect of group ($\chi^2(1) = 6.68$, $p = 0.010$) with CTLs reporting significantly greater DL0 than the LTMs. For DL1 (*relaxation*), there was again no group by block interaction ($\chi^2(3) = 1.86$, $p = 0.60$) but a significant effect of *block* ($\chi^2(3) = 10.35$, $p = 0.016$), with significantly greater DL1 during M1 ($t(78.38) = -2.81$; $p = 0.031$) and a trend for greater DL1 during CH ($t(78.65) = -2.47$; $p = 0.073$) and M2 ($t(78.83) = -2.51$; $p = 0.066$) compared to BL (p-values for all post-hoc comparisons adjusted using Tukey method for a family of 4 estimates). For DL2 (*concentration*), there was again no *group* by *block* interaction

($\chi^2(3) = 2.14$, $p = 0.55$) but a significant effect of both *block* ($\chi^2(3) = 24.36$, $p < 0.001$) and *group* ($\chi^2(1) = 5.86$, $p = 0.016$). There were significantly greater experiences of DL2 during CH ($t(78.49) = -2.96$; $p = 0.021$), M1 ($t(78.66) = -4.48$; $p < 0.001$) and M2 ($t(78.66) = -4.00$; $p < 0.001$) compared to BL. At the same time, the LTMs also reported higher DL2 experiences compared to CTLs ($t(26.16) = -2.42$; $p = 0.023$). For DL3 (*transpersonal qualities*), there was a significant *group* by *block* interaction ($\chi^2(3) = 9.19$, $p = 0.027$). This interaction was due to an increase in DL2 reports during CH ($t(75.20) = -4.00$; $p < 0.001$), M1 ($t(75.20) = -4.36$; $p < 0.001$) and M2 ($t(75.20) = -4.82$; $p < 0.001$) compared to BL only for the LTMs but not the CTLs (CH: $t(75.42) = -0.71$, $p = 0.89$; M1: $t(75.63) = -0.86$; $p = 0.82$; M2: $t(75.63) = -1.56$; $p = 0.41$). DL2 was also higher in LTMs compared to CTLs during CH ($t(43.78) = -3.04$; $p = 0.004$), M1 ($t(43.83) = -3.15$; $p = 0.003$) and M2 ($t(43.83) = -3.04$; $p = 0.004$) but not during BL ($t(42.83) = -1.13$; $p = 0.26$). For DL4 (*nonduality*), there was a strongly significant *group* by *block* interaction ($\chi^2(3) = 21.46$, $p < 0.001$). DL4 reports were higher during CH ($t(75.10) = -5.25$; $p < 0.001$), M1 ($t(75.10) = -6.20$; $p < 0.001$) and M2 ($t(75.10) = -6.24$; $p < 0.001$) compared to BL only for the LTMs and not for the CTLs (CH: $t(75.32) = 0.01$; $p = 1.00$; M1: $t(75.53) = -0.97$; $p = 0.77$; M2: $t(75.53) = -1.23$; $p = 0.61$). They were also higher in LTMs compared to CTLs following CH ($t(43.36) = -2.86$; $p = 0.005$), M1 ($t(43.41) = -2.86$; $p = 0.007$) and M2 ($t(43.41) = -2.87$; $p = 0.006$) but not BL ($t(42.43) = 0.14$; $p = 0.89$). As

expected, both DL3 and DL4 were selectively enhanced during the meditation compared to baseline for LTMs but not CTLs.

Relationship between neuro-physiological measures and meditation depth

We hypothesised that one or more of the seven NPMs (*theta*, *alpha*, *beta*, and *gamma*, *RR*, *HR* and *HRV*) would be related to meditation depth, either specifically in one group (as a 3-way interaction with *group* and *depth-level* when regressed upon self-reports) or across both groups (as a 2-way interaction with *depth-level*). We used a top-down stepwise approach to model reduction to obtain significant interactions. Figure 2A depicts this model-reduction process with columns showing steps and rows showing the interactions modelled at each step. At Step 1 all interactions are included and at each subsequent step the weakest one is dropped till only significant ones remain. The final reduced model revealed two highly significant 2-way interactions of *depth-level* with *alpha* ($\chi^2(4) = 68.23$, $p < 0.001$) and *theta* ($\chi^2(4) = 55.38$, $p < 0.001$) amplitude.

While LMMs with 2- and 3-way interactions show which NPMs impact meditation depth, they are unable to reveal how individual depth levels are related to the NPMs. For this, we performed post-hoc tests by regressing alpha and theta amplitude upon self-reports for each depth-level separately. Figure 2B shows the *t*-values for each of the 5 depth-levels for *alpha* and *theta* (negative *t*-values indicate negative correlations with self-reports). Correlations of *alpha* and *theta* with depth followed a strikingly complementary pattern. *Alpha* was significantly negatively correlated with DL0 ($t(81.00) = -4.20$, $p < 0.001$ (FDR adjusted)) and positively correlated with DL3 ($t(87.68) = 3.16$, $p = 0.009$) and DL4 ($t(75.17)$

= 2.88, p = 0.016). *Theta* was significantly positively correlated with DL0 (t(66.61) = 4.19, p < 0.001) and negatively correlated with DL3 (t(62.27) = –2.60, p = 0.045).

Next, we plotted brain topographies of the strength of the 2-way interactions of *theta* and *alpha* with *depth-level* to investigate the brain regions corresponding to the experience of deepening meditation (Figure 3A). Theta oscillation correlations were observed primarily over medial and lateral prefrontal cortex and occipital cortex (Figure 3A). Interestingly, alpha oscillation correlations were also observed over similar regions in addition to the left parietal cortex (Figure 3B).

Next, we tested if the dependence of meditation depth on *alpha* and *theta* was present in both groups (or driven by one group). For this, we modelled regressed interactions of *alpha* and *theta* with *depth-level* in the two groups separately. The two interactions were indeed highly significant in both LTMs (*alpha*: $\boldsymbol{\chi}^2(4) = 17.30$, p = 0.002; *theta*: $\boldsymbol{\chi}^2(4) = 17.71$, p = 0.001) and CTLs (*alpha*: $\boldsymbol{\chi}^2(4) = 22.04$, p < 0.001; *theta*: $\boldsymbol{\chi}^2(4) = 18.76$, p < 0.001). We also investigated if the two groups showed similar or different brain regions for the two frequency bands, as the latter may indicate differences in cognitive processes or strategies for evaluating self-reported meditation depth. For the LTMs (Figure 3B), theta and alpha were related to depth-level over medial prefrontal cortex and occipital cortex negatively and positively respectively. For the CTLs, theta was negatively related to depth-level over left and

right lateral prefrontal cortex as well as occipital cortex. Alpha was related to depth-level over medial and bilateral prefrontal cortex along with occipital and left parietal cortex.

Control analysis

While the LTMs engaged in silent self-guided meditation, CTLs engaged in audio-guided practice. To ensure that differences in topographies between groups were not due to auditory stimulation, we also analysed the topographies using only the last 6 minutes of M1 and M2 (Supplementary Figure 1). These topographies were very similar to the topographies in Figures 3B—C indicating that group differences could not be explained by differences in auditory stimulation.

While M1 and M2 practices for CTLs are commonly used as part of mindfulness-based interventions, CH is not. To ensure the applicability of our results to mindfulness-based interventions, we also plotted the topographies by excluding the CH block (Supplementary Figure 2). These topographies were again similar to when the CH block was included though with reduced effect sizes, as expected.

Exploratory analysis of physiology and meditation depth

Our planned analysis did not reveal a significant relationship between meditation depth and the physiological measures. It is however possible that if there were such a relationship, it was explained away by the neural correlations. We performed exploratory analysis by regressing the 3- and 2-way interactions from only RR, HR and HRV upon self-reports. Model reduction revealed three significant interactions. There was a 3-way interaction of HR with *depth-level* and *group* ($\chi^2(4) = 13.48$, $p = 0.009$). Post-hoc LMMs revealed that this was due to opposite patterns of how HR was related to self-reports across depth levels in the two

groups; with decreasing correlations in the CTLs and increasing correlations in the LTMs (Figure 4A). For the CTLs, there was a strong negative relationship between HR and DL3 ($t(20.20) = -2.89$, $p = 0.045$), while no relationship between HR and any of the individual depth-levels was observed in LTMs. There were also significant 2-way interactions of RR ($\chi^2(4) = 14.79$, $p = 0.005$) and HRV ($\chi^2(4) = 13.48$, $p = 0.009$) with depth-level. Post-hoc analysis revealed that this was due to a decrease in the association between RR and self-reports with depth-level and a decrease with HRV (Figure 4B). At individual depth-levels, RR was significantly correlated to DL4 ($t(86.00) = -3.42$, $p = 0.005$), while HRV was not correlated with any of them.

Discussion

We observed the expected changes in self-reported meditation depth both with long-term meditation training and following periods of meditation practice. The CTLs reported significantly more *hindrances* during meditation compared to the LTMs. Both groups reported heightened experiences of *relaxation* and *concentration* following practice compared to baseline, indicating a state manipulation. For the deepest experiences—*transpersonal qualities* and *nonduality*—LTM reported significant heightening following the two types of practices but CTL did not. These results validate the ability of MEDEQ to successfully measure state manipulations of meditation depth (Piron, 2001, 2003).

When modeling the covariation over blocks of the different neural and psychophysiological measures with self-reported meditation depth, we found a strong association between the amplitude of alpha and theta neural oscillations and meditation

depth. Interestingly, the two neural measures were related to meditation depth in a precisely opposite manner. While theta correlated positively with experiences that hinder meditation, alpha correlated negatively. As meditation experience deepened, however, the association of self-reports became more positively correlated with alpha and more negatively correlated with theta. Moreover, the association of alpha and theta with meditation depth was strongly significant within both groups separately. This suggests that despite the two groups engaging in different styles of meditation practices and having vastly different amounts of meditation experience, self-reported meditation depth relied on somewhat similar aspects of brain function.

Alpha oscillations are closely linked to inhibitory processing in the brain and in the context of attention are often related to suppression of distractors (Jensen and Mazaheri, 2010; Klimesch, 2012; Clayton *et al.*, 2015). Whereas, theta oscillations are generally related to attentional monitoring, control or selection (Cohen, 2014; Clayton *et al.*, 2015). As meditation deepens, we would expect a greater suppression of distractors and thus increased alpha. And, once the distractors have been suppressed during a deep state, there would be less of a need for cognitive control (and thus a more effortless quality of attention (Lutz *et al.*, 2015)), which was likely what was reflected in the reduction in theta. In this sense, alpha and theta would act in a complementary way. This complementary relationship between alpha and theta was also evident in the similar set of brain regions where they were related to meditation depth, i.e., lateral and medial prefrontal, and occipital cortex.

In addition to mechanisms shared by the two groups, we also investigated group-specific mechanisms. While alpha and theta correlations were present over the occipital

cortex for both groups—indicating suppression of visual sensory activity—there were differences in where these correlations were focused over the frontal cortex. Notably, the negative correlation of theta with meditation depth was present over the frontal-midline cortical regions in LTMs and frontal-lateral regions in CTLs. Medial and lateral prefrontal regions have been found to be broadly involved into two different aspects of executive (or metacognitive) processing—monitoring and regulation—respectively (Botvinick *et al.*, 2001; Kerns *et al.*, 2004). Frontal midline theta, previously localised to the anterior cingulate cortex (ACC) (Ishii *et al.*, 1999; Tsujimoto *et al.*, 2006), is a classical signature of conflict monitoring (Cohen, 2014; Clayton *et al.*, 2015). At the same time, growing evidence suggests that lateral frontal theta is related to top-down regulation (Fellrath *et al.*, 2016; Rajan *et al.*, 2019; Spooner *et al.*, 2020; Zamorano *et al.*, 2020). Both these processes would be essential during meditation and especially when the mind is highly influenced by distractions; monitoring to ensure one is attending the meditative target, and if not, downregulating distractors and upregulating the target (Hölzel *et al.*, 2011; Tang *et al.*, 2019). However, as distractions subside with practice, the need for executive processing would reduce and if anything hinder uninterrupted deep absorbed meditative experiences. Our results show that such deep meditation experiences occur through different strategies of suspending executive processing depending on the amount of meditation training. While untrained meditators have a deep experience by suspending neural signatures of top-down regulation, trained practitioners suspend a neural process that computationally precedes regulation, i.e., monitoring. In other words, long-term training allows a practitioners' brain to learn that there are no more distractors to be downregulated, and thus reduce conflict monitoring of the contents of their consciousness. This finding is consistent with past work demonstrating

an inverted U-shaped response of lateral prefrontal cortex with meditation training as well as reduced ACC activation in highly trained compared to untrained meditators (Brefczynski-Lewis *et al.*, 2007), and higher response inhibition despite reduced midline frontal theta in long-term meditators (Andreu *et al.*, 2019).

Although meditation depth was not related to psychophysiological measures when modelled in combination with the neural measures, we did observe such a relationship when physiology was modelled separately. This indicates that neural activity in alpha and theta bands effectively "explained away" variance of the physiological measures. Respiration-rate was negatively correlated with the deepest (*nondual*) meditation experiences. This extends previous anecdotal evidence of extreme slowing down of respiration-rate accompanying deep meditation experiences (Corby *et al.*, 1978). We also observed that heart-rate was negatively correlated with *transpersonal qualities* in CTLs but not LTMs. This is interesting with respect to theories of subjective experience that posit a central role for interoceptive and embodied processes (Gallagher, 2006; Seth, 2013; Allen and Friston, 2018). Seth (2013) for example posits that conscious experience relies on predictive processing in the brain about interoceptive signals. In this sense, heart-rate constituted interpersonal conscious experience for CTLs but not LTMs. This implies that prolonged meditation training may reduce the influence of certain interoceptive/autonomic processes as somatic "markers" of deep meditation experiences.

Finally, meditation depth was not related to beta and gamma oscillations, which have previously been related to altered meditative experiences (Dor-Ziderman *et al.*, 2016; van Lutterveld *et al.*, 2017). We suspect two reasons for this. First, we analysed our data

differently from past studies. Previously different frequency bands have been correlated with self-reports using separate statistical models and not using multivariate models as in our analysis. The advantage of the multivariate approach is that it enables a parsimonious discovery of correlates while accounting for covariation between them. Second, we measured the correlates of a relatively broad idea of meditation depth that encompass a variety of different experiences including self-dissolution and effortless, the two experiences investigated in past work. This enabled us to discover more mechanistic-level neurocognitive correlates of altered conscious experiences during meditation.

Our meditation-naïve control group engaged in practices that are widely used in mindfulness-based interventions for improving mental health. During such practices, deeper meditation experience (such as relaxation and mindfulness) corresponded to a reduced neural signature of executive processing. Currently, a large majority of theoretical literature focuses on how mindfulness practices train executive processes such as attentional control and emotional regulation ((Lutz *et al.*, 2008; Hölzel *et al.*, 2011; Malinowski, 2013; Leyland *et al.*, 2019), however, see (Lutz *et al.*, 2015)). Our findings suggest that executive processes, while necessary for meditation, may not be the sole mechanisms involved in the pro-adaptive impact of mindfulness practices on mental health. Further studies of the impact of post-executive-processing-related deeper meditation experiences on clinical and positive health aspects of mindfulness training are needed.

One limitation of the present study is that because we used LTMs belonging only to a single meditation tradition, the LTM-specific reduction in midline frontal theta—and thus reduced executive monitoring as a mechanism for deeper meditation experiences—may not

be generalisable to meditators doing other types of practices. However, considering that ACC-related activity reduces with long-term training (Brefczynski-Lewis *et al.*, 2007) despite increase with short- to medium-term training (Hölzel *et al.*, 2007; Tang *et al.*, 2009) in meditators from other traditions, it is likely a general feature of meditation training. Another limitation is that we did not measure high-density EEG along with individual structural anatomies, and were thus unable to source-localise the lateral prefrontal cortical regions where theta was related to meditation depth. Future replication studies are advised to do so.

To summarise, both of the previous meta-analyses of neurophysiology literature on meditation and mindfulness training have concluded that alpha and theta oscillations are the most reliable neurophysiological signatures for them (Cahn and Polich, 2006; Lomas *et al.*, 2015). And while there have been several speculations about the role of alpha and theta in meditation (Lomas *et al.*, 2015; Brandmeyer and Delorme, 2016; Tang *et al.*, 2019), until now no studies to the best of our knowledge have empirically differentiated the distinct roles played by these two frequency bands in meditation practice. This is because previous studies did not take different levels of subjective experiences associated with meditation practice into account. By doing so, our results strongly indicate that while alpha increases as meditation experiences are deepened, theta decreases. Topographies of the correlations of alpha and theta with meditation depth combined with their previously known functional cognitive roles moreover indicate that increased alpha is likely associated with greater inhibition of distractions, while reduced theta is associated with a reduction in effortful control (at the level of monitoring in the LTMs and at the level of regulation in the CTLs) during meditation practice. We also found that prolonged meditation training may reduce the impact of certain autonomic signals, particularly heart-rate, on conscious experience.

Finally, as our meditation-naïve control group engaged in secular mindfulness practices used in mindfulness-based interventions for improving mental health and well-being in clinical and positive psychology settings, our results are directly applicable to such scenarios.

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Conflicts of Interest

None

Ethical Standards

The authors assert that all procedures contributing to this work comply with the ethical standards of the relevant national and institutional committees on human experimentation and with the Helsinki Declaration of 1975, as revised in 2008.

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Figure Legends

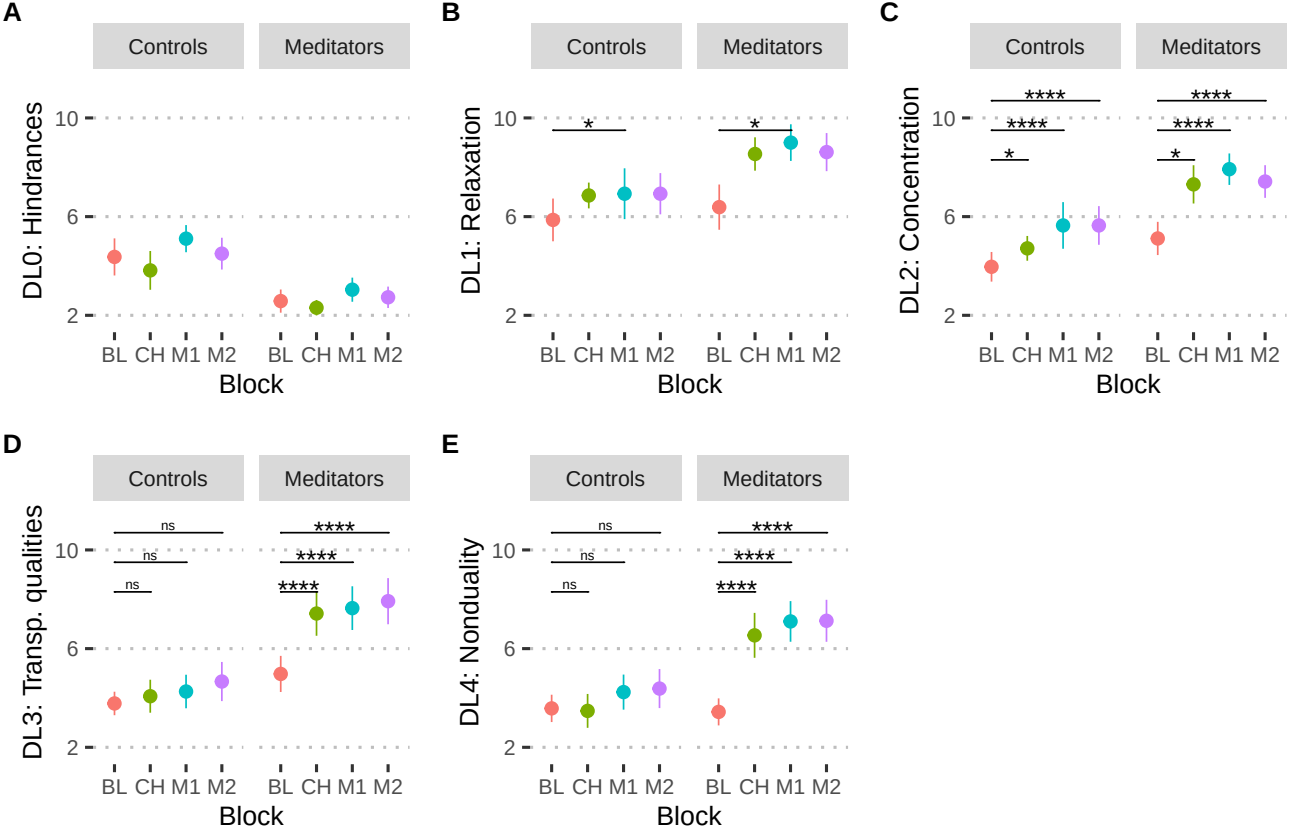
Figure 1. Self-reports of meditation depth for the five depth-levels, **A)** Hindrances (DL0), **B)** Relaxation (DL1), **C)** Concentration (DL2), **D)** Transpersonal Qualities (DL3), and **E)** Nonduality (DL4). Each depth-level is plotted for the two groups Controls and Long-term Meditators and for four time-points, baseline (BL), chanting (CH), first meditation practice (M1) and second meditation practice (M2). The error bars indicate standard errors of the means. Significance levels: * $p < 0.05$; ** $p < 0.01$; $p < 0.005$; ****$p < 0.001$.

Figure 2. **A)** Stepwise model reduction. Columns show the steps and rows show the 3 and 2-way interactions modelled at that step. The square-root of the $\chi 2$ value of the interaction is shown in shades of grey. Step 1 included all interactions. At each step the weakest interaction was dropped. The final reduced model revealed two significant 2-way interactions; depth-level x alpha and depth-level x theta. **B)** *t* values of the regression of alpha and theta upon self-reports at each depth-level. Filled triangles denote significant correlations ($p < 0.05$; FDR-corrected).

Figure 3. Topographic plots of the relationship between theta (left) and alpha (right) amplitudes and meditation depth in the **A)** two groups combined, **B)** long-term meditators, and **C)** controls. Plotted are the square-root of the $\chi 2$ values of the interaction effects between depth-level, and theta and alpha amplitude regressed upon self-reports. The values are signed by the direction of relationship, which was negative for theta and positive for alpha at all channels. Asterisks denote channels with significant interaction effects, thresholded for A) at Bonferroni-corrected $p < 2.5e{-}8$ and B—C) at Bonferroni-corrected *p*

< 0.025.

Figure 4. **A)** *t* values of the correlation between subjective reports of depth at each of the five depth-levels with heart-rate for the two groups, controls and long-term meditators. **B)** *t* values of the correlation between subjective reports at each of the five depth-levels for heart-rate variability and respiration-rate. Filled triangles denote significant correlations (p < 0.05; FDR-corrected) at that depth-level.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Meditators
DL0: Hindrances
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B
Controls
Meditators
DL1: Relaxation
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Controls
Meditators
DL2: Concentration
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DL3: Transp. qualities
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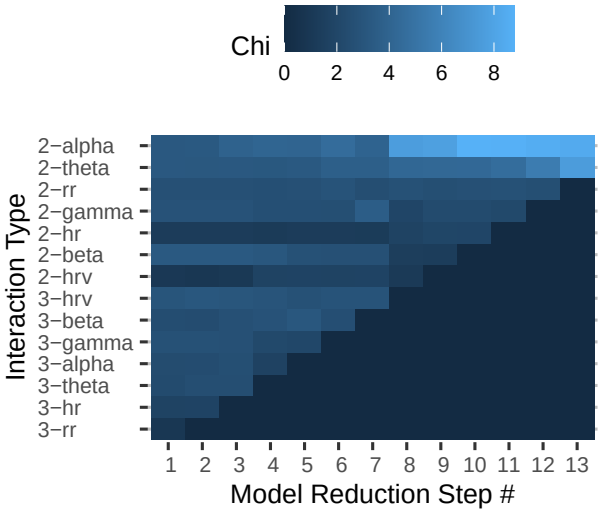
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Interaction Type
2−alpha
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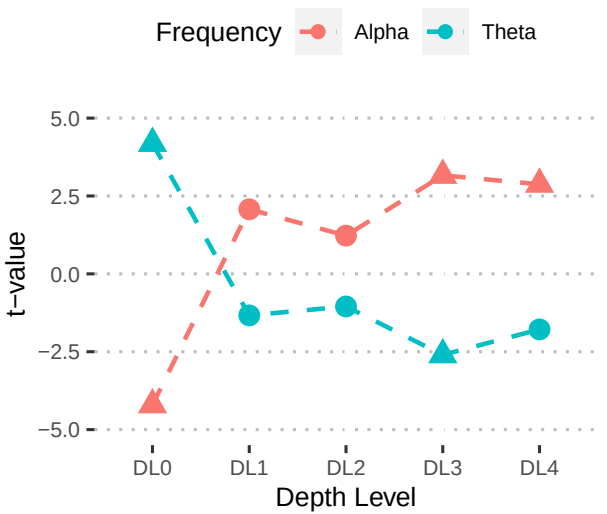
Model Reduction Step #

B


Frequency
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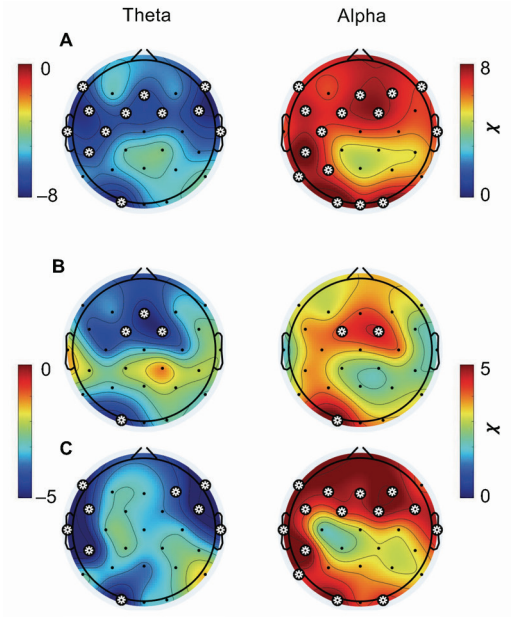
DL0
DL1
DL2
DL3
DL4
Depth Level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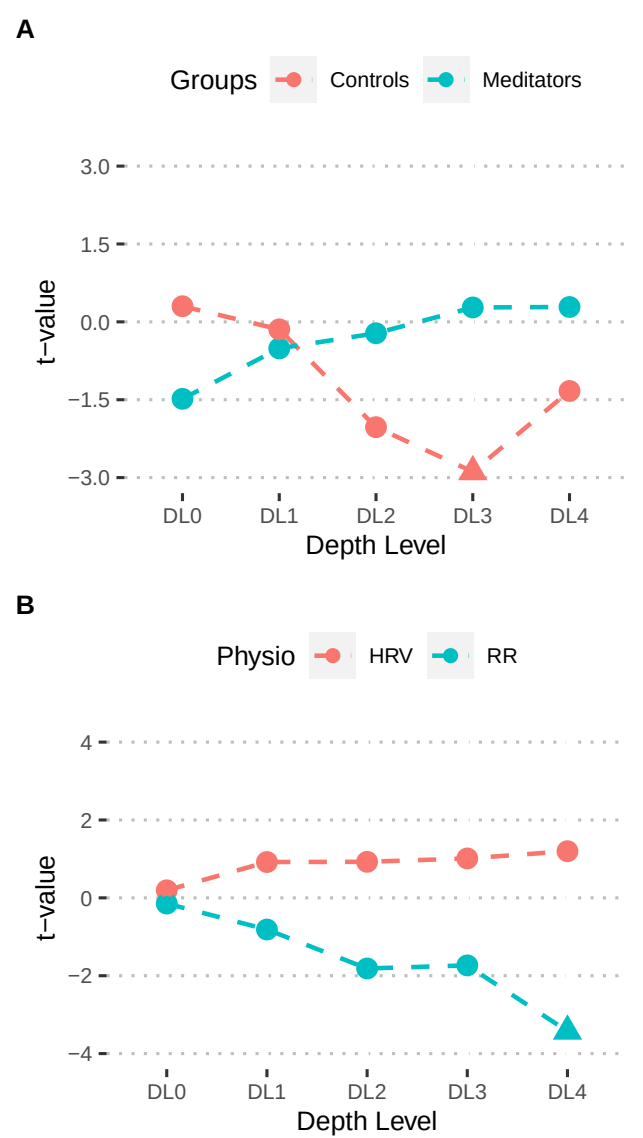
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Depth Level

Supplementary Materials

Participant recruitment

Long term meditators (LTMs) were recruited from a single meditation tradition (*Ananda Marga*; English translation: Path of Bliss) through their regional email lists in the Bay Area and national email lists in the United States. This tradition was selected because an older study from this tradition anecdotally reported a practitioner entering a deep state of meditative trance (*samadhi*) but no follow-up studies have been conducted since (Corby *et al.*, 1978). The LTMs were included based on >10 years of regular practice of at least 1 hour/day, although most reported 2—3 hours of daily sitting practice. Nine of the fifteen long-term meditators were monastics. The practitioners reported engaging in multiple practices as part of their daily regimen. This included a system of moral guidelines that are part of the Yogic tradition (*yama* and *niyama*), yoga postures (*asanas*), controlled breathing (*pranayama*), visualisation practice where the participants try to withdraw attention from the external senses (*pratyahara*), concentration on a point and an internally repeated phrase (*mantra*), as well as nondual absorptive meditation (*dhyana*).

Control participants (CTLs) were recruited through online forums and by posting fliers in public and university libraries in the Sacramento/Davis area.

Meditation Practices

Before beginning measurements, participants were asked to familiarise themselves with the MEDEQ questions and ensure they were clear about their meanings. For BL, participants were asked to keep their eyes closed and listen to a podcast lasting approximately 9 minutes

(*The Memory Palace*; Episode 36). For CH, participants again kept their eyes closed while listening to an audio that included a musical chant (available online at: osf.io/sfkte). The chant included a repetitive singing of a sanskrit mantra, *Baba Nam Kevalam*. LTMs were familiar with this chant and could use this as a tool for meditation according to its meaning ("love is the essence of everything"). CTLs were also told the meaning of the chant and asked to simply listen to the music and relax before starting meditation. For M1 and M2, the LTMs engaged in two different styles of practices that were part of their daily regimen. During M1, they practiced concentrating with eyes closed on an internally visualised point accompanied by silently repeating a personal *mantra* (that was assigned to them by a meditation instructor when they first learnt this practice). During this practice, the mantra repetition is accompanied by a contemplation that their individual self-consciousness is part of a larger transcendental consciousness and is merging in it. During M2, they engaged in a "non-dual" practice, which involves contemplating suspension of their intentional agency (e.g., "I am meditating") into the idea of a transcendental consciousness. The idea of transcendental consciousness in *Ananda Marga* philosophy (Anandamurti, 1998) is closer to a Husserlian transcendental consciousness (Husserl, 1999) than to the more commonly known concept of "pure consciousness" described in TM literature (Travis and Shear, 2010), in that the former evades any reflection or noemetisation (Hewitson, 2014).

To the control group, we administered audio recordings with instructions of commonly known meditation practices through headphones. For the first practice, they followed instructions from a 20-minute recording of focused attention mindfulness of breath practice. For the second practice, they listened to a 15-minute recording of a "loving-kindness" meditation towards a stranger, a close other, and themselves.

Subjective report about experience

We selected the following questions from the MEDEQ such that they would capture all five depth levels: 2, 4, 6, 8, 10, 11, 12, 15, 19, 22, 23, 24, 26, 27 (Piron, 2001).

Missing data

Due to technical difficulties, we did not obtain pulse and respiration measures on one of the control participants. In addition, in 3 (of 112) blocks participants missed filling out the questionnaire.

EEG and physiology preprocessing

We used EEGLAB (Delorme and Makeig, 2004) and customized MATLAB code to conduct EEG data analysis. Raw EEG data were first downsampled to 250 Hz then band-pass filtered between 0.1–80 Hz, notch filtered with a 1 Hz bandwidth to exclude electrical line noise at 60 Hz, and re-referenced to the average of all electrodes. We then used Independent Component Analysis (ICA; as implemented in EEGLAB) to remove ocular and muscular artifacts (Delorme *et al.*, 2007). Despite ICA, however, the four peripheral-most lateral channels (FT9, FT10, TP9, TP10) still appeared to be contaminated with muscle artifacts in many subjects. Moreover, midway through the study, the lead of one of the front-polar channels (FP2) was corrupted. Accordingly, for final analysis we excluded a total of six channels (FT9, FT10, TP9, TP10, FP1, FP2). Results were however very similar when these channels were included in analysis.

For computing our seven neuro-physiological measures, we first split each of the four measurement periods, BL, CH, M1 and M2 into continuous 60-sec epochs with 40-sec overlaps. As M1 was 20 minutes and M2 was 15 minutes, we used only the last 15 minutes of M1 (and M2) as well as the entire duration of BL and CH for analysis. We then calculated the average amplitude in four frequency bands corresponding to *theta* (4–7 Hz), *alpha* (7–13 Hz), *beta* (15–25 Hz), *gamma* (30–50 Hz) oscillations at all the channels using MATLAB's FFT function and then averaged these measures across all epochs. Respiration-rate (RR), heart-rate (HR) and heart-rate variability (HRV) were also calculated in similar 60-sec epochs. For calculating RR, we filtered the respiration data between 0.04—0.4 Hz and calculated the median of the inverse time difference between peaks corresponding to the inhale phase within each epoch. Epochs where peak-duration differences were highly variable (interquartile range > 5) were marked as artifactual and excluded from analysis; results were similar for a wide range of interquartile range thresholds (e.g., 5 < interquartile range < 10). Heart measures, HR and HRV, were calculated in the 60-epochs using *HRVTool* toolbox (version 0.3) for MATLAB (Vollmer, 2019), which provides a function to filter out artifactual pulses. HRV was calculated in the high-frequency range (0.15–0.4 Hz) consistent with previous literature (e.g., Lumma *et al.*, 2015).

Statistical analyses

For statistical analysing, we used linear mixed models (LMM) as implemented by the *lme4* package (version 1.1.21) in R (Bates *et al.*, 2014). The intercept for individual participants was used as the random effect for all LMMs. Even though the self-report data was based on a

Likert scale, which is otherwise ordinal, when using more than four or five levels (we used a 12-point scale) allows its treatment as continuous data (e.g., Johnson and Creech, 1983; Norman, 2010). LMMs were ensured to reasonably satisfy assumptions of linearity, homoscedasticity, and normality of residuals.

The interaction effects were evaluated using type II Wald $\chi 2$ tests through the *Anova* function in the *car* package (version 3.0.2). Post-hoc differences were evaluated using *lsmeans* function, which uses the Kenward-Roger method for estimating the degrees of freedom and performs a multiple comparison correction uses the Tukey method for a family of 4 estimates. The main effects for individual-depth-level plots (Figure 2B and Figure 4) were obtained using *t*-tests to obtain the sign of the correlation through the *summary* function of the *lmerTest* package (version 3.0.1), which uses Satterthwaite's method to estimate the degrees of freedom. The *p*-values for the 5 individual depth-levels were corrected for multiple comparisons using false discovery rate.

Self-reports

For self-reports, we were interested in validating our manipulations of state (meditation or chanting vs. baseline blocks) and group (long-term meditators vs. controls). For this we tested if 1) the meditation blocks increased ratings for DL1 (*personal self*) through DL4 (*nonduality*), 2) if the control group reported higher DL0 (*hindrances*) compared to the long-term meditators during the meditation epochs, and 3) if long-term meditators reported stronger experiences for DL3—DL4 (*transpersonal qualities* and *nonduality*) typically associated with long-term meditation training (Piron, 2001). For this, we separately

modelled each of the 5 *depth-levels* (DL0—DL4) with 2 levels of *group* (long-term meditators, controls) and 4 levels of *block* (BL, CH, M1, M2) as fixed effects.

Covariation of self-reports and neuro-physiology

We expected to study the relationship between self-reports of meditation depth and neural oscillatory amplitude and physiological measures, in all 7 different neuro-physiological measures (i.e., NPM). For this, we used a stepwise top-down model reduction approach on multilinear mixed models for obtaining the NPMs that predicted meditation depth.

For an NPM to be related to meditation depth (in one or more of its five levels), we expected that its covariation with self-reported experiences across the four blocks to be significantly different across depth level. For example, if higher alpha amplitude is related to greater meditation depth, then the correlation between alpha and self-reports across blocks would be low (or even negative) for DL0 and would gradually increase for DL4. Such an effect could be statistically determined by investigating the 2-way interaction between alpha amplitude and depth-level when regressed upon self-reports. Furthermore, if a particular NPM was related to self-reported meditation depth in one group but not the other, then we would observe a 3-way interaction between that measure, the depth-level and group in predicting self-report.

We started by modeling self-reports as a combination of multiple 3- and 2-way interactions along with main effects using maximum likelihood (ML) estimation (Zuur *et al.*, 2009). The 3-way interactions were between the 7 NPMs (theta, alpha, beta and gamma, RR, HR and HRV), depth-level and group. The 2-way interactions were between the 7 NPMs and

depth-level. For evaluating the 3-way interactions, the other two sets of 2-way interactions between the NPMs and group, as well as group and depth-level were also included in the complete model. In a top-down approach to model reduction, we first stepwise reduced the 3-way interactions and then the 2-way interactions by removing the interactions with the lowest effect sizes that did not significantly (alpha = 0.05) contribute to the model. When removing the 3-way interaction for an NPM, we also removed its associated NPM by group interaction. Similarly, when removing a 2-way interaction, we also removed the corresponding main effect of the NPM. We then evaluated the reduced model with restricted maximum likelihood estimation (REML) to obtain accurate statistical parameters corresponding to the remaining effects (Zuur *et al.*, 2009).

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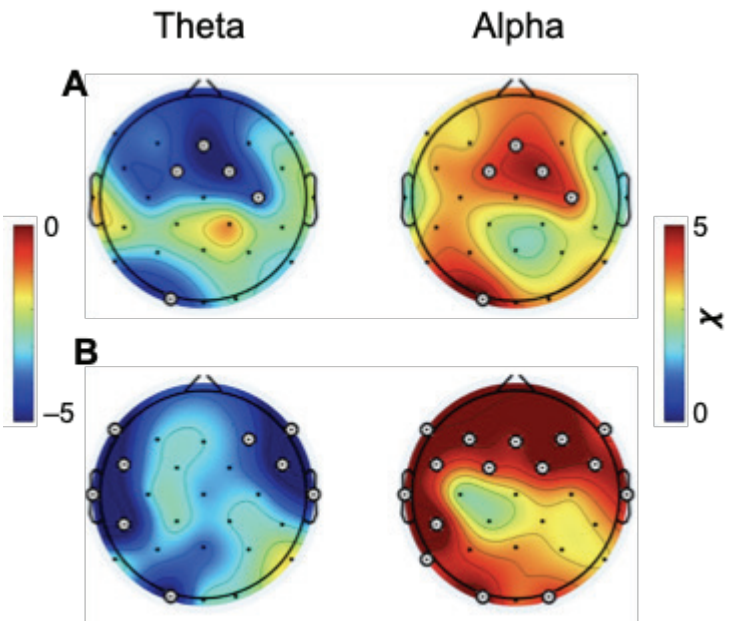
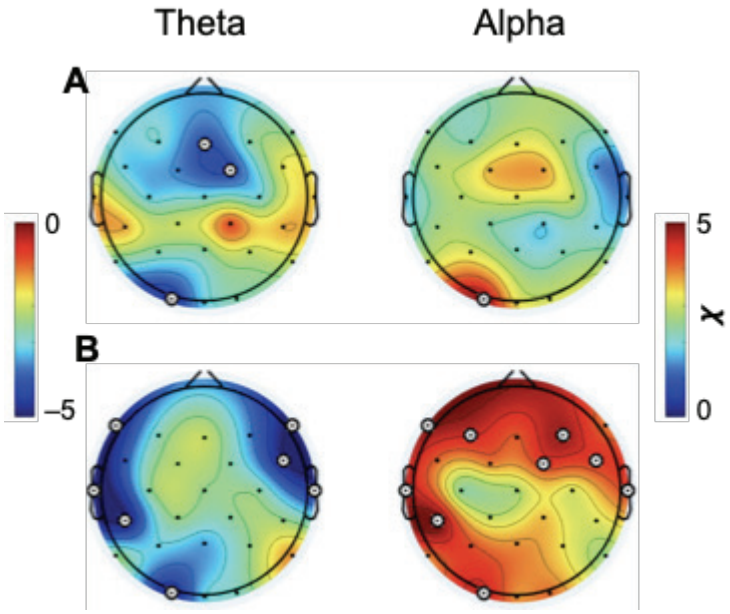
Supplementary Figures



Supplementary Figure 1. Topographic plots of the relationship between theta (left) and alpha (right) amplitudes and meditation depth in **A)** long-term meditators, and **B)** controls for only the last 6 minutes of the meditation block. Plotted are the square-root of the $\chi 2$ values of the interaction effects between depth-level, and theta and alpha amplitude regressed upon self-reports. The values are signed by the direction of relationship, which was negative for theta and positive for alpha at all channels. Channels with asterisks show significant interaction effects thresholded at Bonferroni-corrected $p < 0.025$.



Supplementary Figure 2. Topographic plots of the relationship between theta (left) and alpha (right) amplitudes and meditation depth in **A)** long-term meditators, and **B)** controls evaluated while excluding the chanting block. Channels with asterisks show significant interaction effects thresholded at Bonferroni-corrected $p < 0.025$.