Neuropsychologia 119 (2018) 92–100

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Differential effects of non-dual and focused attention meditations on the formation of automatic perceptual habits in expert practitioners

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ARTICLE INFO

Keywords:
Attention
Auditory oddball
EEG
Gamma
Mindfulness
Predictive coding

ABSTRACT

Non-dual meditation aims to undo maladaptive cognitive and affective patterns by recognizing their constructed and transient nature. We previously found high-amplitude spontaneous gamma (25–40 Hz) oscillatory activity during such practice. Nonetheless, it is unclear how this meditation state differs from other practices, in terms of perceptual information processing. Here, we hypothesized that non-dual meditation can downregulate the automatic formation of perceptual habits. To investigate this hypothesis, we recorded EEG from expert Buddhist meditation practitioners and matched novices to measure two components of the auditory evoked response: the Mismatch Negativity (MMN) and the Late Frontal Negativity (LFN), a potential observed at a latency sensitive to attentional engagement to the auditory environment, during the practices of Open Presence (OP) and Focused Attention (FA), as well as during a control state, in the context of a passive oddball paradigm. We found an increase in gamma oscillatory power during both meditation states in expert practitioners and an interaction between states and groups in the amplitude of the MMN. A further investigation identified the specific interplay between the MMN and the LFN as a possible marker to differentiate the two meditation states as a function of expertise. In experts, the MMN increased during FA, compared to OP, while the opposite pattern was observed at the LFN latency. We propose that the state of OP in experts is characterized by increased sensory monitoring and reduced perceptual inferences compared to FA. This study represents a first attempt to describe the impact of non-dual meditation states on the regulation of automatic brain predictive processes.

1. Introduction

We recently proposed a novel classification system that categorizes various styles of meditation into attentional, constructive, and deconstructive families based on their primary cognitive mechanisms and their specific impact on self-related processes and different aspects of well-being (Dahl et al., 2015). While attention-based meditation and compassion-based practices (i.e., the constructive family) are increasingly studied as tools for cognitive neurosciences, little is still known about the basic neurophysiological and cognitive processes underlying the so-called “deconstructive family” (Dahl et al., 2015). Deconstructive style of meditation aims to undo maladaptive cognitive and emotional patterns (e.g. rumination, neuroticism) by exploring the dynamics of perception, emotion, and cognition and generating insights into one's internal models of the self, others, and the world. This self-inquiry can involve exploring self-related processes with discursive analysis, akin to cognitive-based therapy, or by direct examination of conscious experience through phenomenological methods. This latter approach is especially cultivated in so called non-dual forms of meditation, and familiarity with the contemplative methods involved requires intensive training. Contemplative traditions allege that non-dual meditation practices are important for alleviating suffering, and such practices also play a role in many contemporary mindfulness-based interventions (Dunne, 2011). Apart from very few studies (e.g. (Josipovic, 2014)), the clinical benefits of this approach and its behavioral and neurophysiological mechanisms are still largely unknown.

To explore this topic, we studied the meditative state of “Open Presence” (OP) in Tibetan Buddhist traditions as a paradigmatic case of

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https://doi.org/10.1016/j.neuropsychologia.2018.07.025
Received 31 January 2018; Received in revised form 15 July 2018; Accepted 20 July 2018
Available online 21 July 2018
0028-3932/

non-dual meditation. Styles of meditation that cultivate OP are described as inducing a phenomenal experience where the intentional structure involving the duality of object and subject is attenuated. In this sense, such styles of contemplative practice are "non-dual" (Lutz et al., 2007). One important phenomenological element of the state of OP is a spontaneously occurring suspension of the representational models of the self and objects in the world. At the same time, OP styles of meditation are said to instantiate a state of relaxed lucidity, where perceptual phenomena are experienced with more saliency and clarity, without acting upon them or avoiding them. In such a way, perceptual phenomena in OP spontaneously appear and vanish in the field of awareness like "patterns drawn on water" (Dowman, 1994).

Based on these phenomenological descriptions, we hypothesized that OP practice downregulates the formation of perceptual habits while increasing the monitoring of the sensory environment, modulating brain predictive processes in relation to a specific profile of spontaneous brain activity. As the stability of OP is considered to require extensive training, we expected this effect to be present in expert practitioners only. To test this hypothesis, we used electroencephalography (EEG) to study a well-characterized component of the auditory-evoked potential, the Mismatch Negativity (MMN) (Näätänen et al., 2004), which measures implicit perceptual learning processes. The MMN reflects the violations of predictions that the brain casts over the regularity of the auditory environment, following the presentation of a "deviant" stimulus after several "standard" tones (Garrido et al., 2009). We expected to observe a decrease in MMN amplitude in experts, compared to novice practitioners, during the practice of OP and compared to a control state where attention is diverted from the auditory stream. To characterize the specificity of OP meditation, we compared this state to a control state of concentrative meditation, or Focused Attention (FA) (Lutz et al., 2008). FA meditation requires the practitioner to monitor ongoing distractors while maintaining attention on the chosen object. During FA, we expected the increased monitoring of task-unrelated events to enhance the brain responses to deviations of the auditory environment, as measured by increased MMN amplitude. Furthermore, we looked at later latencies (after 200 ms) of the auditory-evoked response to characterize differences between states and groups in terms of monitoring and saliency of the sensory environment (e.g. Escera and Corral, 2007; Chennu et al., 2013). As stated above, we expected both meditation states to result in increased monitoring of the incoming stimuli, but having a different impact on brain predictive processes. Previous studies have investigated biomarkers of different meditative practices, focusing especially on brain oscillatory activity (e.g. Cahn and Polich, 2006 for a review). In the present study, we aimed at confirming previous findings in this domain, as well as investigating a putative functional relationship between specific oscillatory profiles and the hypothesized modulation of predictive processes in non-dual practices. More specifically, we predicted increased power of oscillatory activity in the alpha (8–12 Hz) frequency range during meditation, as a correlate of general relaxation and in line with previous studies (Cahn and Polich, 2006). In addition, we also predicted that higher activity in faster oscillatory rhythms (i.e. 25–40 Hz) at frontal scalp regions would underlie the state of high meta-awareness and perceptual saliency in OP, a profile previously identified during a similar form of non-dual practice (Lutz et al., 2004).

2. Materials and methods

2.1. Ethics statement

All study and task details were approved by the UW-Madison Health Sciences Internal Review Board. Participants provided written informed consent for all study procedures.

2.2. Subjects

Sixteen long-term meditation practitioners (43.4 ± 9.4 years old, 12 males and 4 females) and fifteen age-matched controls (42.4 ± 11.4 years old, 13 males and 2 females) participated in the study. Long-term meditation practitioners were selected based on a criterion of at least 10,000 h of formal meditation practice in the Nyingma and Kagyu traditions of Tibetan Buddhism, which have very similar styles of practice (mean: 28,990 h, SD: 13.88). The length of their training was estimated based on their daily practice and the time they spent in meditative retreats. Ten hours of sitting meditation were counted per day of retreat. Based on this criterion, these practitioners are referred to as "experts" here for brevity. Control participants were recruited from the local community and had no previous experience with any type of meditation, but expressed interest in learning meditation. Subjects in the control group were familiarized with the meditation instruction for one week before the experiment and were guided by verbal instructions during the practice.

2.3. Meditation practices and training

Open Presence (OP) styles of practice are found in both the Mahāmudrā or Chagchen (Tibetan, *phyag chen*) and the Dzogchen (Tibetan, *Rdzogs chen*) traditions of Tibetan Buddhism (Van Schaik, 2004). In this regard, these contemplative traditions overlap so significantly that Tsele Natsog Rangdrol, an influential Tibetan author from the 17th century, combines the Tibetan terms for these two traditions into a single moniker, "Chag-zog" (2). The main focus for Chag-zog styles of practice is to recognize the "nature of the mind" (Tibetan, *sems nyid* or *sems kyi rang bzhin*) or one's fundamental "awareness" (Tibetan, *rig pa*) and then to sustain that recognition. In this study, the term "rigpa chok zhag" (Tibetan, *rig pa cog bzhag*)—literally, "placing the mind directly in fundamental awareness"—was the term used for OP practice, but various other terms for OP practice are also widely known and are essentially synonymous (Lutz et al., 2007; Rangdrol, 2011). Referring to the Tibetan Chag-zog traditions as "systems of definitive meaning," Rangdrol describes the key features of OP practice in this way:

> "Let go into your natural state, with no need to cling or fixate on even the impetus or the attitude, "I meditate!" Without disturbing yourself with any ambition, such as hoping for a good meditation or fearing it won't succeed, to let be in unfabricated naturalness free from concepts is the meditation state of all the systems of definitive meaning" (Rangdrol, 2011).

Based on its traditional presentation (Namgyal, 2001; Third Dzogchen Rinpoche, 2008; DBaṅ-phyug-rdo-rje, 2009; Rangdrol, 2011) and scholarly analysis (Lutz et al., 2007; Dunne, 2011, 2015), OP practice is viewed here as an advanced form of Open Monitoring (OM) practice (Lutz et al., 2008), in which practitioners might be found at various levels of achievement. OP meditation consists theoretically of a state where the qualities of effortless openness and acceptance are vividly experienced with minimal control-oriented elaborative processes. The lack of explicit monitoring in OP meditation is the pivotal but finely grained difference from OM practice, and this distinction concerns the Buddhist notion of "reflexive awareness," as discussed by Buddhist scholars (Coseru, 2012; Dunne, 2015). Briefly, in OP practice, an awareness of whatever emerges in experience continues without the effortful vigilance that characterizes OM styles of practice. For reasons of simplicity, we will continue to use the term "monitoring" in this scientific context to describe this aspect of OP, with the understanding that this term takes a slightly different meaning in OP and OM. In addition to the OP meditation of "placing the mind directly in awareness," practitioners also engaged in a Focused Attention (FA) style of practice known as "one-pointed concentration" (Tibetan, *rtse gcig ting nge'dzin*; see Namgyal, 2001). As with any FA style of practice, in one-pointed concentration one maintains selective attention on a chosen object, and in this case sustained attention was directed at a fixation cross. This FA style of practice is considered here as second meditation condition to determine the specificity of effects observed in the OP practice. Control participants were given instructions written by a scholar who is familiar with the practices (see Supplementary material 1), and then told to practice at home 30 min a day for 7 days prior to the experiment.

2.4. Auditory paradigm

Subjects underwent a passive auditory oddball task (Näätänen et al., 2004), consisting of the variable repetition of a standard tone (1000 Hz; 60 ms duration; 10 ms rise and fall; 80 dB SPL) followed by the presentation of a frequency deviant tone (1200 Hz; 60 ms duration; 10 ms rise and fall; 80 dB SPL). Each block of the task contained 80% standard tones (n = 200) and 20% deviant tones (n = 50) with a variable interstimulus interval of 800–1200 ms (block duration: 4m15s on average). Each subject underwent three blocks per condition and three different conditions: Open Presence (OP), Focused Attention (FA), and Reading (RE) as a control condition. The two meditative practices, OP and FA, are described above. During the control condition (RE), subjects were instructed to read a newspaper and ignore the auditory stimulation. The order of blocks was randomised and each subject underwent the same order, as follows: RE1 - OP1 - FA1, FA2 - OP2 - RE2, OP3 - FA3 - RE3.

2.5. EEG recording

EEG data were recorded at standard extended 10–20 positions with a 128-channel Geodesic Sensor Net (Electrical Geodesics, Eugene, OR), sampled at 500 Hz, and referenced to the vertex (Cz). Data were filtered, using an analogue band-pass filter, between 0.1 and 200 Hz. A digital notch filter was applied to the data at 60 Hz to remove any artefacts caused by alternating current line noise. Bad channels were replaced by using spherical spline interpolation (Perrin et al., 1989).

2.6. Data pre-processing

Data were first converted into EEGLAB software format (Delorme and Makeig, 2004), which was used for the first pre-processing steps. Data were filtered between 0.5 and 100 Hz and manually cleared of large movement-related artefacts. Independent Component Analysis (ICA) was applied to the raw data of each participant (on those channels that were not interpolated) using the Runica algorithm (Makeig et al., 2002) to identify and remove artefacts caused by blink, saccades, and cardiac (EKG) and muscular activity. We further investigated ICA profiles to determine whether some specific components that are prevalently found in expert meditation practitioners, which are characterized by a sustained peak of gamma activity distributed in several locations over the scalp, had to be rejected as caused by muscular activity or rather had to be kept in the EEG analysis as genuine contributions to the brain signal (see Supplementary material 2.1 for a detailed description of these profiles and the methods used to test their contribution to the ERP). After ICA correction, data were re-referenced offline to the average of both mastoids, a non-causal band-pass 1–60 Hz digital filter was applied, and two-second epochs centred on stimulus presentation (− 1 to 1 s) were generated. For each subject and for each state we generated a "deviant" condition, comprised only of epochs centred on deviant tones, and a "standard" condition, comprised only of epochs centred on standard tones that were presented just before a deviant tone. After manually rejecting artefacts, the number of trials did not differ significantly between states, conditions, and groups. Although there was a trending difference between states ($F(2, 58) = 3.38$; $p = 0.054$ Huynh-Feldt corrected), we did not take it into account in further data analysis, since the largest difference between states (FA – RE) in the number of trials was only 3% (see Supplementary material 2.2 for descriptive statistics). The epoched data were baseline-corrected by subtracting the mean value of the signal during the 100 ms before stimulus presentation.

2.7. Event-related potentials

We converted data from EEGLAB into SPM8 (Wellcome Department of Imaging Neuroscience, London, UK) software format, which was used for the following steps of event-related potentials (ERPs) analysis. After conversion into SPM8, we generated ERPs for each subject, state, block, and stimulus type using the robust averaging method implemented in SPM8. We used this procedure as a complementary artefact-correction for any artefacts that were not removed by previous artefact-rejection methods. Since robust averaging can re-introduce high frequencies into the signal, we filtered data again at 1–20 Hz and reapplied baseline-correction. We then performed two streams of analysis to investigate differences between groups and states that appeared in the MMN and later latencies, respectively. Statistical analyses were performed using R software (version 3.4.2)(R core team, 2017).

To identify the MMN, we computed difference waveforms from the grand average for each group and state, subtracting responses to standard stimuli from those to deviants. We used an a priori region of interest (ROI) for the assessment of this component, basing our ROI on previous literature (e.g. (Duncan et al., 2009; Näätänen et al., 2011)), resulting in a frontal ROI comprised of twelve electrodes, including Fz (see Fig. S1). Our selection of this ROI was confirmed by observation of the topography of the standard and deviant waveforms and difference waveforms (MMN) across all subjects and states, as well as those for each state and group taken separately.

We computed the mean amplitudes of MMN for each participant and state over a time-window of 90–180 ms after stimulus onset. This time-window was in line with previous literature (e.g. (Opitz et al., 2002)) and confirmed through the observation of the time-course of the MMN waveforms in the main region of interest. We then fitted a linear mixed-effects model using the R package lme4 (Bates et al., 2014). The model comprised the average MMN amplitude as dependent variable, the interaction between STATE (FA, OP, RE) and GROUP (Experts, Novices) as fixed effect, and subjects as random effect. The model was tested using an ANOVA analysis of variance (Type II Wald chi-square test). Paired *t*-tests, corrected for multiple comparisons using Tukey honestly significant difference test (HSD), were used as post-hoc tests comparing least-squared means.

As a second line of analysis that would focus on differences between groups and states in late latencies (after 200 ms), we looked for a time window for which the signal in response to standard tones, within the a priori ROI used for the MMN, was significantly different between the meditation (both FA and OP) and control (RE) conditions, across groups. We corrected for multiple comparison using a non-parametric, permutation-based, cluster-level statistical test (Maris and Oostenveld, 2007) in MNE v0.14 (cluster-defining threshold = 0.01; cluster-level threshold = 0.05; 10,000 permutations). A temporal cluster was found between 280 and 400 ms post-stimulus. We used this time-window for subsequent analyses of the late negative ERP component, henceforth referred to as Late Frontal Negativity (LFN). We fitted a linear mixed-effects model comprising the average LFN amplitude (combining standard and deviant stimuli) as dependent variable, the interaction between STATE and GROUP as fixed effect, and subjects as random effect. The model was tested using an ANOVA analysis of variance (Type II). Paired *t*-tests, corrected for multiple comparisons using Tukey HSD, were used as post-hoc tests comparing least-squared means.

Finally, we explored in a post-hoc analysis the interplay between early (MMN) and late (LFN) components of the auditory evoked potential as a mean of investigating differences between states and groups in terms of monitoring and perceptual inference. Data from each participant and state for the two ERP components was mean-centred by subtracting to each observation the average of the corresponding component across states and groups. Data were then entered in a two-way repeated measures ANOVA (rmANOVA), with STATE (three levels: FA, OP, RE) and COMPONENT (two levels: MMN and LFN) as within-subject factors and GROUP (two levels: EXPERT, NOVICE) as a between-subject factor.

2.8. Spectral analysis

For spectral analysis, we used epoched data before conversion to SPM8 (filtered between 1 and 60 Hz), combining epochs derived from all stimuli (all standard and deviant tones). We computed the power spectral distribution for each electrode and for each 2-s epoch using Welch's method (Welch, 1967), which averages power values across sliding windows (window width = 500 ms, overlap = 50%). We averaged the results from all epochs to obtain the mean power spectral density (PSD) for each experimental condition. We created two sets of data by averaging and log-transforming PSD over two frequency bands: alpha (8–12 hz) and gamma (25–40 Hz).

The aim of the spectral analysis was to investigate in two different brain rhythms the presence of: 1) main effects of meditation states across both groups, 2) differences between OP and FA meditation, and 3) whether these differences were specific to expert practitioners. For this purpose, we first entered log-transformed data in a comprehensive general linear model with STATE (FA, OP, RE), FREQUENCY (alpha, gamma), and ROI (frontal, occipital [see Fig. S2]) as within-subjects and GROUP (Experts, Novices) as between-subjects factors. The model was tested using repeated-measures analysis of variance (rANOVA). If interactions were present, different linear mixed-effects models were fitted for each frequency and ROI. Paired and independent-samples *t*-tests, corrected for multiple comparisons using Tukey HSD, were used as post-hoc tests comparing least-squared means.

In some cases, and for illustrative purposes, we performed whole-scalp statistical inferences to identify electrodes that showed significant effects for contrasts of interest. We used a cluster-based approach to control for multiple comparisons, and a permutation scheme to relax the assumptions usually required by parametric methods. More specifically, we used the threshold-free cluster enhancement strategy developed by Smith and Nichols (2009), which offers better localization than other cluster-based methods by performing inference at the electrode level.

3. Results

3.1. Auditory event-related potentials

Fig. 1 B shows the topographies at the scalp level for the mean amplitude of the MMN (90–180 ms) for experts and novices, and for each experimental condition. To test our hypothesis of a down-regulation of the MMN during OP in expert meditators only, we tested a linear mixed-effects model at the frontal ROI (Fig. S1). In line with our prediction, we found a significant STATE by GROUP interaction (χ^2 (2) = 7.81; p = 0.02), showing how different meditative states modulate the amplitude of the MMN differently for expert and novice practitioners (Fig. 1A). More specifically, in the expert group, the MMN amplitude marginally increased during FA, compared to RE (t-ratio (58) = − 2.3; p = 0.06) while no difference was found between OP and RE (t-ratio (58) = − 0.3; p = 0.94). Contrary to our hypothesis, the increase in FA, compared to OP, was present only as statistical trend (t-ratio (58) = − 1.9; p = 0.12) (Fig. 1C). In novice practitioners, the MMN amplitude was marginally higher during OP, compared to RE (t-ratio (58) = 2.2; p = 0.06), while no difference was observed between

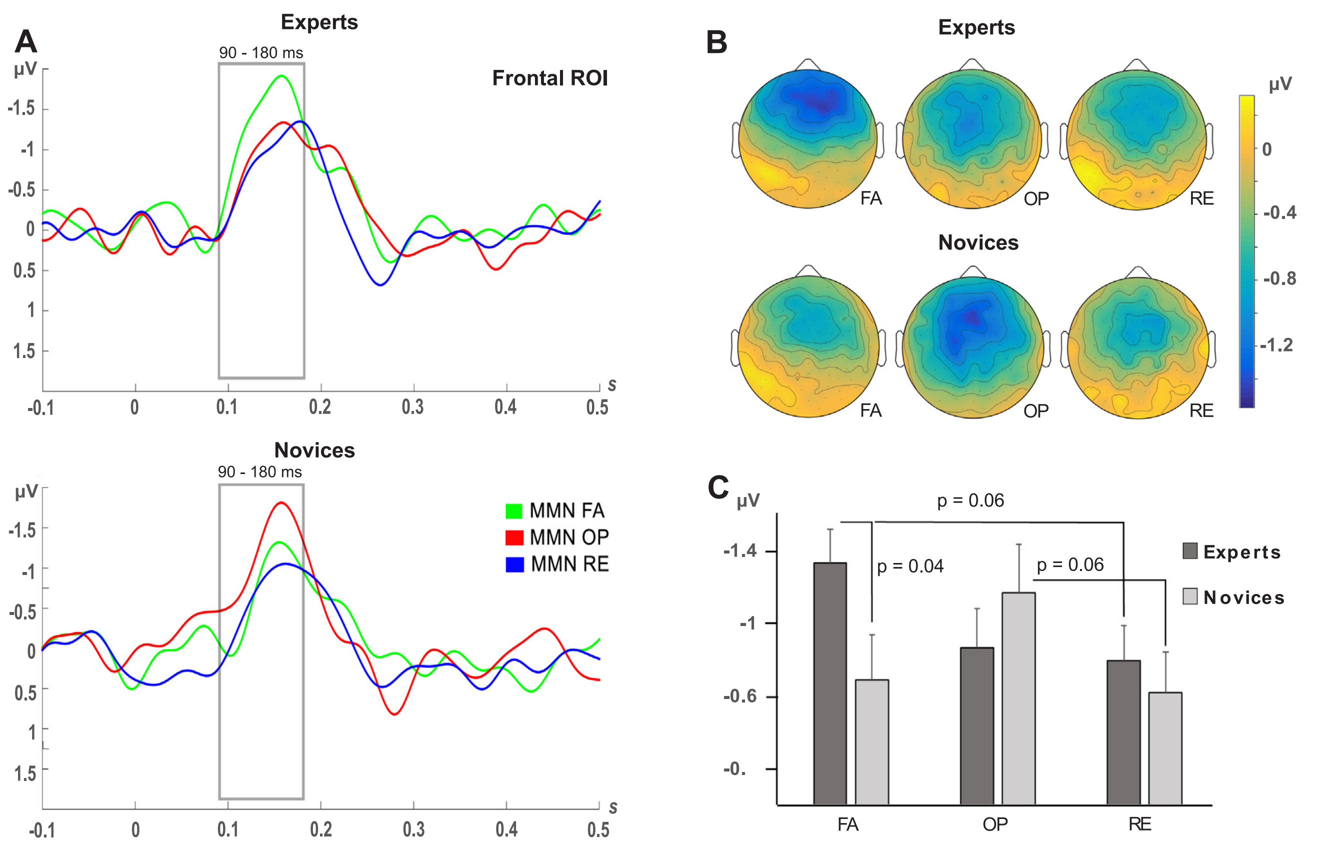

Fig. 1. Meditation states modulate mismatch negativity (MMN) differently between expert and novice meditators. (A) Subtraction (deviant minus standard, i.e. MMN) waveforms at frontal ROI (see Fig. S1) for FA, OP and RE conditions (FA: focused attention meditation, OP: open presence meditation, RE: reading a newspaper) in experts (top) and novices (bottom). (B) Average voltage scalp maps of MMN between 90 and 180 ms after stimulus onset for experts (top) and novices (bottom) during FA, RE and OP. (C) Mean values of MMN from (B) at frontal ROI. Error bars represent standard errors of the mean. P-values indicate significant and marginally significant differences within groups, between experimental conditions, as a result of paired *t*-tests (Tukey HSD corrected).

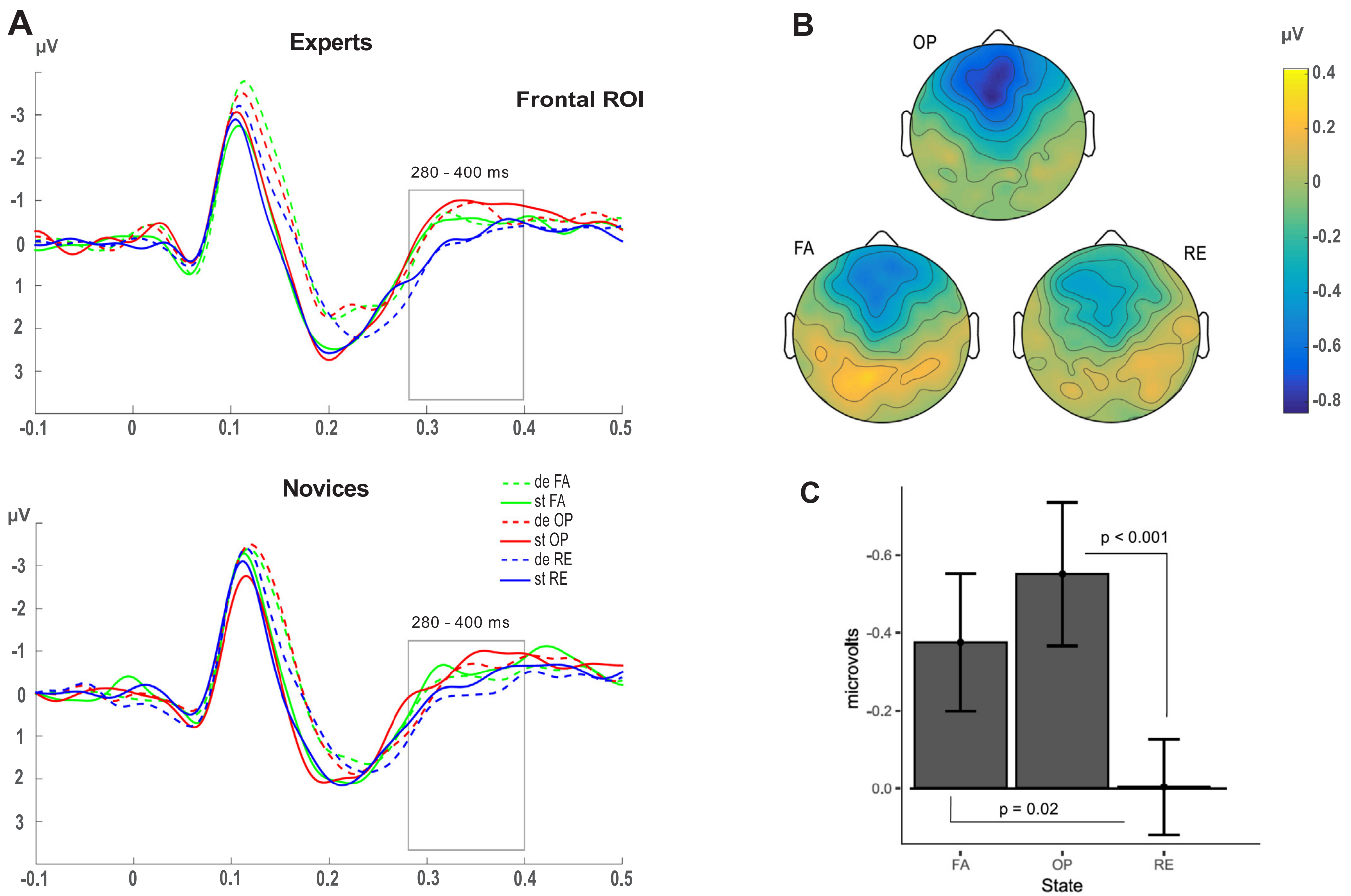

Fig. 2. Open Presence meditation modulates late auditory evoked-potential (Late Frontal Negativity, LFN) in expert and novice practitioners (A) Event-related responses to standard (solid lines) and deviant (dashed lines) tones at frontal ROI (see Fig. S1) during FA, OP and RE in experts (top) and novices (bottom). (B) Average voltage scalp maps, combining standard and deviants and the two groups, between 330 and 500 ms after stimulus onset. (C) Mean values of LFN from (B) at frontal ROI. Error bars represent the standard errors of the mean. P-values indicate significant differences between experimental conditions, as a result of paired *t*-tests (Tukey HSD corrected).

FA and RE (t-ratio (58) = − 0.2; p = 0.95) and an increase in OP, compared to FA, was observed only as statistical trend (t-ratio (58) = − 1.9; p = 0.12) (Fig. 1C). We also explored differences in MMN amplitude between groups for each state separately. We found a significantly higher MMN amplitude in experts, compared to novice practitioners in the FA condition (t-ratio (62.4) = − 2; p = 0.04). Contrary to our hypothesis, no group difference was found in OP (t-ratio (62.4) = − 0.5; p = 0.5). In line with our prediction that reading was a non-specific control state, there was no group difference RE conditions (t-ratio (62.4) = − 0.9; p = 0.35).

Additional statistical analysis, performed separately on standard and deviant stimuli, did not yield informative results regarding the specific contribution of each stimulus type to the observed differences in the MMN amplitude (see Supplementary material 2.3 for details).

We assessed differences in stimulus attendance and attentional monitoring, between states and groups, that could have contributed to the modulation of the auditory-evoked potential in the earlier latency (MMN), by looking at later latencies of the evoked response (see Methods section).

Fig. 2B shows topographies at the scalp level for the mean values of the Late Frontal Negativity (LFN), combining responses to both standard and deviant stimuli, in the selected time window (280–400 ms) for experts and novices and for each experimental condition. The ANOVA performed at the frontal ROI (Fig. S1) yielded a significant effect of STATE (χ^2 (2) = 16.7; p < 0.001; Fig. 2A). We further investigated differences between each state (Fig. 2C). A significant increase in the amplitude of the LFN was found in OP and FA compared to RE (t-ratio (58) = − 3.9; p < 0.001 and t-ratio (58) = − 2.711; p = 0.02 respectively), while no difference was found between FA and OP (t-ratio (58) = − 1.7; p = 0,18).

To determine whether the interplay between attentional monitoring and perceptual habits formation would represent a more sensitive marker to differentiate the two practices in expert meditation practitioners, we included data from the MMN and the LFN in an integrated model. We performed an exploratory analysis on the interaction between MMN and LFN in expert and novice practitioners and between experimental conditions (Fig. 3). A statistically significant interaction between STATE, COMPONENT and GROUP resulted from the repeated-measures ANOVA (F (2, 58) = 3.42; p = 0.03). Given this interaction, we investigated the two groups separately. A marginally significant interaction between STATE and COMPONENT was present in experts (F (2, 30) = 3.07; p = 0.06), while a main effect of STATE was present in the novice group (F (2, 28) = 5.28; p = 0.01). We further tested interactions between pairs of states and the two components in the expert group to investigate the sensitivity of this combined measure to differentiate each pair of states. An interaction between STATE and COMPONENT was present when comparing FA and OP (F (1, 15) = 5.6; p = 0.03), showing how the LFN amplitude increased during OP while the MMN amplitude increased during FA. An interaction between STATE and COMPONENT was also present when comparing OP and RE (F (1,15) = 3.8; p = 0.06), showing an increase in the LFN but not in the MMN amplitude during OP compared to RE. Finally, a main effect of STATE was present when focusing on FA and RE (F (1,15) = 11.08; p = 0.004) showing how the amplitude of both components increased

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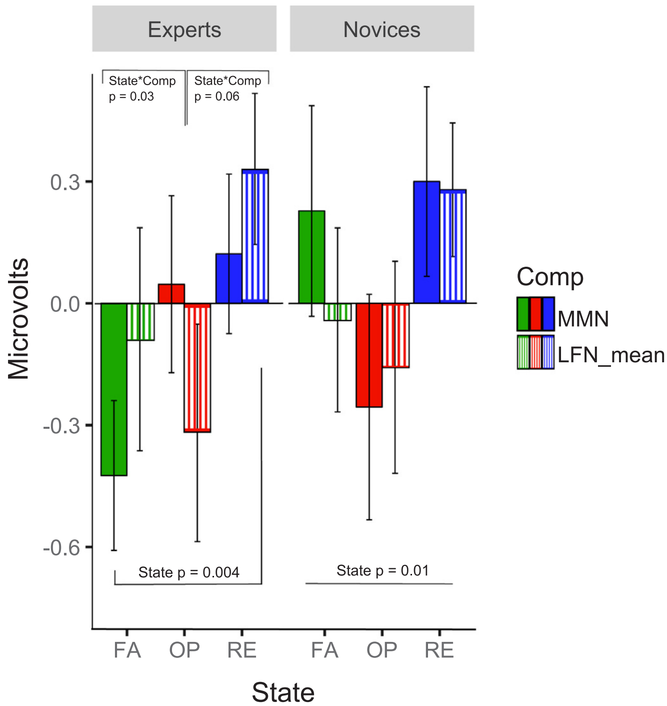

Fig. 3. Different interplay between LFN and MMN amplitudes between experimental conditions as a function of meditation expertise. Mean difference in microvolts, relative to the average across groups and conditions, of MMN (full colour) and LFN (lines pattern) in FA (green), OP (red) and RE (blue). P-values indicate significant main effects and interactions resulting from repeated-measures ANOVAs. A significant three-way interaction was found between states, components and groups (F (2, 58) = 3.42; p = 0.03). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

during FA compared to RE. Altogether this composite analysis revealed a double dissociation in experts between OP and FA and RE, respectively.

3.2. Spontaneous Alpha (8–12 Hz) and gamma (25–40 Hz) EEG oscillatory activity

Fig. 4A shows mean log-values of alpha and gamma power, in two different ROIs, for expert and novice practitioners; Fig. 4B shows the topographical distribution of these oscillatory activities. A statistically significant interaction between STATE, FREQUENCY, ROI and GROUP resulted from the main model tested (F (1.7, 49.9) = 3.87; p = 0.03; Huynh-Feldt corrected). Given the significant interaction, we investigated the two frequency bands and ROIs separately.

A significant effect of STATE on average alpha power was present in both the frontal and occipital ROIs (χ^2 (2) = 43.1; p < 0.001 and χ^2 (2) = 9.8; p = 0.007, respectively). This analysis showed how alpha power increases in both groups during meditation and how, between the two practices, OP meditation is characterized by the most powerful alpha oscillatory activity in the frontal ROI (OP vs RE: t-ratio (58) = 6.4, p < 0.001; FA vs OP: t-ratio (58) = − 2.4, p = 0.05; FA vs RE: t-ratio (58) = 4, p < 0.001). The main effect of state observed at the occipital ROI was mostly caused by the increased alpha power during OP compared to RE (OP vs RE: t-ratio (58) = 3.1, p = 0.008; FA vs RE: t-ratio (58) = 1.6, p = 0.24; FA vs OP: t-ratio (58) = − 1.4, p = 0.31).

As for the differences in gamma power, we found a significant STATE by GROUP interaction at the frontal ROI (χ^2 (2) = 7.87; p = 0.02), showing how gamma oscillatory power increased during OP, compared to RE, in experts only (t-ratio (58) = 3; p = 0.008) while no difference was found between FA and RE, and OP and FA (t-ratio (58) = 1.5; p = 0.27 and t-ratio (58) = − 1.5; p = 0.28, respectively). No difference between states was found in the novices. Between-group *t*-tests highlighted a significant increase in gamma oscillatory power in experts, compared to novices, during OP and FA (t-ratio (42.8) = 3.3; p = 0.002 and t-ratio (42.8) = 2.1; p = 0.03, respectively), but not RE (t-ratio (42.8) = 1.2; p = 0.23). At the occipital ROI, a significant main effect of state was present (χ^2 (2) = 45,3; p < 0001), showing how gamma power increased during RE compared to OP and FA (t-ratio (58) = − 6.4; p < 0.001 and t-ratio (58) = − 4.8; p < 0.001, respectively). We did not find a relationship between spontaneous gamma activity and hours of meditation practice in expert practitioners. This hypothesis was tested at the frontal ROI used in the present study, as

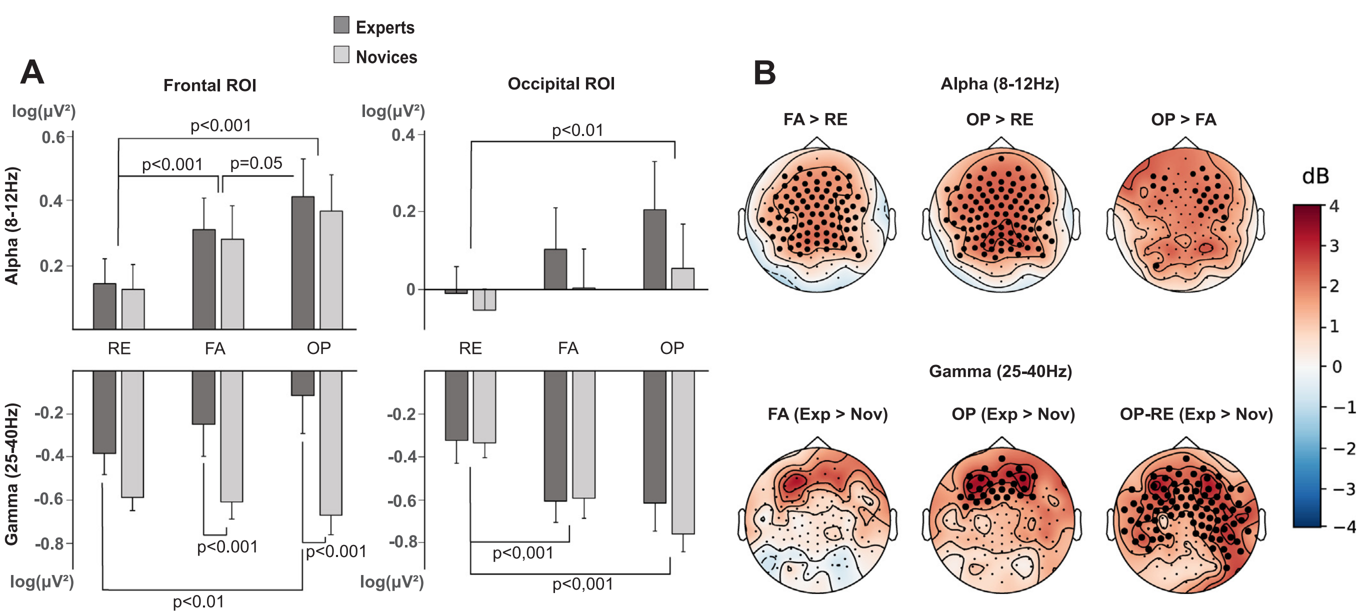

Fig. 4. Meditation states differently modulate spontaneous oscillatory activity between expert and novice meditators. (A) Mean log-transformed values of spectral power in alpha (8–12 Hz) and gamma (25–40 Hz) frequency bands at the frontal ROI and occipital ROI for experts and novice practitioners. Error bars represent standard errors of the mean. P-values indicate significant differences between groups and between experimental conditions within groups, as a result of paired *t*-tests (Tukey HSD corrected). *(B)* Corresponding whole-scalp topographies for a few selected contrasts. Large dots indicate electrodes for which the contrast is statistically significant (p < 0.01, corrected for multiple comparisons: see Section 2).

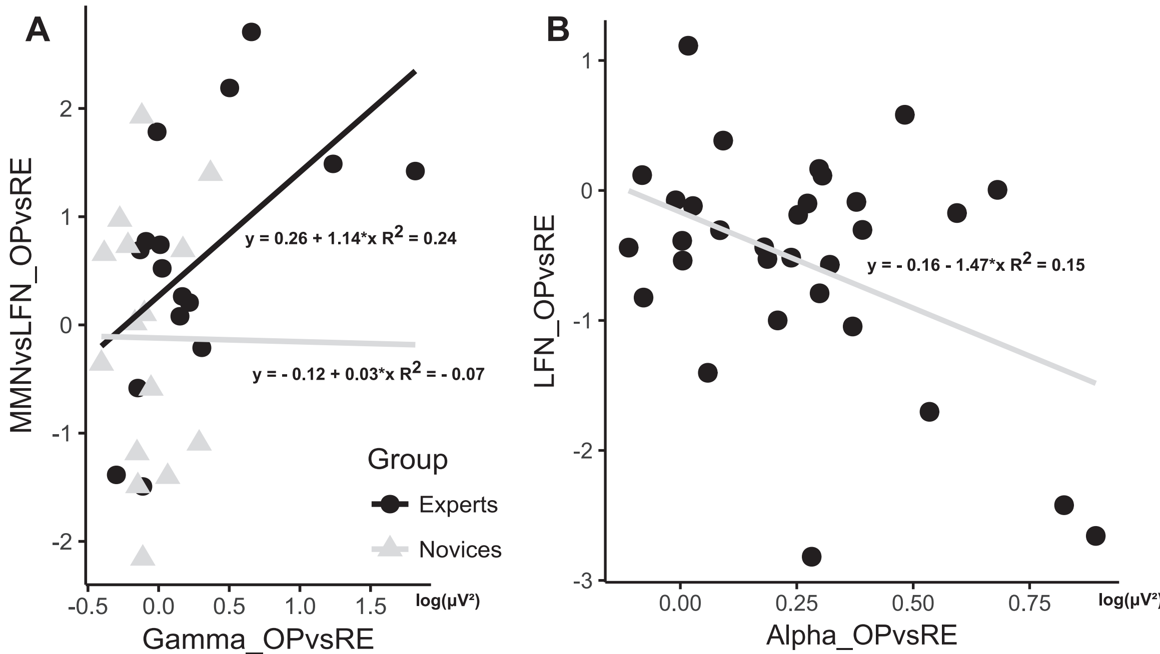

Fig. 5. Spontaneous oscillatory activity in the gamma and alpha range correlates with changes in the auditory evoked potential between OP and RE conditions. (A) Scatter plot for single-subject mean values of difference in gamma (25–40 Hz) power between OP and RE (x-axis) and difference between MMN and LFN between OP and RE (y-axis) for novice (grey) and expert (black) practitioners. Regression lines and relative equations, as well as R-squared values, show the direction of the correlation for each group. (B) Scatter plot for differences in alpha (8–12 Hz) power between OP and RE (x-axis) and difference in LFN amplitude between OP and RE (y-axis) across both groups. Regression line and relative equation, as well as R-squared value, show the direction of the correlation across subjects.

well as at the ROI used in a previous study, when a relationship was found (Lutz et al., 2004).

3.3. Correlation between spontaneous oscillatory activity and auditory evoked responses

Following the results obtained after the analysis of ERP components and oscillatory power, we aimed to further characterize the relation between state measures and brain responses to auditory stimuli (Fig. 5). Firstly, we explored the relationship between the difference between MMN and LFN amplitude and the frontal gamma activity, as both measures exhibited a group by state interaction, particularly between OP and RE, as both states differed for experts only on these two measures. We found a significant correlation between these two measures in experts, but not novices ($\rho_{X,Y} = 0.54$; $p = 0.03$ and $\rho_{X,Y} = -0.006$; $p = 0.98$ respectively) and this correlation was marginally different between the two groups (z-score = 1.5; $p = 0.06$ following (Cohen et al., 2014)). Secondly, the common profile of the state effect found in both LFN amplitude and frontal alpha activity suggested a possible relationship between them, particularly in the contrast between OP and RE (see Figs. 4 and 2). We found a negative correlation between the increase in alpha power and the increase in LFN amplitude during OP, compared to RE condition; this effect was present across both groups ($\rho_{X,Y} = -0.42$; $p = 0.01$).

4. Discussion

In the present study, we showed how an Open Presence style of nondual meditation can be differentiated from a style of concentrative meditation, named Focused Attention, in terms of the interplay between saliency and monitoring of the sensory environment and perceptual learning processes as measured by a composite measure of EEG ERPs. The observed patterns are in line with the specific phenomenology of the two different states. Moreover, both meditation states are characterized by increased power of brain rhythms in the gamma frequency range in experts compared to novices, and by increased power in alpha frequency range for both groups. We also found some relationship between meditation-induced changes in ERPs and meditation-induced changes in brain oscillatory rhythms in both gamma and alpha frequency bands.

Theoretical accounts of the MMN suggest that it is a neural correlate of prediction error signals (Garrido et al., 2009; Lecaignard et al., 2015). Elaborating on this notion, recent studies have highlighted the role of attention in increasing the precision of such prediction errors, resulting in an increase of the MMN amplitude (e.g. (Chennu et al., 2013; Auksztulewicz and Friston 2015)). These studies are in line with theoretical and experimental work on the role of attention in modulating prediction error signals in different sensory domains (e.g. (Feldman and Friston, 2010; Kok et al., 2012)). In the present study, we found that two meditation practices and a control state differently modulate the MMN amplitude in groups of expert and novice practitioners. During the state of Focused Attention, the MMN amplitude increases in experts compared to a control, Reading condition and compared to novices. Contrary to our hypothesis, the MMN in OP was not statistically different from FA, even if there was a trend toward this effect. The increase in FA compared to RE could be related to the specific task-set of focusing on and selecting a perceptual object, which increases the saliency of task-unrelated stimuli and entails higher meta-awareness of the sensory environment (Lutz et al., 2015). Previous studies have reported an increase of the MMN during concentrative meditation (Srinivasan and Baijal, 2007) and in expert practitioners (Biedermann et al., 2016). Nonetheless, these studies presented several limitations such as the lack of a control condition and the assessment of the MMN amplitude at unconventional scalp areas. In line with our findings, a previous study showed how the MMN increased during a concentrative state (breath-counting task), compared to mind-wandering (Braboszcz and Delorme, 2011). In the novice group, the MMN amplitude increases during the practice of OP compared to RE, while a difference between OP and FA was observed only as a statistical trend. Higher MMN during OP meditation in novices could also reflect higher attentional resources being allocated to the auditory stream of the oddball paradigm, compared to Reading, in line with the recent literature on attention modulation of prediction error signals. This view is corroborated by the effect of meditation states on the late negative component of the auditory evoked response, here referred to as Late Frontal Negativity, which is highly similar, in terms of location and latency, to previously observed components that have been linked to stimulus attendance and attention orienting (e.g.(Karayanidis and Michie, 1996; Bendixen et al., 2007)). The fact that there was no increase in MMN in FA versus RE in novices could reflect a less stable capacity to maintain attentional focus compared to experts.

Based on the results obtained from separate tests performed on the two components of the auditory evoked potential, we sought to characterise the interplay between attentional monitoring of the sensory environment (indexed by the LFN amplitude) and the modulation of predictive processes (reflected in the MMN amplitude). This exploratory analysis was driven by the interest in highlighting specific profiles of perceptual information processing in line with our operational hypotheses regarding the two different meditation states in expert practitioners. In this group, indeed, the practices of OP and FA have a different impact on the two ERP components, when compared between them and to the RE condition. More specifically, the state of OP increases the LFN amplitude, compared to RE, but not the MMN, whereas during FA both components show a higher amplitude compared to RE. Finally, compared to FA, the state of OP shows higher LFN amplitude but lower MMN. As stated earlier, we hypothesized that the distinct phenomenology of OP in expert practitioners would correlate with a reduction of the interpretation of sensory information across time by perceptual habits. The modulation of the strength of prior predictions on the auditory environment could be, in this case, a suitable mechanism underlying this hypothesized process. This modulation would be orthogonal to the increased saliency of perceptual stimuli. By contrast in novices, the dissociation between these two processes was not found, as reflected by a state effect but not by a state by component interaction: increasing perceptual saliency during OP condition (i.e. high LFN) was associated to increase in MMN, whereas decreasing perceptual saliency during RE condition (i.e. lower LFN), was associated to decrease in MMN (Fig. 3). In line with the phenomenological description, the specific pattern of auditory response in MMN combined with LFN observed in expert practitioners represents a key finding of the present study. Such modulation of predictive processes could also explain results from a previous studies that found a reduction of the auditory startle response in one expert meditator during OP (Levenson et al., 2012) and a reduction of habituation to startle stimuli in expert practitioners (Antonova et al., 2015).

Expert meditators also show increased gamma oscillatory power over the frontal scalp region during both meditative states compared to the control condition and to novices. These results are in line with a previous study characterizing an increase in gamma power in experts during a non-dual form of compassion meditation (Lutz et al., 2004) and in contrast with a recent study that did not find an interaction between states and group, but rather a trait effect in gamma power (Braboszcz et al., 2017). Yet, in this last study, novice practitioners did not engage in the same practice as the experts, and the inclusion criteria for experts, as well as the type of practices, were different from the present study.

Fast frequency oscillatory activity (> 25 Hz) is considered to play a prominent role in a variety of mental processes, such as attention, feature integration and conscious perception (e.g. Lachaux et al., 2012; Fries, 2015). It has been previously hypothesized that, in the context of nondual meditation states, modulation of endogenous gamma activity could reflect changes in the quality of awareness, especially regarding the chronometry of stimulus processing (Lutz et al., 2004). We explored a possible relation between the difference in gamma power between OP and RE in experts and the difference between the same states in modulating the interplay between MMN and LFN amplitude (Fig. 5). The relationship we observed in expert practitioners between these two measures points towards a putative link between spontaneous profiles of oscillatory brain activity during meditation and the modulation of information processing. Nonetheless, as no difference was found between OP and FA in the power of frontal gamma, this analysis remains exploratory. Further studies should clarify whether a direct relationship exists between spontaneous gamma and auditory predictive processes in meditation.

Finally, an increase in alpha oscillatory power was found across both groups during meditation, compared to the RE condition, and especially during OP. Since early studies, increased alpha power during meditation has been consistently reported (see (Cahn and Polich, 2006) for a recent review) and linked to a general increase in relaxation as a state effect of numerous practices. Nonetheless, more recent theories describe the prominent role of alpha oscillatory activity in inhibiting task-unrelated stimuli when attention is sustained (Clayton et al., 2015; Fries, 2015), as well as when it is redirected to a specific task-set (Jensen et al., 2002), hence its involvement in working memory. In a recent study, alpha power increased during the transition from mind-wandering to breath-focus (Braboszcz and Delorme, 2011). Here we found a correlation between the increase in alpha power and the increase in LFN amplitude during OP compared to RE, across both groups. This finding highlights a putative link between alpha oscillatory activity in meditation and attentional processes (e.g. reorienting attention from auditory stimuli to the main task-set of the practice).

This study presents some limitations: first of all, while a complete cessation of the MMN response would not be plausible (MMN has been consistently observed during sleep and even in minimally-conscious patients (Atienza and Cantero, 2001; Boly et al., 2011)), one might expect OP meditation in experts to have a deeper impact on predictive processes and to actually reduce the MMN amplitude, compared to a control condition. The reason why we did not observe such modulation could be due to the relatively small sample size and, most importantly, to the various degrees at which the state of OP could be achieved and maintained between experts and, within the same session, by the same subject. This heterogeneity is also a possible reason why we did not find a significative difference between FA and OP in MMN and frontal gamma power in expert practitioners. When the state of OP is not fully realised, some degree of concentration might be required, hence sharing brain processes with the state of FA. On the other hand, once the “nature of the mind” is realised, it will be always present to some extent, therefor reducing the gap between OP and FA in terms of spontaneous brain activity. Future studies should address differences in the subjective experience of expert practitioners during advanced nondual states, relating quantitative data to online self-reports and qualitative accounts of single-subject profiles. Finally, future research should explore the mechanisms underlying the modulation of the MMN by OP meditation implementing trial-by-trial analysis of the auditory responses, based on strong computational hypotheses and modelling (e.g. (Lieder et al., 2013)).

Overall, the present study provides evidence of the brain processes underlying a non-dual meditation practice and describes the impact of meditation on predictive processes. This will foster the understanding of the brain mechanisms involved in the formation of perceptual habits and shed light on the mechanisms of meditation practices in clinical settings.

Acknowledgments

This work was supported by grants from the National Center for Complementary and Integrative Health (NCCIH) to Richard J. Davidson (P01AT004952); a core grant to the Waisman Center from the National Institute of Child Health and Human Development (NICHD) (HD003352); by the LABEX CORTEX of Université de Lyon (ANR-11-LABX-0042), within the program “Investissements d’Avenir” (ANR-11-IDEX-0007), by an European Research Council grant ERC- Consolidator 617739-BRAINandMINDFULNESS to Antoine Lutz and by a gift from the Adam J. Weissman Foundation.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neuropsychologia.2018.07.025.

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