

RESEARCH ARTICLE

Mindfulness meditators show altered distributions of early and late neural activity markers of attention in a response inhibition task

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Abstract

Attention is vital for optimal behavioural performance in every-day life. Mindfulness meditation has been shown to enhance attention. However, the components of attention altered by meditation and the related neural activities are underexplored. In particular, the contributions of inhibitory processes and sustained attention are not well understood. To address these points, 34 meditators were compared to 28 age and gender matched controls during electroencephalography (EEG) recordings of neural activity during a Go/Nogo response inhibition task. This task generates a P3 event related potential, which is related to response inhibition processes in Nogo trials, and attention processes across both trial types. Compared with controls, meditators were more accurate at responding to Go and Nogo trials. Meditators showed a more frontally distributed P3 to both Go and Nogo trials, suggesting more frontal involvement in sustained attention rather than activity specific to response inhibition. Unexpectedly, meditators also showed increased positivity over the right parietal cortex prior to visual information reaching the occipital cortex (during the pre-C1 window). Both results were positively related to increased accuracy across both groups. The results suggest that meditators show altered engagement of neural regions related to attention, including both higher order processes generated by frontal regions, and sensory anticipation processes generated by poster regions. This activity may reflect an increased capacity to modulate a range of neural processes in order to meet task requirements. This increased capacity may underlie the improved attentional function observed in mindfulness meditators.

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Introduction

Attention is vital in selecting and maintaining processes most relevant for optimal behaviour [1]. Attentional mechanisms have limited capacity and thus are most effective when allocated to processes that ensure behaviour consistent with the goals of the organism. In particular, attentional resources are most likely to enable optimal goal-oriented responses when the neural processes most at risk of failure are enhanced. In other words, attention improves goal-oriented behaviour by strengthening the weak links in the chain of neural processing that goes from stimulus detection to behavioural response [2, 3].

One method that enhances attention—mindfulness meditation—is conceptualised as a practice of training attention (or awareness) with an attitude of openness and non-judgement towards experiences [4, 5]. Enhanced attention is a key mechanism of action in the improvements associated with mindfulness meditation [1, 5–9]. Notably, meditators demonstrate improvements in sustained attention after both intensive retreats and after attending regular classes [10–12], distribution of scarce attentional resources in time after intensive retreats [13, 14] and distribution of scarce attentional resources in space in highly experienced meditators [15], and attentional control including inhibition of prepotent behaviour after 16 weeks of ten minutes per day of practice and after regular classes [11, 16]. However, although eight-week standardized mindfulness programs improve aspects of cognition such as working memory and cognitive flexibility, they may not improve neuropsychological measures of attention [17]. As such, individual components of attentional processes need further examination to determine the exact parameters of attentional function improvements that result from mindfulness meditation.

Reviews suggest that mindfulness meditation most likely has its impact on attentional functions via changes to the structure and function of numerous regions in the prefrontal cortex, the anterior cingulate cortex, the insular cortex, and the hippocampus and amygdala [18, 19]. As suggested above, sustained attention and inhibition are among the key mechanistic features from both an empirical and theoretical perspective [19]. One task designed to test both inhibition and sustained attention is the Go/Nogo task. The Go/Nogo task presents stimuli to which participants are instructed to respond (Go trials), setting up a prepotent response tendency, and stimuli to which participants are instructed to withhold their response (Nogo trials). This task engages conflict monitoring to allocate neural resources between the two competing processes (response and non-response), keeping track of the alignment between behaviour (or potential behaviour) and the goals held by participants [20]. Nogo trials also engage response inhibition to actively prevent a habitual or prepotent response [21]. The Go/Nogo task also requires successful sustained attention, in order to keep track of stimuli, potential conflicts, and engage response inhibition processes [22]. Improved behavioural performance on the Go/Nogo task has been shown after a three month mindfulness meditation retreat, which was sustained for up to five months, reliably predicting improved socioemotional function [23].

At a neural level, sustained attention and inhibition are reflected by variations in the amplitude and synchronisation of neural oscillations, the average effect of which can be measured using event related potentials (ERPs) [24]. Two ERPs are elicited by the Go/Nogo task: the N2, which is related to conflict monitoring and response inhibition, and significantly larger during Nogo trials [25–28] and the P3, which is generally larger in Nogo trials and associated with the evaluation of response inhibition behaviour in those trials [29]. The P3 is also present in Go trials, and as such is also thought to reflect attentional resource allocation, including inhibition of potentially interfering neural activity that is unrelated to task demands, and as such is related to sustained attention [30, 31]. The N2 is thought to be underpinned by theta activity modulations and generated by anterior midcingulate and left inferior frontal brain regions,

while the P3 is related to delta activity, and generated by precentral, middle frontal, midcingulate, insula and right temporo-parietal regions [29]. Six studies have used the Go/Nogo task to examine the effect of trait mindfulness or mindfulness meditation on ERPs related to conflict monitoring, response inhibition, and sustained attention (see Table A in [S1 File](#) for a summary). Each has studied a different population or intervention, and results between studies are inconsistent [32–37].

The inconsistencies make it difficult to draw meaningful conclusions about the effect of mindfulness meditation on attention. As the potential of meditation to alter neural activity is likely to be most noticeable in those individuals who have engaged in extensive practice, work with this population is crucial to identifying likely benefits of mindfulness meditation. No such research to-date has examined neural response to the Go/Nogo task in long term meditators. Prior studies of neural activity related to mindfulness in the Go/Nogo task all used single electrode measures, further limiting potential conclusions. If meditation alters the P3 distribution, increasing prefrontal engagement (related to attention enhancements), single electrode analyses cannot differentiate these distribution differences from amplitude differences. The inconsistencies in prior studies may also be related to differences in windows and electrodes selected for analysis, and may have missed early processing changes that have been found in meditators in other tasks [15]. An analysis technique encompassing all time windows and electrodes without a priori assumptions may be beneficial, in order to obtain a better understanding of the effect of meditation on neural activity. In particular, previous research has indicated that both voluntary and involuntary attention affects “evoked” sensory processing ERPs such as the C1, P1, N1, and P2 [38–41]. Differences between meditators and controls in these windows are not detectable with research that focuses on typical Go/Nogo a priori windows of interest.

Recently developed EEG analytic techniques [42] enable comparison of neural activity across entire EEG epochs while simultaneously controlling family-wise error. Additionally, this analysis technique enables discrimination of differences reflecting altered overall neural response strength from differences in the distribution of neural activity across regions. As such, this analysis technique could elucidate whether meditation enhances the amplitude of typical neural responses related to sustained attention or inhibitory processes, or trains a completely different pattern of brain region engagement, a question that has not been examined before in studies of meditation.

Aims and hypotheses

The aim of the current study was to assess whether individuals with extensive experience in mindfulness meditation showed differences in neural activity related to inhibition and sustained attention compared to demographically-matched individuals without meditation experience. To achieve this aim, we had participants complete a Go/Nogo task. In order to ensure any potential differences between groups were not due to an interaction between group and the effect of different frequencies of stimulus presentation (rather than attention or response inhibition processes) [43], we used a Go/Nogo task with an equal probability of Go and Nogo trials (which may have reduced response inhibition demands—see the [discussion](#) for further details). We had hypotheses regarding both the amplitude and distribution of neural activity. Regarding amplitude, we hypothesized that: 1) neural activity related to conflict monitoring and response inhibition (the Nogo N2 and Nogo P3) would show larger amplitudes in meditators, reflecting increased engagement of these neural processes as a result of the attention enhancing effect of meditation practice, and 2) neural activity related to attention would show larger amplitudes in meditators (both Go and Nogo P3) reflecting increased engagement of

these neural processes. Previous EEG research has not examined the distribution of neural activity independently of the amplitude of neural activity in meditators. However, research has suggested better attention and inhibition function are related to frontal activity [44, 45]. As such, we hypothesised that the meditators would show more frontal activity in these ERPs, reflecting increased ability to engage the prefrontal cortex to maintain attention and inhibition processes. We also planned: 1) exploratory analysis of accuracy and reaction time data to determine whether any differences in neural activity were concurrent with enhanced behavioural performance (without any specific hypotheses), and covariate analyses of the relationship between any behavioural differences and neural differences to determine whether differences in neural activity in the meditation group were related to improved behavioural performance, 2) exploratory source analyses to assess which brain areas were activated during any topographical differences between groups and 3) microstate analysis to further characterise topographical differences between groups. Previous research in our lab used simplified emotional faces as stimuli for the Go/Nogo task, and found the task design differentiated depressed individuals from healthy controls, but no interaction with emotion [46]. We chose to use exactly the same task in the current study (since it had previously demonstrated ability to differentiate groups). However no interaction between group and emotion was expected, as our previous research suggested the simplified faces were not sufficiently emotionally evocative to generate between group differences [46].

Methods

Participants and self-report data

Thirty-six controls and 34 meditators were recruited through community advertising. Inclusion criteria for meditators involved a current meditation practice, with at least six months of meditation for at least two hours per week. All meditators except three had more than two years of meditation experience. Phone screening and in-person interviews were administered by experienced mindfulness researchers (GF, KR, NWB) to ensure meditation practices were mindfulness-based, using Kabat-Zinn's definition—"paying attention in a particular way: on purpose, in the present moment, and nonjudgmentally" [47]. Further screening ensured meditation practices were consistent with either focused attention on the breath or body-scan. Any screening uncertainties were resolved by between two researchers including the principal researcher (NWB). Control group participants did not have experience with meditation of any kind.

Exclusion criteria involved self-report of current or historical mental or neurological illness, or current psychoactive medication or recreational drug use. Participants were additionally interviewed with the MINI International Neuropsychiatric Interview for DSM-IV [48] and excluded if they met criteria for any DSM-IV psychiatric illness. Participants who scored in the mild above range or above in the Beck Anxiety Inventory (BAI) [49] or Beck Depression Inventory II (BDI-II) [50] were also excluded. All participants had normal or corrected to normal vision and were between 19 and 62 years of age.

Prior to completing the EEG task, participants reported their age, gender, years of education, handedness, and an estimate of the number of years spent meditating and the number of minutes per week spent meditating. Participants also completed the Freiburg Mindfulness Inventory (FMI) [51], Five Facet Mindfulness Questionnaire (FFMQ) [52], BAI, and BDI-II (see Table 1). All participants provided written informed consent prior to participation. The study was approved by the Ethics Committee of the Alfred Hospital and Monash University (approval number 194/14).

Table 1. Demographic and self-report data.

	Meditators <i>M (SD)</i>	Controls <i>M (SD)</i>	Statistics
Age	36.56 (10.88)	35.68 (14.69)	$t(60) = 0.271, p = 0.794$
Gender (F/M)	21/13	17/11	n.s.
Years of Education	16.97 (2.55)	15.87 (2.82)	$t(60) = 1.598, p = 0.115$
Meditation Experience (years)	8.30 (10.28)	0	
Current Time Meditating Per Week (hours)	5.50 (4.15)	0	
BAI score	4.24 (4.68)	4.50 (5.62)	$t(60) = 0.202, p = 0.840$
BDI score	1.06 (1.87)	1.61 (2.69)	$t(60) = 0.944, p = 0.349$
FMI score	45.62 (7.02)	41.12 (7.75)	$t(60) = 2.401, p = 0.019^*$
FFMQ score	152.97 (17.13)	138.39 (12.63)	$t(60) = 3.741, p < 0.001^{**}$

* $p < 0.05$

** $p < 0.001$.

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Select data was excluded from analysis—four controls were excluded due to scoring in the mild depression range on the BDI, two due to misunderstanding task instructions, and one due to non-task completion. One additional control was excluded from neural analysis due to equipment fault. Two additional controls and three meditators were excluded from the behavioural analysis, due to an intermittent button fault during those sessions (enough correct response epochs were left for neural analysis, but accuracy calculations were insufficiently reliable). This left 28 controls for neural analysis (17 female, all right handed) and 27 controls for behavioural analysis. No exclusions were made for the meditators’ neural data, leaving 34 meditators (21 female, 3 left handed), and 31 for behavioural analysis.

Task and stimuli

Participants performed a Go/Nogo task with simplified emotional faces as stimuli while 64-channel EEG was recorded (see Fig 1). Task details were the same as Bailey et al. [46], with two blocks (instead of the four in the original design). The two blocks each included 75 happy and 75 sad faces. The equal trial type frequency was selected to limit between group comparisons to processes related to response inhibition (rather than also including processes related to

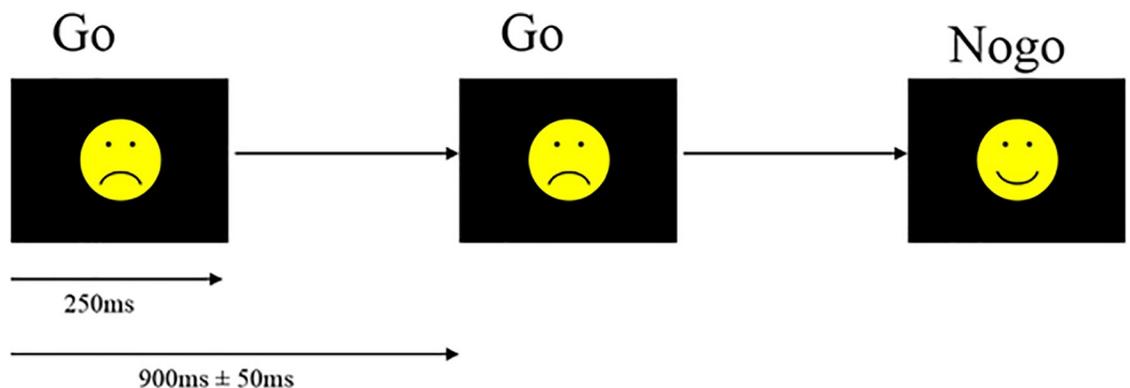


Fig 1. Go/Nogo task design. Go:Nogo ratio was 50:50, with stimulus response pairings switched in the second block so all participants responded to an equal number of happy and sad faces, and stimulus response pairings counter-balanced within each group.

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probability of trial type, as would be the case if Nogo trials were less frequent than Go trials, since factors such as novelty modulate the Nogo N2 amplitude [53]. Participants were instructed to respond by using both index fingers to press separate buttons simultaneously when they saw one emotion, and withhold responses to the other emotion. Stimulus-response pairings were reversed in the second block—participants who responded to happy faces in the first block responded to sad faces in the second block, and vice versa. Button press responses by the dominant hand were recorded. Stimulus-instruction pairing was counterbalanced across participants and groups. Stimuli were presented for 250 ms, with an inter-trial interval of 900 ms (with a random jitter of 50 ms to avoid entrainment of EEG activity). Stimuli presentation was pseudo-random so that no more than four of each trial type was presented consecutively. Prior to beginning the task and again before the second block, participants were presented with a short practice block. The second practice was included to prevent extra errors and switching effects on the N2 amplitude [53]. Percentage accuracy and reaction time (RT) for each trial type were extracted offline.

Electrophysiological recording and pre-processing

A Neuroscan 64-channel Ag/AgCl Quick-Cap was used to acquire EEG through NeuroScan Acquire software and a SynAmps 2 amplifier (Compumedics, Melbourne, Australia). Electrodes were referenced to an electrode between Cz and CPz. Eye movements were recorded with vertical and horizontal EOG electrodes. Electrode impedances were kept below 5k Ω . The EEG was recorded at 1000Hz, with an online bandpass filter of 0.05 to 200Hz.

Data were analysed offline in MATLAB (The Mathworks, Natick, MA, 2016a) using EEGLAB for pre-processing (scn.ucsd.edu/eeGLAB) [54]. Second order Butterworth filtering was applied to the data with a bandpass from 1–80 Hz and also a band stop filter between 47–53 Hz. Correct response trials were re-coded, and data were epoched from -500 to 1500 ms surrounding the onset of the stimulus presentation for each trial; only correct responses were analysed. Epochs were visually inspected by an experimenter experienced with EEG analysis and blinded to the group of each participant, and periods containing muscle artefact or excessive noise were excluded, as were channels showing poor signal. Thirty-five or more accepted epochs were obtained from each participant for each condition, and no significant differences were detected between groups in the number of accepted epochs ($p > 0.10$).

Data were combined with epoched data from another cognitive task (results of which will be presented in a separate publication) for Independent Component Analysis (ICA). AMICA [55] was used to manually select and remove eye movements and remaining muscle activity artefacts. Once artefactual ICA components were rejected, raw data were re-filtered from 0.1–80 Hz, all previous channel and epoch rejections were applied, and rejected ICA components were applied to this 0.1–80 Hz filtered data to avoid rejecting low frequency brain activity around 1 Hz (prior to ICA rejection, data below 1 Hz was filtered out as it adversely impacts the ICA process). Rejected electrodes were re-constructed using spherical interpolation [56]. Data were then visually inspected again by a separate researcher (who was also blind to the group of the data inspected at that time) to ensure the artefact rejection process was successful. Recordings were re-referenced offline to an averaged reference and baseline corrected to the -100 to -10 ms period, and epochs from each condition and participant were averaged for ERP analyses.

Source localisation pre-processing

Estimation of cortical sources during topographical between-group differences was performed using Brainstorm [57] (<http://neuroimage.usc.edu/brainstorm/>). EEG data were co-registered

with the template model (ICBM 152) because individual MRIs were not available. The forward model used the Symmetric Boundary Element Method implemented in OpenMEEG software [58]. The inverse model used the computation of minimum norm estimation, with sLORETA to normalise activity based on the depth of sources [59], with dipole orientations unconstrained to the cortex to minimize the impact of using the MRI template [60]. Differences in estimation were calculated using absolute subtraction. We source localised the well-known P100 occipital ERP (averaged across 50 to 150 ms) to the correct location to demonstrate our source analysis was reliable even in the absence of individual MRI templates (see Figure A in [S1 File](#)) [61]. Statistical comparisons of source localisations were not performed, as scalp comparisons already demonstrated significant differences, and without MRI co-registration source statistical comparisons can be unreliable [62].

Statistical comparisons

Self-report and behavioural comparisons were made using SPSS version 23. Independent samples t-tests were conducted to ensure groups were matched in age, years of education, BAI, and BDI, and to determine whether groups differed in FMI, FFMQ scores. Chi square tests were used for gender and handedness. Percentage correct was compared with a repeated measures ANOVA involving 2 group x 2 Go/Nogo conditions x 2 emotion conditions. RT was compared in Go trials only (as these were the only trials requiring responses) with a repeated measures ANOVA involving 2 group x 2 emotion conditions. Fewer than 2 outliers were Winsorised for each percent correct condition. No outliers were present for cumulative percentage correct, and data met assumptions of normality and equality of variances. The Benjamini and Hochberg false discovery rate (FDR) [63] was used to control for multiple comparisons across behavioural performance measures.

Primary comparisons. Primary statistical comparisons for EEG data were conducted using the Randomised Graphical User Interface (RAGU) to compare scalp field differences across all electrodes and time points with randomisation statistics without making any a priori assumptions about electrodes or windows for analysis [42]. This reference-free method takes advantage of the additive nature of scalp fields to allow comparisons of neural activity between groups and conditions without estimation of active sources by calculating a difference scalp field between groups or conditions. This difference scalp field shows the scalp field of brain sources that differed between the two groups/conditions, while brain sources that did not differ result in zero scalp field difference [42]. RAGU controls for multiple comparisons in both time and space using randomisation statistics (see [42]). To control for multiple comparisons in time (which are made at each time point in the epoch), global duration statistics calculate the duration of significant effects that are longer than 95% of the significant periods in the randomised data, ensuring significant durations in the real data last longer than the random comparison data at $p = 0.05$ [42]. Additionally, area under the curve statistics of significant time points across the entire epoch confirm sufficient control for multiple comparisons in the time dimension.

RAGU also allows for independent comparisons of overall neural response strength (with the global field power—GFP test) and distribution of neural activity (with the Topographic Analysis of Variance—TANOVA). Prior to the TANOVA, a Topographical Consistency Test (TCT) was conducted to ensure a consistent distribution of scalp activity within each group / condition. Lastly, Topographical Analysis of Covariance (TANCOVA) performs the same operations as TANOVA except it compares neural data to a linear predictor instead of between-group comparisons [42].

GFP and TANOVA tests were used to conduct 2 group x 2 Go/Nogo condition comparisons for averaged ERP data from -100 to 700 ms surrounding the onset of the stimulus. Five thousand randomisations were conducted with an alpha of $p = 0.05$. Post-hoc GFP and TANOVA tests to explore interactions were only conducted averaged across time periods of significant interaction after global duration controls.

In order to obtain effect sizes, GFP values were extracted from RAGU and submitted to parametric repeated measures ANOVA in SPSS. For the TANOVA, partial eta squared was computed in RAGU using the amount of variance explained in the difference scalp field by the experimental design.

The Benjamini and Hochberg false discovery rate (FDR) [63] was used to control for multiple comparisons for all comparisons testing primary hypotheses separately from comparisons involving behavioural data. FDR corrections were performed on the area under the curve p-values from each main effect or interaction. Area under the curve p-values were measured as the sum of all time points across the epoch in each comparison (across group main effects and group by Go/Nogo condition interaction). Controlling for multiple comparisons across both GFP and TANOVA tests, as well as across main effects and interactions avoided the hidden multiplicity in ANOVA designs [64]. Post-hoc t-test designs were similarly controlled for using the FDR method. To enable comparison with other research, both corrected and uncorrected p-values are reported for significant comparisons (labelled 'FDR p' and 'p-uncorrected' respectively).

Exploratory analysis. Exploratory analyses were not corrected for multiple comparisons, so should be taken as preliminary findings. In order to assess relationships between behavioural results and neural activity, significant periods from group TANOVA comparisons were averaged and compared using TANOVA tests with linear predictor values from significant between-group differences at the behavioural level.

Microstates are temporarily stable topographies of neural activation lasting approximately 80–120 ms before very quickly (~5 ms) transitioning to another temporarily stable topography, reflecting difference source activations [65]. Identification of microstates, determination of the optimal number of microstates, and statistical analysis was conducted using RAGU [66]. Microstates were identified using atomize and agglomerate hierarchical clustering (AAHC) algorithm, which merges ERP topographies into clusters so that the average topography of the clusters explains maximal variance in the ERP [67]. The optimal number of microstates was computed using cross-validation with the mean ERP from a learning set containing varied numbers of microstate classes and associated timing, which are then applied to the test set comprised of the remaining data. The optimal number of microstates is the point where the mean variance explained in the test set reaches its maximum [66]. Randomisation statistics are then used to compare microstate properties during periods that were significant in the ERP TANOVA and GFP comparisons. Lastly, for comparison to previous literature, traditional single electrode analyses figures are included in the supplementary materials (Figure B in [S1 File](#)).

Results

Demographic and behavioural

The neural analysis was the main focus of the study, so we only examined demographic and self-report differences for the participants included in the neural analysis. Results are summarised in [Table 1](#). For participants included in the neural analysis, no significant differences were present between groups in age, years of education, BAI score, BDI score, gender or handedness (all $p > 0.3$). Meditators showed significantly higher FMI $t(60) = 2.401$, $p = 0.019$ and FFMQ scores $t(60) = 3.741$, $p < 0.001$.

Table 2. Behavioural and accepted epoch data.

	Meditators <i>M (SD)</i>	Controls <i>M (SD)</i>	Statistics
Total Percent Correct	97.13 (2.48)	95.32 (2.99)	$t(56) = 2.511, p = 0.015^*$
Happy Go %	98.19 (3.90)	96.69 (3.52)	
Sad Go %	98.62 (2.11)	96.45 (4.26)	
Happy Nogo %	96.08 (3.44)	94.57 (5.25)	
Sad Nogo %	95.62 (4.16)	93.59 (5.14)	
Total Go RT	389.92 (46.58)	388.47 (55.09)	$F(1,56) = 0.012, p = 0.914$
Happy Go RT	388.31 (47.92)	384.19 (55.77)	
Sad Go RT	391.53 (48.88)	392.75 (57.67)	
Accepted Happy Go Epochs	71.12 (7.37)	68.18 (9.90)	$t(60) = 1.339, p = 0.186$
Accepted Sad Go Epochs	70.41 (8.05)	68.89 (7.52)	$t(60) = 0.762, p = 0.449$
Accepted Happy Nogo Epochs	70.21 (3.52)	68.79 (5.85)	$t(60) = 1.181, p = 0.242$
Accepted Sad Nogo Epochs	69.79 (4.13)	68.21 (5.00)	$t(60) = 1.364, p = 0.178$

* $p < 0.05$ <https://doi.org/10.1371/journal.pone.0203096.t002>

To examine behavioural performance, we compared percentage correct and reaction times. Normality, Box's test, and Levene's test were violated for percentage correct for Go and Nogo trials independently, however no significant interaction involving group was present with repeated measures ANOVA (Go/Nogo \times group $F(1,56) = 0.004, p = 0.952$). Log₁₀, natural log, and z-score transforms were attempted, but data remained non-normal. As such, corrections to normalise data were not performed. Cumulative percent correct across all conditions was calculated and found to be normally distributed. Meditators showed higher cumulative percentage correct with independent samples t-test $t(56) = 2.511, p\text{-uncorrected} = 0.015$ partial eta squared = 0.101, FDR $p = 0.045$.

No significant difference was found for any condition, group or interaction in the number of accepted epochs (all $p > 0.10$). No significant differences were found in reaction time for group comparisons or interactions involving group (all $p > 0.10$, see Table 2).

Within the meditation group, no correlations were significant between cumulative percentage correct and meditation experience (years), minutes per week, or FFMQ scores (all $p > 0.10$).

Neural data

Global field potential test. To assess the strength of neural response to Go/Nogo trials, we analysed the data using the GFP test. A significant group by Go/Nogo trial interaction was present between 336 ms to 449 ms (area under the curve statistic $p\text{-uncorrected} = 0.0198$, FDR $p = 0.0396$), global duration statistic = 33 ms. When activity was averaged across the significant window (336 to 449 ms) to obtain a single value for analysis, the effect was still significant ($p = 0.001$). Post-hoc comparisons within trial type in RAGU indicated that controls and meditators did not differ in Go trial comparisons ($p = 0.298$) nor Nogo trial comparisons ($p = 0.184$). Controls showed a significant difference between Go and Nogo trials—Go trials showed larger amplitude than Nogo trials ($p\text{-uncorrected} < 0.001$, FDR $p = 0.004$). Meditators did not show a difference between Go and Nogo trial amplitudes ($p = 0.743$). See Fig 2 for details. These results suggest that controls generate larger P3 amplitudes during Go trials, and smaller P3 amplitudes during Nogo trials, while meditators showed no differences. No differences were present in the N2 window (thought to reflect inhibition and conflict monitoring).

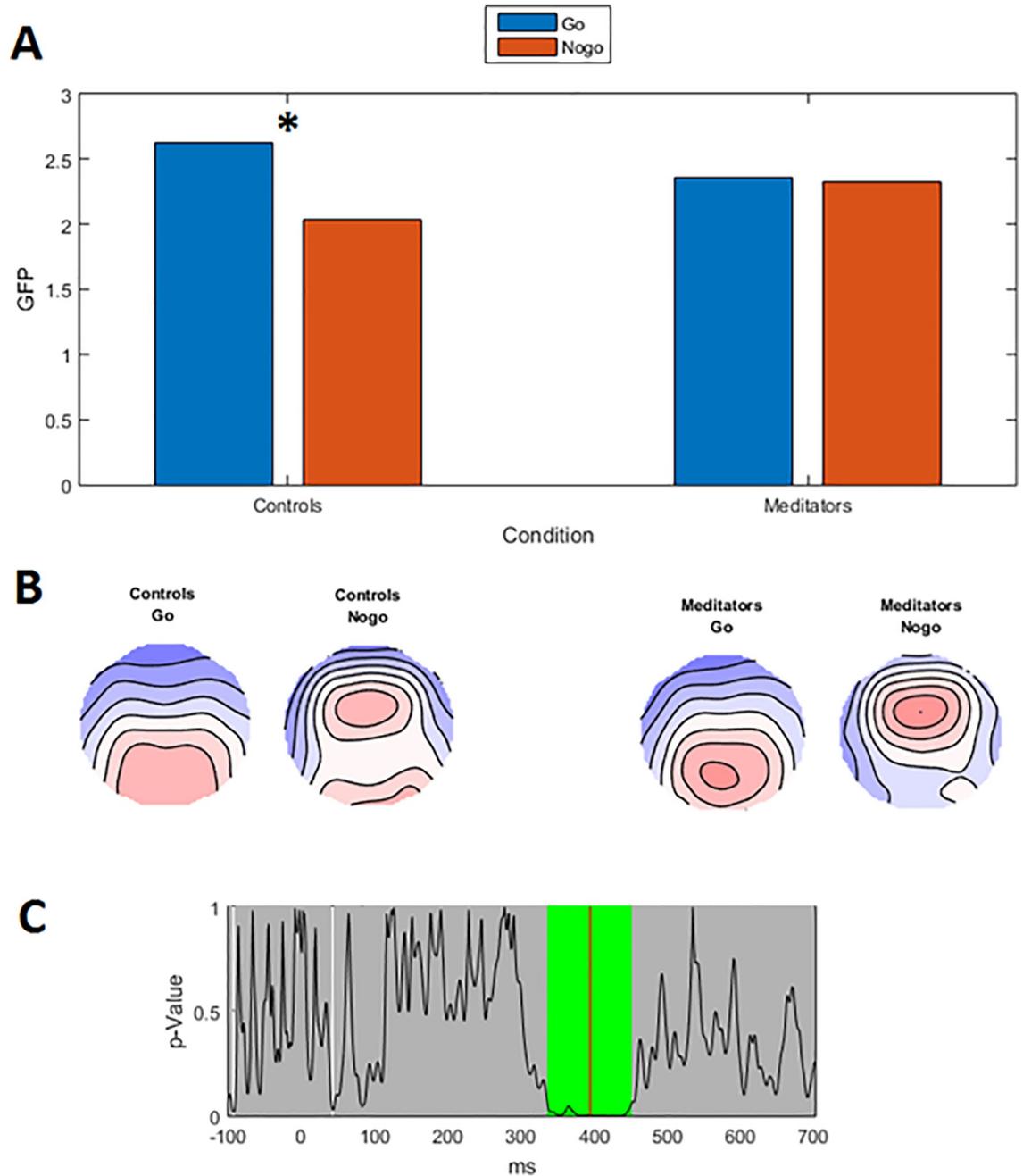


Fig 2. Significant group by Go/Nogo GFP interaction during the P3 window. A—Averaged GFP within the significant 336 ms to 449 ms window (green periods = 46 ms reflect periods that exceeded the duration control for multiple comparisons across time = 33 ms). * p-uncorrected < 0.001 (FDR p < 0.004). B—Averaged topography during the significant window for each group. C—p-values of the group by Go/Nogo trial comparison for the real data against 5000 randomly shuffled permutations across the entire epoch.

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In order to obtain effect sizes, GFP values were extracted from RAGU and submitted to a parametric repeated measures ANOVA in SPSS. Partial eta squared from Group x Go/Nogo interaction in parametric repeated measures ANOVA = 0.098. 95% Confidence intervals for controls Go = 2.253 to 2.999, Nogo = 1.718 to 2.349, meditators Go = 2.022 to 2.699, Nogo = 2.037 to 2.610. There was no main effect of group ($p > 0.1$).

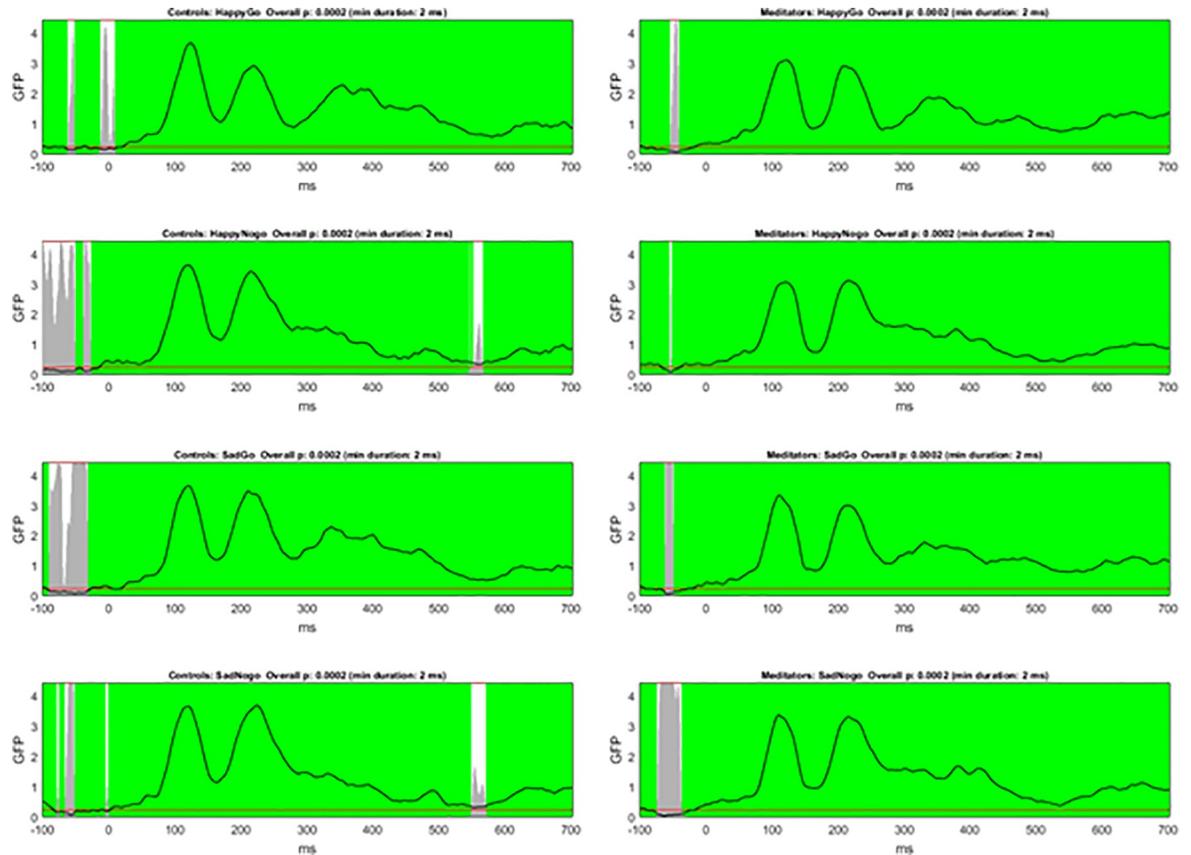


Fig 3. Topographical consistency test. The line indicates GFP values and the grey bars indicate p-values, with the red line indicating $p = 0.05$. White sections indicate regions without significantly consistent distribution of activity within the group/condition, while green periods indicate consistent distribution of activity across the group/condition after duration control for multiple comparisons across time [42]. Note significant consistency across all conditions for both groups except for prior to stimulus onset, and around 550 ms in the Nogo trials for control participants.

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Topographical consistency test. In order to assess consistency of neural activity within groups and trial types, the TCT test was conducted [42]. The TCT showed significant signal indicating consistency of neural activity within all groups / conditions across the entire epoch except prior to the stimulus and during a brief period (< 20 ms) at 550 ms in Nogo trials for controls, see Fig 3). Consistent neural activity within conditions and groups indicates that TANOVA comparisons between conditions and groups are valid.

TANOVA. In order to examine potential differences in the distribution of neural activity in response to the Go and Nogo trials, TANOVAs were conducted. Significant main effects of group that survived duration control for multiple comparisons were present from -1 ms to 62 ms (prior to the C1 period, referred to as pre-C1 henceforth) ($p = 0.003$ averaged across the significant window, partial eta squared effect size = 0.0720), and from 416 ms to 512 ms (during the P3 period) ($p = 0.007$ averaged across the significant window, partial eta squared effect size = 0.0657). The area under the curve statistic for the entire epoch within the group main effect was p -uncorrected = 0.011 (FDR $p = 0.040$), and the global duration control statistic was 46 ms. Figs 4 and 5 depict the topographical differences between groups for the pre-C1 (-1 to 62 ms) and P3 (416 to 512 ms) periods respectively. No significant interaction between group and trial type was present ($p > 0.1$).

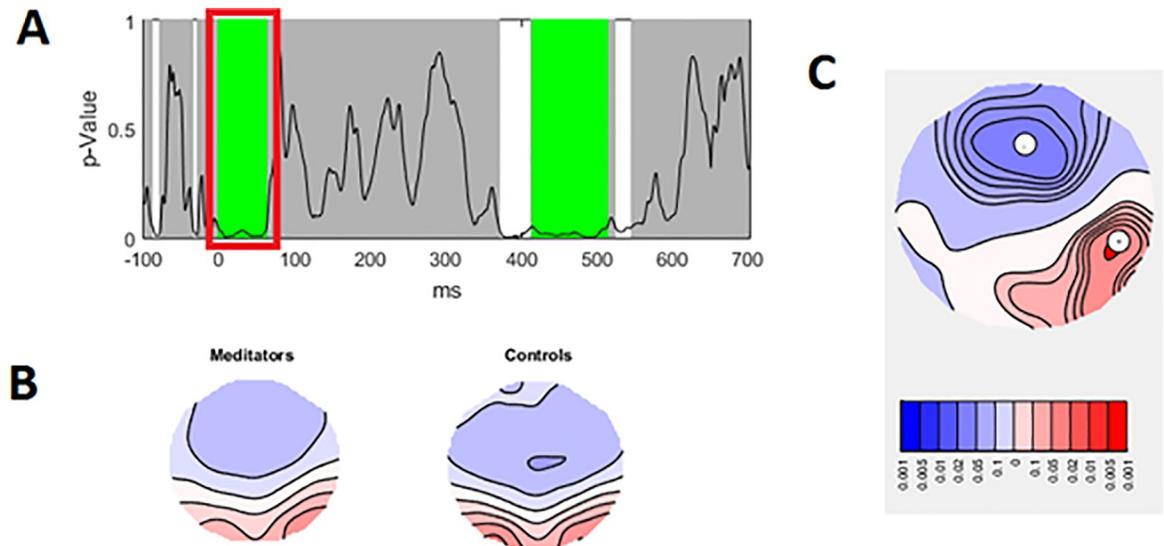


Fig 4. TANOVA main group effect from -1 to 62 ms. A—p values of the between-group comparison for the real data against 5000 randomly shuffled permutations across the entire epoch (green periods reflect periods that exceed the duration control for multiple comparisons across time = 46 ms). B—Averaged topographical maps for each group during the significant time window. C—p-map for meditators topography minus control topography during the significant time window ($p = 0.003$ averaged across the significant window, partial eta squared effect size = 0.0720).

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Overall, the differences indicate more fronto-central negativity and right posterior positivity in the meditation group during the pre-C1 (from -1 and 62 ms). Because the C1 is thought to be the first neural processing of visual stimuli [40, 68], the difference in pre-C1 activity is likely to reflect group differences in anticipatory activity.

The results also reflect more fronto-central positivity during the P3 in the meditation group. Because this difference was present across both Go and Nogo trials, the higher frontal activity in the meditation group may reflect altered attentional function of the P3 rather than altered inhibitory processes. No differences were present in the N2 window (thought to reflect inhibition and conflict monitoring).

TANCOVA. To assess relationships between the altered distribution of neural activity shown by the TANOVA and behavioural performance, TANCOVAs were conducted between significant periods of activity in the TANOVA and cumulative percentage correct. Since participants performed at ceiling, groups were combined to maximise statistical power. TANCOVA between cumulative percentage correct and topographies averaged across the pre-C1 window (-1 to 62 ms) ($p = 0.006$) and the P3 window (416 to 512 ms) ($p = 0.048$) were significant, with positive topographics showing activity more similar to meditators, suggesting those topographies were related to better performance (see Fig 6). However, this may be confounded by group differences in both topographies and performance. When running this analysis just within the meditation group the same pattern was apparent, but non-significant ($p = 0.240$ for -1 to 62 ms, and $p = 0.766$ for 416 to 512 ms), and the same was true for analysis within the control group ($p = 0.112$ for -1 to 62 ms, and $p = 0.182$ for 416 to 512 ms).

Microstates. To further explore the differences in ERPs, we used a microstate analysis approach which clusters different time periods into dominant scalp topographies. Microstate analyses were restricted to durations showing significant group main effects in the TANOVA [66]. Three microstates differed in meditators—microstate 2, reflecting pre-C1 activity, and microstates 5 and 6, reflecting the P3 (see Fig 7 for details). The findings suggested that pre-C1

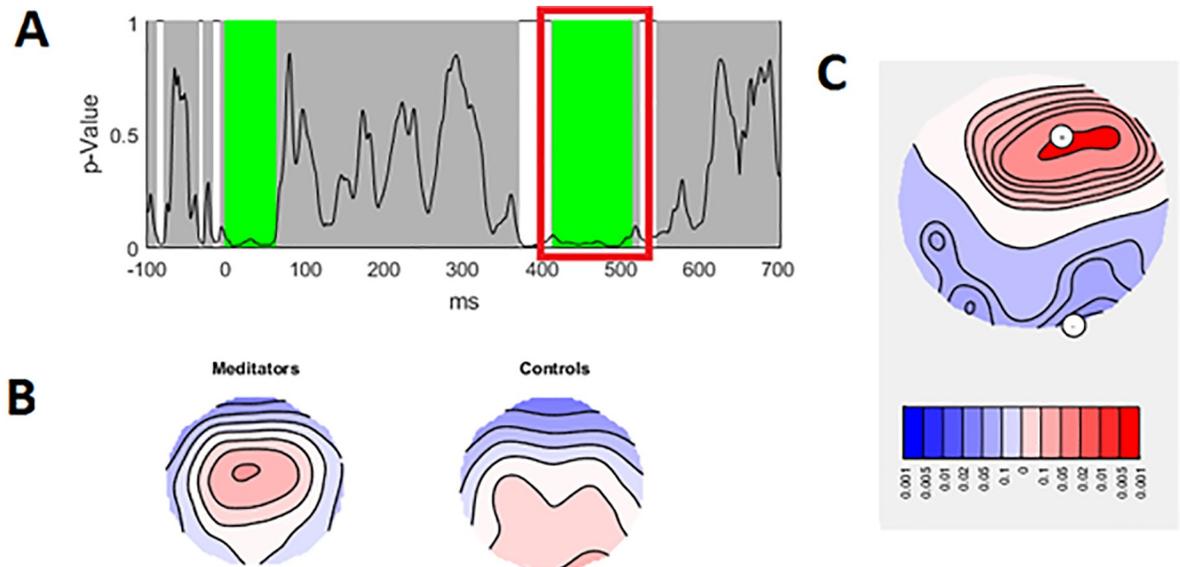


Fig 5. TANOVA main group effect from 416 to 512 ms. A—p values of the between-group comparison for the real data against 5000 randomly shuffled permutations across the entire epoch (green periods reflect periods that exceed the duration control for multiple comparisons across time = 46 ms). B—Averaged topographical maps for each group during the significant time window. C—p-map for meditators topography minus control topography during the significant time window ($p = 0.007$ averaged across the significant window, partial eta squared effect size = 0.0657).

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period neural responses began earlier in meditators compared to controls, and that meditators spend more of the P3 period showing frontally dominant topographies compared to controls. Microstate 2 shows an earlier centre of gravity in meditators (the timepoint reflecting the centre of the GFP area for microstate 2 is earlier in meditators, $p = 0.018$), suggesting earlier

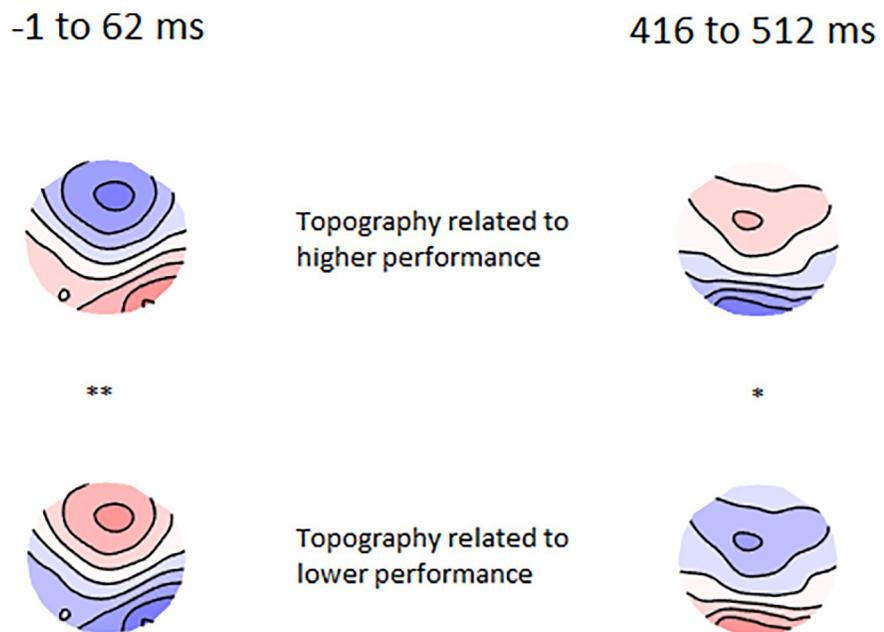


Fig 6. TANOVA topographies depicting the relationship between cumulative percentage correct and averaged topography. From -1 to 62 ms (left) and 416 to 512 ms (right) across both groups. * $p = 0.048$, ** $p = 0.006$.

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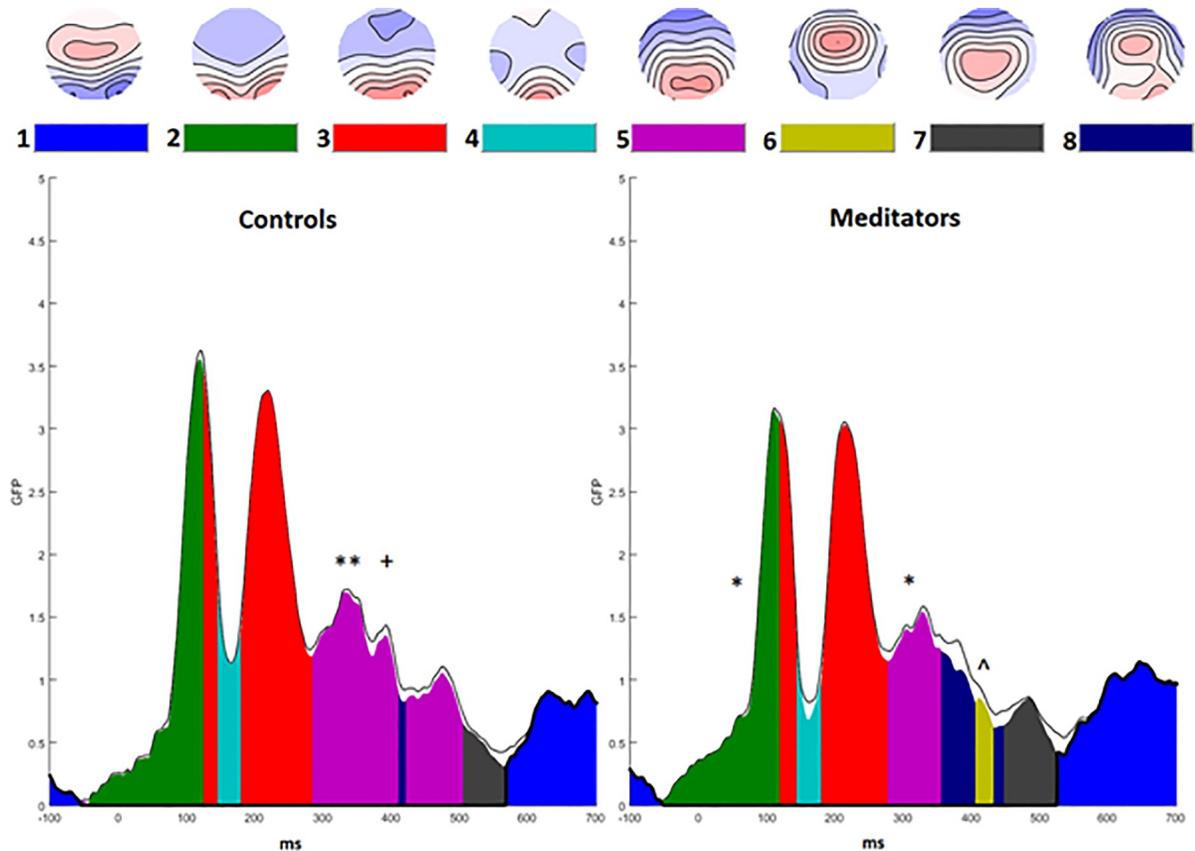


Fig 7. Microstate analysis showing overall between-group effects. Meditators differed in microstate 2 (reflecting pre-C1 activity), and microstates 5 and 6 (reflecting P3 activity). * $p < 0.05$ indicates an earlier centre of gravity in meditators, ** $p < 0.01$ indicates a longer duration in controls, + $p < 0.05$ indicates a larger area under the curve in controls, ^ $p < 0.05$ indicates larger area under the curve in meditators [66].

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processing of the stimuli in this group (the microstate is present from ~0 to ~100 ms following stimuli, matching TANOVA results in the -1 to 62 ms window). Microstate 5 shows a shorter duration in meditators ($p = 0.003$, meditators 78 ms, controls 217 ms). It also shows a smaller area under the curve in meditators ($p = 0.031$, meditators 105.9 ms x microvolts, controls 252.4 ms x microvolts), and an earlier centre of gravity ($p = 0.028$, meditators 318.2 ms, controls 381.9 ms). Microstate 6 shows more area under the curve in meditators ($p = 0.044$, 21.1 ms x microvolts in meditators, 0 ms x microvolts in controls). Microstate 5 is replaced by microstate 6 in meditators (indicating a more frontally distributed P3 during this period) but microstate 5 does not change to microstate 6 at all in controls. These results match the 416–512 ms period of significance in the TANOVA.

Source analysis. To ascertain which brain regions contribute to the differences in scalp ERPs observed between the groups, we estimated the cortical sources of the signal using sLOR-ETA. Source analysis suggested similar distributions of activity between the groups in both the pre-C1 and P3 time periods. Difference maps indicated that meditators showed more pre-C1 activity in right temporal and parietal regions, and a widespread pattern of more P3 activity in the central frontal and parietal regions. See Figs 8 and 9 for details.

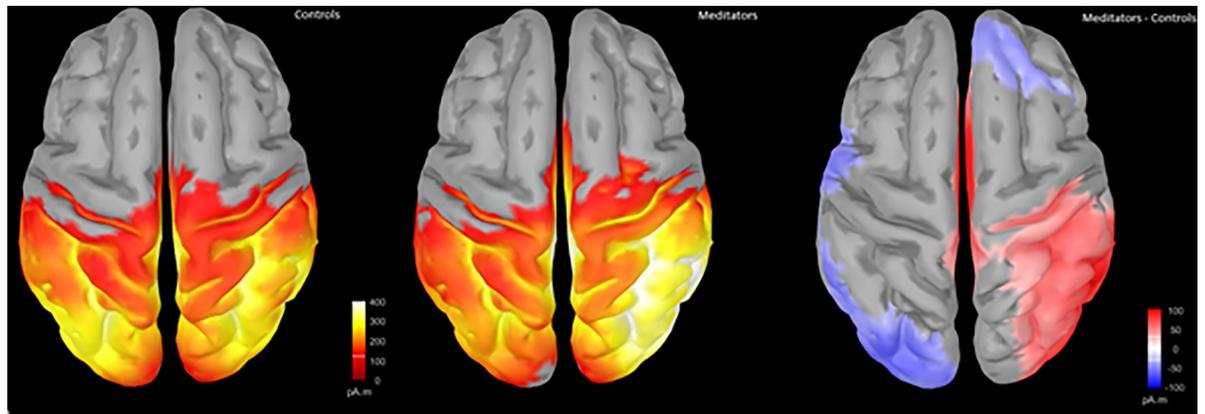


Fig 8. Source reconstruction during the -1 to 62 ms window using sLORETA and minimum norm imaging, unconstrained to cortex (to minimise assumptions). Group averages do not depict positive or negative voltages, only where a region was activated. Difference maps reflect meditator minus control activity (red reflecting more activity in meditators compared to controls, blue reflecting less activity in meditators).

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Discussion

Our study examined whether experienced mindfulness meditators showed differences in neural activity related to conflict monitoring, response inhibition, and sustained attention. The methods used enabled us to separately examine differences in the distribution of activated brain regions from differences in strength of neural activation, which has not been previously studied in meditators. Meditators showed higher accuracy across both Go and Nogo trials and frontally shifted distribution of neural activity during the P3 in both Go and Nogo trials. The latter finding suggests alterations to global attentional processes rather than inhibition specifically. Additionally, meditators showed less differentiation in the strength of neural activity between response and response inhibition trials during the early P3 window. Meditators showed more right parietal positivity during the pre-C1 period, suggesting more anticipatory neural activity for stimulus processing. The distribution of neural activity during both the pre-C1 and P3 significant time periods was correlated with behavioural performance across both

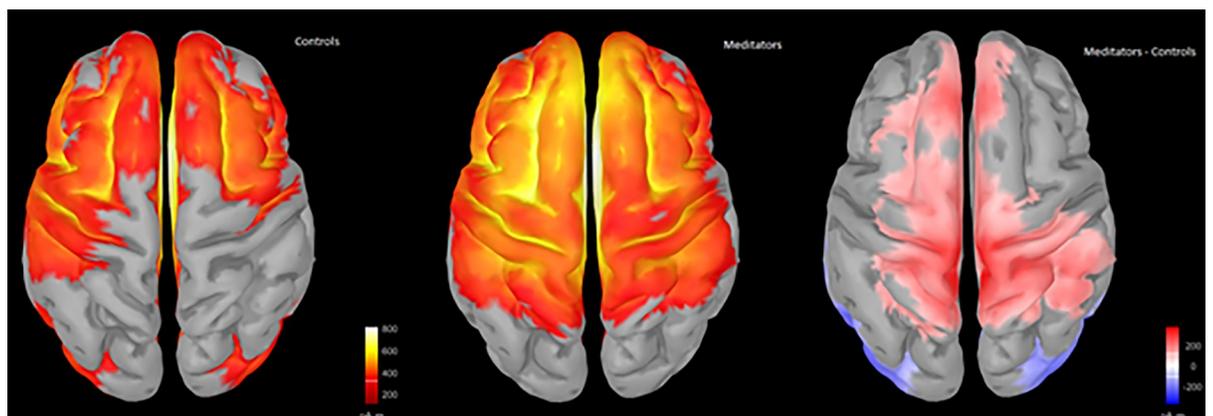


Fig 9. Source reconstruction during the 416 to 512 ms window using sLORETA and minimum norm imaging, unconstrained to cortex (to minimise assumptions). Group averages do not depict positive or negative voltages, only where a region was activated. Difference maps reflect meditator minus control activity (red reflecting more activity in meditators compared to controls, blue reflecting less activity in meditators).

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groups, with better performing participants displaying the same distribution of activity observed in meditators.

These results suggest a range of differences in neural activity in mindfulness meditators compared to demographically matched controls. These differences likely reflect enhanced attentional mechanisms from long-term practice engaging attentional processes. The differences may reflect adaptive adjustments to the neural processes responsible for devoting resources to the functions maximally taxed by task requirements.

A more frontally distributed P3

Meditators showed a more frontally distributed P3 than controls (partial eta squared effect size = 0.0657). Previous research has indicated that engaging response inhibition processes generates a more frontally distributed P3 [29], though no comparable work has explained the function of a more frontal P3 across both Go and Nogo trials. The more frontally distributed P3 in meditators across both trial types suggests that the differences were due to general attention effects rather than response inhibition. Additionally, source analysis indicated more activity in meditators across the superior/medial frontal gyrus, particularly the left hemisphere, as well as the bilateral parietal regions, spreading more laterally in the right hemisphere. Previous research has indicated the superior frontal gyrus to be related to executive function [45]. Activity in the medial frontal gyrus is more pronounced when top-down control is allocated to Go/Nogo stimuli and is usually more related to attentional control than inhibition [44]. Lastly, activity in the parietal cortex is thought to be related to selective and sustained attention, and the right parietal cortex to spatial attention [69, 70]. These results suggest that the altered P3 distribution in meditators is likely to reflect enhanced attentional control. Further support for this conclusion comes from the finding that a more frontally distributed P3 was related to improved behavioural performance.

Smaller P3 amplitude difference between response and response inhibition and No N2 differences in meditators

The meditation group showed no difference between Go and Nogo trials in overall neural response strength during the P3 window, while the control group showed larger neural response strength to Go trials than Nogo trials. However, no difference was found between groups in post-hoc comparisons of Go and Nogo trials independently, suggesting that trial type only differentiates neural response strength within controls rather than that meditators differ from controls. These results were not hypothesized, and contradicted our expectation that the Nogo P3 would be enhanced in the meditation group, reflecting enhanced response inhibition [71]. One potential explanation is that the task was easier for meditators. More difficult Go/Nogo tasks generate larger differences in neural activity between trial types [21]. This explanation aligns with the better behavioural performance in the meditation group, who also showed less difference in neural activity between Go and Nogo trials.

Additionally, research has suggested that Go/Nogo ratios of 50/50 (as used in the current study) reduce response inhibition related neural activity by more than 60% [72]. Equal ratio Go/Nogo tasks may simply compare general response-related activity to trials where response-related activity is never initiated (rather than trials that initiate response activity that subsequently must be inhibited [72]). Single electrode ERP figures for the current data showed larger frontal P3 amplitudes in Nogo compared to Go trials (see Figure B in S1 File), typical of response inhibition activity in Go/Nogo tasks [29]. This suggests the task did engage response inhibition processes. However, the equal ratio of Go and Nogo trials may have meant these inhibitory processes were not difficult to successfully perform, and so were not differentially

modulated by group. As such, observed differences may merely reflect improved attentional control in meditators rather than improved inhibitory processes. In support of this explanation, studies using harder Go/Nogo tasks with lower frequencies of Nogo trials show enhanced Nogo P3 activity in ADHD patients who have undergone meditation training [33]. However, the Go and Nogo P3 is influenced by stimuli frequency [73]. Thus, future research examining response inhibition in meditators should attempt to differentiate between frequency and response inhibition effects.

Additionally, although an interaction between trial type and group was present for P3 amplitudes, no interaction was present in the behavioural data. The lack of behavioural difference likely reflects a ceiling effect—the behavioural results were too consistently high to reveal an interaction, while neural data may be more sensitive. Lastly, we expected the N2 component to be altered in meditators. Previous research with infrequent Nogo trials has demonstrated N2 alterations from meditation, perhaps as a result of the higher demand placed on response inhibition related neural processes [32, 36]. As mentioned with the lack of altered Nogo P3 activity in meditators, the N2 component may not have differentiated the groups in the current research because response inhibition processes were not sufficiently taxed by the equiprobable Go/Nogo task.

More right posterior pre-C1 positivity

The meditators showed a topography with more negative fronto-central activity and more right posterior positivity during the pre-C1 window (partial eta squared effect size = 0.0720). The result reflects differences in neural activity that precedes the earliest point that visual related activity has been shown to reach the occipital cortex (~ 50 ms post stimulus [40, 68]). Meditators showed differences in neural activity *before* stimulus perception. Anticipatory activity is present during periods leading up to stimulus processing, reflecting top-down attentional control to enhance cortical processing of stimuli, ensuring optimal processing [74–77]. In other words, the pre-C1 may reflect enhanced endogenous attention, which has been defined as “*the exercising of an intention to selectively attend, based on some internal representation of what will be attentionally relevant in the near future. This intention interacts with attention deployment systems to reorganize the attentional set of the brain in preparation for incoming stimuli—a preparatory attentional state*” [78].

Such anticipatory activity has been found in the dorsal visual processing stream (in temporo-occipital regions), with top-down influences from lateral parietal attentional gating regions, and frontal control regions [68, 74, 78]. These regions overlap with those shown in our source analysis. These areas may exert an excitatory effect on primary visual areas that increase and prolong stimulus processing in those areas [79]. Thus, this pre-C1 difference may reflect an improved attentional preparedness among meditators, reflecting a greater readiness for stimulus processing and enhanced focus, as is a goal in many early mindfulness meditation practices [4, 6–8, 11].

Additionally, the right occipital and temporal regions have been shown to specialise in processing faces as well as for anticipation of general visual processing, suggesting that higher activity in these regions in the meditation group is likely to assist stimuli processing in the current task [78, 80]. As such, the results could reflect enhancement of the visual processing pathway so the chain of information from perception to performance is more effective [68]. Although unexpected, our pre-C1 results provide further evidence for the suggestion that enhanced attention in meditators reflects a stronger ability to modulate neural activity towards the optimal achievement of goals [2, 81]. As such, this difference in anticipatory pre-C1 activity may reflect an altered top-down brain state that prepares meditators’ brains for the subsequent

perceptual brain states. This may have enabled an increased ability of meditators to sustain attentional focus on the chosen object and by consequence to show enhanced behavioural performance (which in this case are the task stimulus) [7]. The difference in meditator neural activity with such a short latency following the stimuli is currently unique in meditation research simply because the current study is the first to include neural activity with such a short latency following the stimuli in statistical analyses. We suggest that future meditation research would benefit from focusing on this anticipatory activity, particularly using tasks designed to probe the activity more directly (eg.[74, 75–77]).

These results have clinical implications—research indicates that aversive stimuli cause altered visual processing within 60–120 ms [82]. Individuals with anxiety also show stronger neural responses to negative emotional images within the 80 ms C1 period [83]. This early response to aversive stimuli and early over-activation in anxious individuals reflects early sensory processing bias that may be impossible for the higher order functions to later modulate. The clinical benefit of mindfulness may involve alteration to attentional mechanisms that allow modulation of early neural processing, reducing emotional reactivity before emotional reactions are elicited. This may explain why mindfulness has amongst its strongest clinical effects on anxiety [84].

Strengths, limitations and future directions

Although a strength of the current study is the selection of a well-matched control group, the main limitation is the lack of ability to draw conclusions about causation due to the lack of an active control group. It may be that individual differences such as personality factors that predispose that group towards mindfulness meditation are ultimately responsible for the differences. Previous longitudinal research has indicated that mindfulness meditation does alter neural activity [13, 14, 16, 85]. While this does not confirm that the results of the current study are due to mindfulness meditation, the positive results from previous research suggest that it is at least possible that the current results are due to mindfulness meditation rather than factors that predispose individuals towards meditation. Nonetheless, it is difficult to control for potential self-selection biases among those who have chosen to meditate versus those who have not [86]. An active control group involving an intervention that does not modulate the potential mechanisms of action of mindfulness meditation would control for potential self-selection biases and other potential confounds such as group membership. However, recruiting an active control group matched for the extended amounts of practice time as our meditation group is difficult (although long term athletes may be one solution [87]). Without an active control group, a parsimonious and robust interpretation of the current conclusions (and those of other cross-sectional studies of experienced meditators) is that differences relate to “leading a life that involves meditation” but the research offers no information as to whether meditation is causal in the differences.

Related to this point, the current study included a range of different meditation techniques that fit under the umbrella term “mindfulness meditation”. While steps were taken to ensure techniques were attention based and body focused (using Kabat-Zinn’s definition—“paying attention in a particular way: on purpose, in the present moment, and nonjudgmentally” [47] and screening to ensure practices were involved focused attention on the breath or body), it may be that different techniques result in differences in the attentional processes being trained [12, 88]. However, a strength of the current study is the confirmation that both the meditation and control groups showed consistent topographical activation patterns prior to performing between-group comparisons (with the TCT test). As such, when neural activity was averaged across the group, the meditation group showed differences in attention related neural activity

that were demonstrated to be consistent within the group. This suggests that even though different meditation practices may train different attention functions, there were still consistent changes from the umbrella definition of “mindfulness meditation” to neural activity related to attention. The within group consistency is also important, because it eliminates the possibility that differences in within-group variability could explain between-group differences, despite absence of signal within one of the groups (because the signal was variable in that group and averaged out to zero).

Future research would do well to examine the commonalities and differences between altered neural activity in mindfulness meditators across different tasks. This is necessary to answer questions about whether the neural effects of mindfulness meditation are process-driven or domain-specific [9]. Our suggestion is that the changes that result from meditation reflect enhancement not of one specific neural process, but of the modulation of a range of oscillatory activity, in order to strengthen the weakest link in the chain of neural processes. As such, we would expect that the process most pressured by a specific task may demonstrate enhanced function in meditators who have improved attentional function. We recommend including easy and hard conditions for research comparing meditators to controls. This would enable identification of neural processes that are upregulated to enable performance in the hard condition, allowing determination of whether that process is specifically affected by enhanced attention in mindfulness meditators.

A propositional integrative interpretation

Overall, the results show differences in both anticipation of sensory processing and top down attention related differences in neural activity in mindfulness meditators, in alignment with previous research [13, 14, 16, 85]. The altered topographies suggest that different neural assemblies are recruited in meditators to perform the same task but with increased accuracy, rather than the same neural assemblies being more strongly activated.

We suggest that the differences in meditators reflect improved attentional function, and this improved attentional function provides enhancements to neural processes that are maximally taxed in the task, or processes that are the ‘weakest link’ in achieving task-oriented goals [2, 81, 89]. This improved attentional function provides increased support to the processes most likely to fail in the chain of neural activity that takes place from stimulus processing to behavioural response, reducing the chance of failure at those most vulnerable points and enhancing the probability of successful task performance. For example, in the current study the more frontally distributed P3 in the meditators may reflect an increase in the inhibition of potentially interfering neural activity that is not related to task demands [29]. Similarly, the pre-C1 topography differences in meditators may reflect enhanced neural activity related to the anticipation of visual processing, in order to improve the probability that these sensory processes would lead to the correct discrimination of the two stimuli, enabling higher accuracy of Go or Nogo responses. This adaptive adjustment to provide extra resources to neural processes that are maximally taxed by task requirements has been shown previously with cued attentional manipulations, but has not yet been shown as a result of attention training [2, 81, 89].

In this context, differences between meditators and controls are likely to be task-specific rather than neural activity or region-specific. For example, fronto-midline theta activity generated by the anterior cingulate cortex has been shown to differentiate meditators from controls while participants are resting or meditating [90, 91]. However, tasks that do not lead to modulations in theta oscillations, but do challenge other frequencies (such as alpha) are unlikely to show differences between meditators and controls in theta activity (and may be more likely to

show differences in alpha activity). As such, tasks other than that used in the current study are likely to demonstrate different effects from meditation depending on the neural processes most taxed by the task, for example alpha modulation enhancements to reduce somatosensory distraction [92], or theta synchronisation to stimulus in attentional blink tasks [14]. Indeed, the current sample of meditators showed an alternative profile of differences compared to controls than the differences found in the current study when they performed both a colour and emotional Stroop task (Raj et al. in preparation) and an N-back task with a tactile distractor (Wang et al. in preparation), and no differences in error processing [93]. These differences in comparisons between meditators and controls dependant on the neural processes most challenged by the task may occur even for subtle differences in task design, for example equiprobable Go/Nogo tasks may reveal differences in attentional processes as per the current results, compared to Go/Nogo tasks with more frequent Go trials which may reveal differences in response inhibition processes. This interpretation may provide an explanation for the variation in findings between studies comparing meditators to controls, as different neural processes are engaged by different tasks and varied task parameters. We hope that the results of the current study can be interpreted and contextualised within this framework, in combination with future research, to provide a more sophisticated understanding of how neural activity differs in meditators.

Supporting information

S1 File. Table A. Previous mindfulness research using the Go/Nogo task. Figure A. Source reconstruction during the well-known P100 occipital ERP, averaged across the 50 to 150 ms window across both groups using sLORETA and minimum norm imaging, unconstrained to cortex (to minimise assumptions). This was performed to demonstrate our source analysis was reliable even in the absence of individual MRI templates [61]. Note that the average does not depict positive or negative voltages, just whether a region was activated. **Figure B. Single electrode ERP waveforms for both groups and conditions.** These are depicted for comparison with traditional ERP analyses. Note that no statistics have examined data from single electrodes.

(DOCX)

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