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ORIGINAL PAPER

The Mindful Brain at Rest: Neural Oscillations and Aperiodic Activity in Experienced Meditators

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Abstract

Objectives Previous research has demonstrated that mindfulness meditation is associated with a variety of benefits, including improved mental health. Researchers have suggested these benefits may be underpinned by differences in neural oscillations. However, previous studies measuring neural oscillations have not controlled for non-oscillatory neural activity, the power spectrum of which follows a 1/f distribution (whereby the power of neural activity at each frequency is inversely proportional to that frequency (such that as frequency increases, power decreases)) and contributes to power measurements within oscillation frequencies of interest. We applied recently developed methods to determine if past findings related to neural oscillations in meditation are present even after controlling for non-oscillatory 1/f activity.

Method Forty-eight experienced meditators and 44 demographically matched non-meditators provided resting electroencephalography (EEG) recordings. Whole-scalp EEG comparisons (topographical ANOVAs) were used to test for differences between meditators and non-meditators in the distribution or global power of activity for theta, alpha, beta, and gamma oscillations, and for the 1/f components slope and intercept using the extended Better OSCillation detection toolbox.

Results Results indicated that meditators showed differences in theta, alpha, and gamma oscillatory power compared to non-meditators (all $p < 0.05$). Post hoc testing suggested that the oscillatory differences were primarily driven by differences in the distribution of neural activity between meditators and non-meditators, rather than differences in the overall power across all scalp electrodes.

Conclusions Our results suggest that experience with meditation is associated with higher oscillatory power and altered distributions of theta, alpha, and gamma oscillations, even after controlling for non-oscillatory 1/f activity. Band-specific differences in oscillatory activity may be a mechanism through which meditation leads to neurophysiological benefits.

Preregistration This study was not preregistered.

Keywords EEG · 1/f slope · Frequency band power · Mindfulness · Meditation

Mindfulness meditation (MM) has gained significant traction in the general population as a tool that may aid in the alleviation of daily stress and negative emotions. MM requires individuals to pay attention to the present moment with a non-judgemental awareness of the inner or outer experiences (Kabat-Zinn, 1994). Accumulated evidence suggests that MM can lead to a variety of benefits, through physiological, emotional, and cognitive changes (Chiesa et al., 2011; Chiesa & Serretti, 2010). These benefits are supported by extensive evidence from research and meta-analyses of clinical-based interventions that target stress, depression, and anxiety, such as mindfulness-based stress reduction (MBSR) and mindfulness-based cognitive therapy (MBCT) (Chiesa & Serretti, 2010).

Previous research has indicated that changes in the power of neural oscillations, as measured by electroencephalography (EEG), may be a neurophysiological mechanism that underpins the benefits of MM, with significant evidence in support of meditation-related differences in theta and alpha

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oscillatory activity (Dietl et al., 1999; Kerr et al., 2011; Lomas et al., 2015; Sauseng et al., 2010). Theta activity (voltage amplitudes that cycle from negative to positive approximately 4 – 8 times per s, or at 4 – 8 Hz) has been shown to be associated with working memory processes (Klimesch et al., 2005; Sauseng et al., 2010), anxiety, cognitive control, and decision-making processes (Cavanagh & Frank, 2014; Cavanagh & Shackman, 2015) as well as attention and the processing of information (Dietl et al., 1999; Grunwald et al., 1999; Klimesch et al., 1997). Alpha activity (voltage amplitudes that cycle from negative to positive approximately 8 – 13 times per second, or at 8 – 13 Hz) is primarily generated by parietal and occipital regions, and evidence suggests alpha activity reflects the inhibition of brain regions that are not involved in the completion of a task (Cooper et al., 2003; Jensen & Mazaheri, 2010; Klimesch et al., 2007; Mathewson et al., 2011). Previous evidence suggests that meditators may be able to modulate alpha activity to a greater degree than non-meditators, both when selecting stimuli for attentional focus between two different sensory modalities, and when required to focus attention away from certain stimuli (Kerr et al., 2011; Wang et al., 2020). In addition, higher power for both theta and alpha oscillations in the frontal and temporal regions has been associated with a variety of types of meditation, both during meditation practice and while at rest (Kerr et al., 2011; Lee et al., 2018; Lomas et al., 2015; Wong et al., 2015).

Less focus has been given to the study of associations between beta and gamma oscillatory activity and meditation. Beta activity (voltage amplitudes that cycle from negative to positive approximately 12 – 25 times per second, or at 12 – 25 Hz) has been linked with activation of the default mode network (DMN) — a network of neural regions involved in self-referential processing, reflective thoughts, emotional monitoring, and maladaptive rumination (Buckner et al., 2008; Gusnard & Raichle, 2001; Hamilton et al., 2011; Hölzel et al., 2011; Jang et al., 2011; Raichle et al., 2001; Taylor et al., 2013). Specifically, a limited number of findings suggest that when compared to a resting condition, meditation is associated with decreased beta activity (Faber et al., 2015), reduced coherence of beta oscillations (as well as alpha and gamma) (Lehmann et al., 2012), and conversely greater beta amplitudes — but only for certain brain regions (Dunn et al., 1999).

Gamma activity, which typically exceeds 25 Hz, has been linked to cognitive processes such as attention, working memory, and sensory information processing (Kambara et al., 2017; Lee et al., 2018; Pritchett et al., 2015). In relation to meditation practice, greater gamma activity has been found in meditators compared to non-meditators when actively engaged in a meditative state (Lutz et al., 2004). Gamma activity has also been positively correlated with experience in meditative practices (Lee et al., 2018).

A limitation of previous research using EEG to examine neural oscillations in the context of meditation is that it has not accounted for the contribution of “non-oscillatory” neural activity (neural activity that generates voltage shifts that do not show oscillations, or a regular repeating cycle). This non-oscillatory neural activity (or “aperiodic” activity) follows a 1/f “power law”, whereby the power of neural activity at each frequency is inversely proportional to that frequency (such that as frequency increases, power decreases) (Ouyang et al., 2020; Voytek et al., 2015). Recent research has shown that the 1/f activity is also important to behavioural function (Ouyang et al., 2020; Voytek et al., 2015). However, the neurophysiological mechanisms that govern 1/f activity are still unclear (Ouyang et al., 2020). Most notably, traditional measures of EEG oscillatory power have not disentangled oscillatory power from 1/f non-oscillatory activity. Previous research on resting-state neural activity in experienced meditators has not controlled for the contribution of non-oscillatory 1/f activity. If not addressed, this non-oscillatory 1/f activity can completely account for differences in power when measuring neural activity within specific oscillatory frequencies, such that researchers cannot draw substantiated conclusions about neural oscillations (Cahn & Polich, 2006; Kosciessa et al., 2020; Lomas et al., 2015; Takahashi et al., 2005; Voytek et al., 2015). Furthermore, research measuring EEG power in lower frequency oscillations (e.g. theta (4–8 Hz) compared to gamma (>25 Hz)) is more likely to be impacted by this 1/f activity, as the amplitude of the 1/f activity in the lower frequency bands is much higher than the amplitude of the oscillatory activity (Voytek & Knight, 2015). As such, although differences in power may be detected within predetermined frequency ranges, these differences do not necessarily reflect differences in oscillatory power. The contribution of 1/f activity can thereby lead to misinterpretation of data, as there may be a number of alternative physiological processes that explain differences in frequency power measures (such as a reduction in true oscillatory power, a shift in the peak frequency of the oscillation, a reduction in power across all frequencies, or a change in the 1/f slope) (Donoghue et al., 2020). In consideration of this possibility, conclusions drawn by previous research regarding an association between meditation and differences in oscillatory activity may in fact be driven by non-oscillatory activity, where 1/f activity has confounded the measurement of the strength of the oscillations.

Evidence has also suggested that a flatter 1/f slope may be associated with more asynchronous neuronal firing (Voytek & Knight, 2015), as weaker synaptic inputs are associated with greater variability in synaptic input response (leading to a flatter spectrum). Alternatively, greater local positive excitatory feedback may be driven by an increased excitation/inhibition (E/I) ratio within the cortex, as higher levels of synchronous neural spiking are associated with a steeper

1/f slope (Voytek & Knight, 2015). A well-regulated E/I balance is vital for maintaining neural homeostasis, is reflective of healthy neuronal communication, and is implicated in cognitive functions such as working memory (Gao et al., 2017; Robertson et al., 2019). Conversely, an imbalance has been associated with cognitive impairments or neurological disorders, and in certain disorders (such as schizophrenia) 1/f activity may actually be more predictive of impaired functioning than neural oscillations (Peterson et al., 2023). Thus, exploring potential differences in the 1/f slope and intercept may provide valuable insight into the function of 1/f activity, and comparing 1/f activity between meditators and non-meditators may indicate whether the E/I balance is modified by meditation. Previous research on resting-state neural activity in experienced meditators has not examined these parameters of the 1/f activity.

While previous research into EEG activity associated with meditation is informative, notably, many of the differences in neural activity that have been associated with meditation have been identified through investigation of neural activity during the performance of cognitive tasks, or whilst actively engaged in a meditation practice. These measurements obtained while participants are actively engaged in a meditation practice provide an indication of activity during the meditation state, which can be defined as a temporary adoption of mindful principles in the context of a formal practice, which may relate to specific neural activities that do not extend to periods outside of the meditation state, even in experienced meditators. In contrast, changes in resting-state EEG data allow us to capture and thus provide novel information indicative of trait-related neural changes, specifically without the engagement of attention mechanisms that may be associated with the performance of a cognitive task or of meditation (Cahn & Polich, 2006; Lutz et al., 2006). *Traits* refer to persistent changes in neural activity that remain evident outside of active meditation periods, for example meditators may show a shift in one's relationship to thoughts, emotions, or a deepened sense of calmness, which may extend beyond of the period of meditation and evident in resting-state EEG analyses (Cahn & Polich, 2006; Lutz et al., 2006).

Given this background, the present study utilised the extended Better Oscillation Detection (eBOSC) algorithm to identify and control for 1/f activity, in order to measure resting-state oscillatory activity from meditators and non-meditators without the confound of the 1/f activity (Kosciessa et al., 2020; Whitten et al., 2011). eBOSC also provides the ability to distinguish periods of EEG activity that show oscillations in specific frequencies from periods that do not show oscillations. This novel contribution enables comparisons of the time spent showing oscillations above the 1/f activity in addition to oscillatory power (reflected by the measure "percentage of EEG trace"; see Supplementary Information) (Donoghue et al., 2020; Kosciessa et al., 2020). In addition to measuring oscillatory power without 1/f activity and the slope and intercept components of the 1/f activity, the eBOSC algorithm allows analysis of peak oscillatory frequencies. Further information regarding these variables can be found in the Supplementary Information.

The primary aims of the present study were to determine if differences in oscillatory power were present between meditators and non-meditators during resting-state EEG (whilst applying a novel method to control for 1/f activity), and examining whether meditators and non-meditators differ in the 1/f components, including slope and intercept. It was hypothesised that meditators would demonstrate greater oscillatory power for all frequency bands compared to non-meditators after controlling for 1/f activity, based on the prior research that examined oscillatory activity without controlling for 1/f activity which was summarized earlier in our introduction (Dunn et al., 1999; Kerr et al., 2011; Lee et al., 2018; Lomas et al., 2015; Lutz et al., 2004; Wong et al., 2015). It was also hypothesised that there would be differences in the 1/f slope and intercept between meditators and non-meditators (reflecting differences in E/I balances). Due to the limited research examining 1/f in the context of meditation (see Rodriguez-Larios et al., 2021), this hypothesis was non-directional. Finally, as there is a limited amount of research on the topographical distribution of these differences in activity, we also formed an exploratory and non-directional hypothesis that both the global amplitude of the different oscillations and 1/f parameters, and the topographical distribution of each oscillation would differ between groups, reflecting both an increase in the overall amplitude of oscillations in meditators and differential patterns of brain region engagement in meditators compared to non-meditators. The novel application of these innovative methods to control for and measure the 1/f activity provides the potential to advance our understanding of the relationship between MM and neural oscillations, providing clarity as to whether the underlying processes do indeed show oscillatory differences between meditators and non-meditators, or whether previously identified differences might instead reflect differences in 1/f non-oscillatory activity.

Method

Participants

Data were collected in the context of two broader studies that examined EEG activity during cognitive tasks, which were conducted from 2016 to 2019 (results of which have already been published; see Bailey et al., (2019a, 2019b, 2020, 2023a), Payne et al., (2020), Wang et al., (2020)). Participants were recruited through community advertisement and from advertisements at meditation centres. Completing the resting EEG recordings was optional for participants, as the EEG recording sessions were long in duration, so not all participants provided a resting recording. The overall sample of resting recordings available from these two studies included 98 participants, of which 50 were experienced meditators and 48 non-meditators. Participants ranged from 19 to 64 years old. Inclusion criteria for meditators consisted of having a current meditation practice involving at least 2 hr per week of practice, with at least 6 months of meditation experience, that were mindfulness-based and met the requirements of the Kabat-Zinn definition of "paying attention in a particular way, on purpose, in the present moment, and non-judgmentally" (Kabat-Zinn, 1994, p. 124). Non-meditators were only included if they had less than 2 hr of lifetime experience with any kind of meditation. Exclusion criteria included self-reported mental or neurological illness, current or previous, as well as current use of psychoactive medication or recreational drugs. The Beck Depression Inventory (BDI-II) and the Beck Anxiety Inventory (BAI) were administered to screen for depression and anxiety (Beck et al., 1996; Brenner, 2011). For the BDI-II, participants who scored at or above the threshold for the mild range were excluded (≥ 19), whilst participants who scored at or above the threshold for the moderate range in the BAI were excluded (≥ 21). Trait mindfulness was also assessed using the Five Facet Mindfulness Questionnaire (FFMQ) (Baer et al., 2006). Data from four non-meditators were excluded due to the following: insufficient EEG data (one participant), moderate anxiety (one participant), or a previous history of meditation (two participants). Data from two meditators were excluded due to a history of mental illness (one participant) or insufficient weekly meditation practice time (one participant). This left 48 meditators (27 females, age *M* (*SD*) = 37.15 (12.11)) and 44 non-meditators (24 females, *M* (*SD*) = age 33 (12.98)), and a total of 92 participants in the final sample (see Table 1 for participant demographics). The study was approved by the ethics committees of the Alfred Hospital and Monash University, and all participants gave written informed consent.

Procedure

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), as the Quick-Cap provides a full distribution of electrodes to measure neural signals from all scalp regions, with high-quality signals that have been extensively validated in previous research (Bailey et al., 2019b, 2023b). Electrodes were referenced to an electrode between Cz and CPz as is standard for the Quick-Cap system, and data were collected from all electrodes for both eyes closed (EC) and eyes open (EO) conditions. Electrode impedances were adjusted to below 5 kΩ prior to the start of each of the (3-min) resting recordings, but were not adjusted during the recordings. The EEG was recorded at 1000 Hz, with an online bandpass filter of 0.05 to 200 Hz.

The EEG session typically lasted between 2.5 and 3.5 hr. Participants who had resting data collected during

Table 1 Bayesian, robust, and parametric tests for demographic and self-report data

	Meditators *M (SD)* *Median and MAD used for robust tests*[a]	Non-meditators *M (SD)* *Median and MAD used for robust tests*[a]	BF_{01}	BF_{10}	Statistics
Sample size	48	44			
Age	37.15 (12.11)	33 (12.98)	1.52		$t(90) = -1.59, p = 0.116$
Gender (F/M)	27/21	24/20	3.89		$X^2\ (1, n = 92) = 0.03, p = 0.869$
Years of education	17.13 (2.43)	16.62 (2.89)	3.15		$t(89) = -0.91, p = 0.364$
Preferred hand (R/L/ambidextrous)	44/4/0	42/1/1	24.96		$\chi^2\ (2, n = 92) = 2.68, p = 0.262$
BAI	4.83 (5.35)	5.34 (5.28)	4.17		$t(90) = 0.46, p = 0.648$
BDI-II	$0^a\ (0^a)$ Mean 1.5 (*SD* = 2.54)	$0^a\ (1^a)$ Mean 3.30 (*SD* = 4.70)		2.20	$t(32.26^a) = 1.61^a, p = 0.116^a$
FFMQ	154.25 (15.4)	134.80 (13.87)		1.104e+6	$t(90) = -6.35, p < 0.001$

Statistics refer to Student's *t*-test (or robust Yuen's *t*-test) and independent chi-squared tests. [a]Robust Yuen's *t*-tests. The median and MAD are reported for robust tests. *MAD*, median absolute deviation. The mean and standard deviation (*SD*) are reported for parametric tests. Robust tests are based on a trimmed sample and so the degrees of freedom (if given) will not be the same for other measures. *BF*, Bayes factors. BF01 > 1 favours the model of the null hypothesis. BF10 > 1 favours the model of the alternative hypothesis. BF01 (BFexcl) is reported for non-significant findings whilst BF10 (BFincl) is reported for significant findings. Higher-order interactions are excluded. All significance levels (α) set at 0.05. NB. The mean BDI-II score for meditators was 1.5 (*SD* = 2.54) and that for non-meditators 3.30 (*SD* = 4.70) and is provided here for additional clarification as a median of 0 may not be of value to interpret on its own participation in the first study completed five cognitive tasks across the session, whilst participants involved in the second study completed three cognitive tasks during participation. Participants recruited from the first study completed a Go/No-Go task and a colour Stroop task prior to their resting EEG recording. Participants recruited from the second study only completed a Go/No-Go task prior to their resting EEG recording. All participants completed the eyes closed resting recording first, and then the eyes open component. Analysis of the task related data can be found in previous studies (Bailey et al., 2019a, 2019b, 2020, 2023a, Payne et al., 2020, Wang et al., 2020). During the resting recording, participants were explicitly instructed "to rest, not to meditate", to exert no deliberate control over their mental state, and to let their mind "do whatever it wants to". Prior to the EEG recording, participants were also shown the EEG activity being recorded, and the influence of eye movements, head movements, and muscle activity on the EEG data. Participants were informed (in an unscripted, conversational manner) that the aim of the study was to record brain activity, and that the eye movements, head movements, and muscle activity disrupted our ability to measure that activity. This explanation was followed by a request to participants to minimize actions that contributed these artefacts to the EEG recordings as much as possible.

Measures

Pre-processing and analysis of EEG data from eyes closed and eyes open conditions were conducted for each recording separately, using the toolboxes EEGLAB (Delorme & Makeig, 2004) and FieldTrip (Oostenveld et al., 2011) in MATLAB R2018b and R2020a (The MathWorks, USA). EEG data were cleaned using the RELAX cleaning pipeline (Bailey, Biabani, et al., 2023b; Bailey, Hill, et al., 2023c). Firstly, EEG data were filtered using a fourth-order Butterworth filter with a bandpass of 1 to 80 Hz and a second order 47 to 53 Hz notch filter. The "Pre-processing" (PREP) pipeline was used to remove noisy electrodes (Bigdely-Shamlo, et al., 2015). Further remaining extreme outlying electrodes and data periods were rejected using multiple approaches as per the default settings in RELAX (full details are reported in Bailey, Biabani, et al. (2023b) and Bailey, Hill, et al. (2023c)). Objective artefact detection procedures were then used to identify eye movements and blinks, voltage drifts, and muscle activity. Three sequential Multiple Weiner Filter (MWF)'s were then used to filter out these artefacts and leave only clean data (Somers et al., 2018). Following the MWF cleaning, wavelet-enhanced independent component analysis was applied to reduce the artefactual components identified by ICLabel (Pion-Tonachini et al., 2019) in order to clean any remaining artefacts. This application of MWF cleaning followed by wavelet-enhanced independent component analysis was demonstrated in previous research to provide optimal reduction of non-neural artefacts concurrent with good preservation of oscillatory neural signals (Bailey, Biabani et al., 2023b), which is critical to enable our comparisons between meditators and non-meditators. Further details regarding the RELAX data cleaning steps can be found in Bailey, Biabani, et al. (2023b) and Bailey, Hill, et al. (2023c). Lastly, the EEG data was split into epochs of 5 s in length with a 1.5-s overlap on each side. This provided 2 unique seconds within each epoch for frequency-power computation, and a sufficient buffer on each side of the epoch to prevent edge effects from influencing frequency-power computations. Epochs that showed improbable voltage distributions or kurtosis values exceeding 5 standard deviations for any single electrode, or 3 standard deviations for all electrodes, were rejected. In line with previous research, no more than 15% of epochs or 20% of electrodes were rejected from any participant (Bailey, Biabani et al., 2023b; Kosciessa et al., 2020; see Supplementary Information).

The eBOSC toolbox was used for the detection of theta (4–8 Hz), alpha (8–12 Hz), beta (12–25 Hz), and gamma (> 25 Hz) oscillations, and the 1/f slope and intercept for each participant (Kosciessa et al., 2020; Whitten et al., 2011). The eBOSC toolbox marked periods of the EEG as containing oscillatory rhythms if the rhythmic activity exceeded the power threshold provided by the algorithm's estimate of the power within the 1/f aperiodic background at each frequency, and if it was distinctly different from the 1/f activity (as demonstrated by showing a minimum number of oscillatory cycles) within the predetermined oscillatory frequency bands. The eBOSC algorithm estimates the 1/f aperiodic activity by computing a robust regression on the Morlet wavelet transform power-spectrum slope after excluding an individualized alpha peak from each participant to improve the regression fit. For the present study, rhythmic activity was defined as activity showing more than three cycles of the frequency of interest. Three cycles were specifically set as the threshold for this study, as transient oscillations between one and three cycles are likely to reflect a different physiological mechanism to stable (> 3 cycles) oscillations (Kosciessa et al., 2020). To obtain estimates of oscillatory power without the contribution of the 1/f non-oscillatory activity, we computed the power within specific frequency bands of interest during periods showing oscillations above the 1/f activity, as well as the power within the same frequency bands during periods that did not show oscillations above the 1/f activity. The mean power within the non-oscillatory periods reflects the 1/f non-oscillatory activity, so these values were subtracted from the power within the oscillatory periods to provide the estimate of oscillatory power without the contribution of the 1/f non-oscillatory activity. Within the eyes closed resting EEG recordings, 12 participants showed no periods without theta oscillations and 11 participants showed no EEG data periods without alpha oscillations. Since we required periods showing non-oscillatory activity to compute the oscillatory power after controlling for the influence of non-oscillatory activity, these participants were excluded from our analysis of theta and alpha power, as we were unable to determine the 1/f power for these participants. The mean peak frequency and percentages of the EEG trace showing oscillations for each frequency of interest were also computed by eBOSC. Further details of the eBOSC calculations and these analyses can be found in the Supplementary Information.

Data Analyses

For statistical comparisons of each primary measure, a whole scalp analysis was conducted using the Randomisation Graphical User Interface (RAGU) (Koenig et al., 2011). RAGU uses randomization statistics that are robust to the assumptions of parametric statistical tests, combined with the difference root mean square (dRMS) value. This dRMS value enables all electrodes to be included in statistical tests concurrently, and is implemented by subtracting the mean value at each electrode in one group from the mean value at each electrode in the other group, followed by the computation of the dRMS value across all electrodes for this difference. The dRMS value provides a measure of the strength of the topographical and global amplitude differences between the two groups, which can be compared to the dRMS value obtained by randomly shuffling participants between the groups and re-computing the dRMS value for the permuted data. In our study, we compared our real group differences to 5000 random shuffles, providing an estimate of the proportion of the null shuffled data that the size of the real group differences exceeded. This enabled computation of *p*-values and effect sizes for the between-group comparisons. RAGU allows for a combined test of potential differences in overall neural strength and distribution of activity using the topographic analysis of variance (TANOVA), which implements the aforementioned dRMS test. Separate TANOVAs were used to conduct repeated measures ANOVA design statistics examining 2 group (meditators vs non-meditators) × 2 condition (eyes closed vs eyes open) for theta, alpha, beta, and gamma oscillations after the removal of 1/f activity. These same tests were performed for the 1/f components slope and intercept. Further details regarding the application of RAGU can be found in the Supplementary Information.

To determine whether any significant differences might be due to differences in either global power or differences in the scalp distribution of activity independent of potential differences in global power, post hoc exploratory analyses were conducted using a root mean square (RMS) test (which tests for differences in global power by computing the RMS within each participant, in contrast to the dRMS between participants used by the TANOVA). Post hoc exploratory analyses were also conducted with an L2 normalised TANOVA (which tests for differences in the distribution of neural activity controlling for the influence of differences in global power, by normalising RMS values within each participant to 1 prior to computing the dRMS and conducting the TANOVA test). Partial eta squared (ηp^2) effect sizes were computed in RAGU for all comparisons of interest. Post hoc t-maps were also produced in RAGU for all measures of interest that demonstrated significant differences for each relevant TANOVA. These t-maps are equivalent to subtracting the control group data from the meditation group at every electrode. The t-maps indicate the *t*-values for differences at all electrodes, with the t-min value indicating where meditators showed smaller values than non-meditators, and the t-max value indicating where meditators showed larger (more positive) values than non-meditators.

Bayes factors (BF) were also calculated in JASP for all analyses (JASP Team, 2020). BF reflect the likelihood a model can be attributed to the alternative hypothesis over the null hypothesis or vice versa, with a BF10 of 3 indicating that the alternative hypothesis is three times as likely as the null hypothesis given the observed data, providing advantages over frequentist statistics which only provide a "significant or non-significant" result (Rouder et al., 2017). Interaction effects were also tested for (noted by BF_{incl}/BF_{excl} values), which are calculated by comparing models that contain the effect to equivalent models stripped of the effect. BF_{01} (and BF_{excl}) is reported for non-significant findings whilst BF_{10} (and BF_{incl}) is reported for significant findings. A priori power analyses were not conducted, as the sample was a convenience sample obtained by combining two planned studies, and an advantage of the use of Bayesian statistics is that they can give an indication of the confidence in null results even in the absence of a power analysis (Rouder et al., 2017).

Traditional frequentist statistical analyses were also conducted in R using the WRS2 package to implement robust statistics for mean peak frequency, RMS for all oscillations measured, and the 1/f components (Mair & Wilcox, 2020; R Core Team, 2020). For any variables which demonstrated violations in homogeneity of variance, the robust Yuen *t*-test was used instead of the independent samples *t*-test. The robust Yuen *t*-test provides an analogue of the traditional parametric independent samples *t*-test that is robust to parametric assumptions, by testing for the difference between trimmed means (Mair & Wilcox, 2020; R Core Team, 2020). As these analyses were exploratory, their full details are provided in the Supplementary Information.

In order to control for the likelihood of increased false positive results due to the number of hypothesis tests, the Benjamini and Hochberg method ("BH") was implemented across all primary comparisons by inserting the *p*-values from all primary tests into the mafdr function in MATLAB (with the "BHFDR" parameter set to "true"), and reporting the adjusted p-values for each of the primary tests (Benjamini & Hochberg, 1995). Primary statistical comparisons involved the main effect of group for the following variables: theta power without 1/f, alpha power without 1/f, beta power without 1/f, gamma power without 1/f, 1/f slope, and 1/f intercept. Adjusted p-values are specified in the results by BH-p, and uncorrected p-values are also reported to enable comparison with previous and future research. Many of the statistics we report require three decimal places to enable optimal understanding of the reported value, or differences between reported values for different analyses (for example, ηp^2 values). As such, we have reported three decimal places of precision as standard, with the exception of some values that are reported to fewer decimal places for brevity.

Results

Demographics and Self-reported Data

No differences were present between groups for any demographic variable (all $p > 0.10$ and $BF_{01} > 1.5$), with the exception of FFMQ scores ($t(90) = -6.35$, $p < 0.001$) and BDI-II scores. For BDI-II scores, robust testing (by the Yuen's t test) did not demonstrate a significant difference ($t(32.26) = 1.61$, $p = 0.116$, $BF_{10} = 2.20$) (Table 1).

Tests for Overall Differences in Oscillatory Power

Results from the TANOVAs without L2 normalisation demonstrated significant differences between meditators and non-meditators for the distribution or amplitude of activity in the theta, alpha, and gamma power bands (see Figs. 1, 2, and 3 and Table 2 for all results, all $p < 0.01$, all BH-$p < 0.015$).

There was a significant difference in the pattern of neural activity between groups for theta power ($p < 0.001$, BH-p $= 0.003$, $\eta p^2 = 0.139$). The t-map of meditator activity minus control activity for theta power was characterised by higher power in the meditator group across all electrodes, with a maximal difference at right posterior regions (t-max $= 4.575$ at PO6, t-min $= 0.648$ at C4) (Fig. 1a and b).

For alpha power, there was also a significant difference found between groups ($p = 0.006$, BH-p $= 0.014$, $\eta p^2 = 0.066$) which was indicated by slightly larger values for controls over right central regions (t-min $= -0.435$ at C4), but larger values for meditators over other regions, with a maximal difference over central posterior regions (t-max $= 5.367$ at PZ) (Fig. 2a and b).

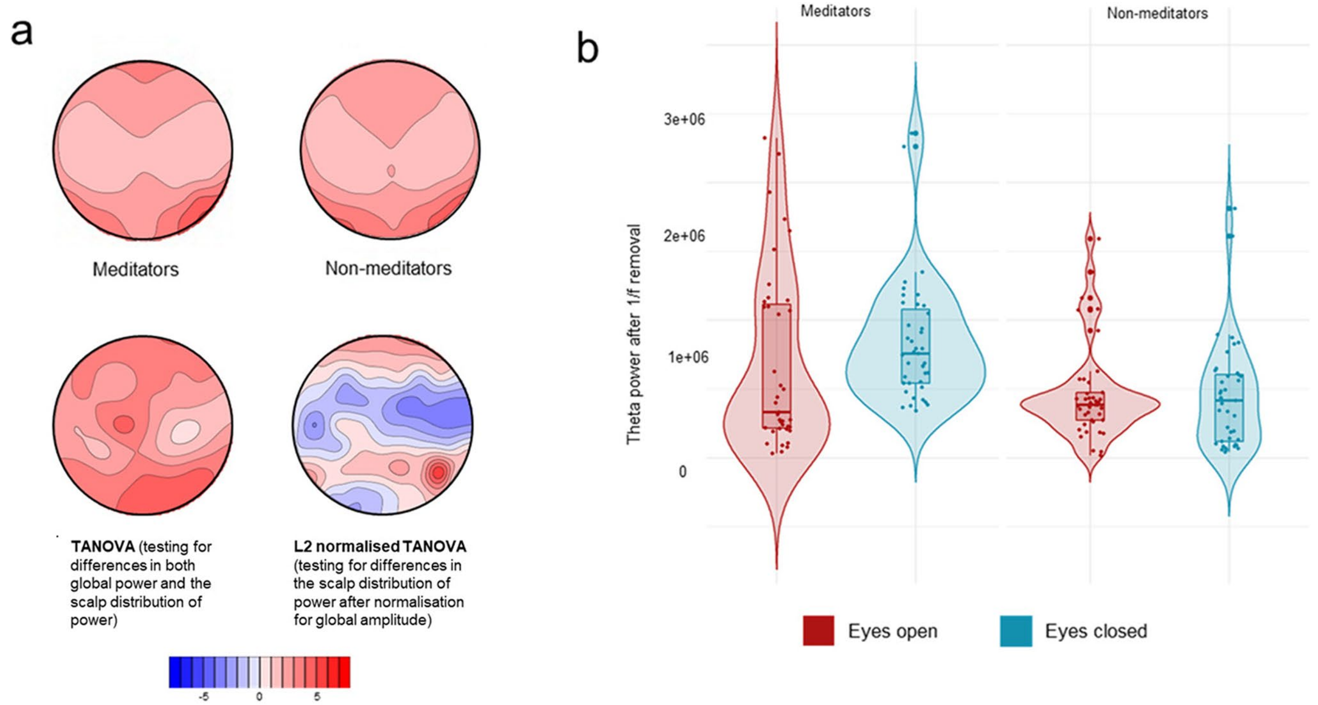
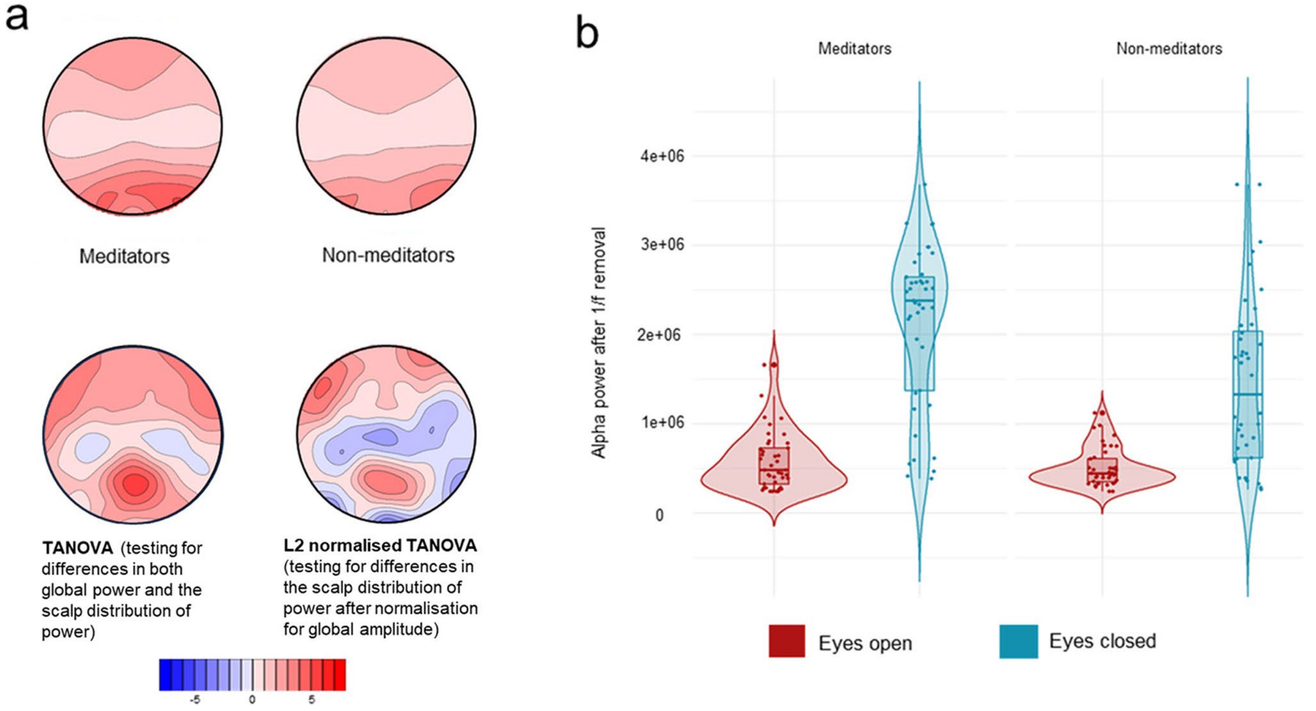


Fig. 1 Tests for overall effect for theta power. **a** TANOVA graphs demonstrating the distribution and amplitude effect of theta power for meditators, non-meditators, the main effect (TANOVA without L2 normalisation), and the post hoc t-test (TANOVA with L2 normalisation). The blue reflects subtraction of the non-meditator group data from the meditation group data (in red). **b** Violin plots demonstrating the distribution of values for the RMS analyses of theta power for both meditators (left) and non-meditators (right), with the eyes open condition depicted in red, and eyes closed condition in blue



TANOVA (testing for differences in both global power and the scalp distribution of power)

L2 normalised TANOVA (testing for differences in the scalp distribution of power after normalisation for global amplitude)

Fig. 2 Tests for overall effect for alpha power. **a** TANOVA graphs demonstrating the distribution and amplitude effect of alpha power for meditators, non-meditators, the main effect (TANOVA without L2 normalisation), and the post hoc *t*-test (TANOVA with L2 normalisation). The blue reflects subtraction of the non-meditator group data from the meditation group data (in red). **b** Violin plots demonstrating the distribution of values for the RMS analyses of alpha power for both meditators (left) and non-meditators (right), with the eyes open condition depicted in red, and eyes closed condition in blue

A significant difference in gamma power was also found between groups ($p < 0.001$, BH-p = 0.003, $\eta p^2 = 0.191$), and the t-map of meditator activity minus control activity was characterised by higher power values in meditators at all electrodes, with a maximal difference in middle anterior regions (t-max = 6.344 at F2, t-min = 2.912 at TP7) (Fig. 3a and b). However, no differences were found between groups for beta power, or the 1/f components slope and intercept (all $p > 0.05$, see Table 2), and no interactions between group and condition survived multiple comparison control (all BH-p > 0.05).

As expected, significant differences were also found between conditions (eyes closed vs eyes open) for most oscillatory frequencies and 1/f components, with larger values in the eyes closed condition for the majority of variables (see Table 2, Figs. 1, 2, and 3, and Supplementary Information). Previous evidence has demonstrated that differences in oscillatory power exist between eyes closed and open conditions whilst at rest, and as such was not of primary interest to the present study and will not be explored in detail (Kirschfeld, 2005; Kosciessa et al., 2020).

Exploratory Analyses

Further exploratory and post hoc tests were conducted to determine whether the significant results reported in our primary analyses reflected differences in the global power of the oscillation (RMS comparison) or differences in the distribution of activity across the head (reflecting a differential pattern of brain regions engaged — tested by the TANOVA with L2 normalisation).

To determine the level of support for the differences between groups in neural distribution (as demonstrated by the TANOVA with L2 normalisation), a follow-up factorial Bayesian ANOVA was conducted in JASP that included all electrodes. Prior to testing the interaction between group and electrode, the data was L2 normed and so the BF value for the interaction between group and electrodes reflects the equivalent of the normalised TANOVA (and therefore does not confound both global amplitude and distribution differences).

For theta power, both the RMS and TANOVA with L2 normalisation analyses were significant (see Tables 2, 3, and 4; all $p < 0.001$), indicating significant differences between groups in both global power and the distribution of activity across the scalp. The t-map of meditator activity minus control activity for theta power after L2 normalisation demonstrated positive values over right posterior regions (t-max 5.971 at P6, where the meditator group showed higher theta power values) and negative values over fronto-central regions (t-min − 3.541 at FC2, where the meditator group showed lower theta power values) (Fig. 1), reflecting the

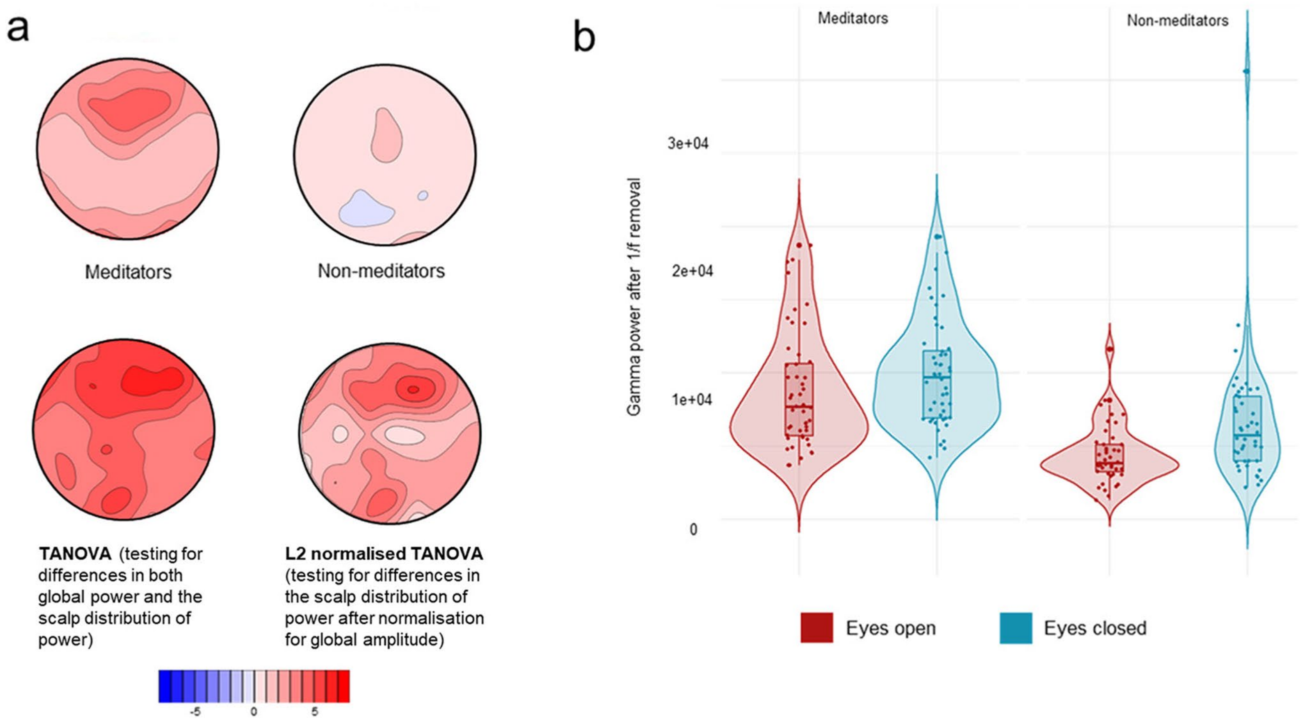


Fig. 3 Tests for overall effect for gamma power. **a** TANOVA graphs demonstrating the distribution and amplitude effect of gamma power for meditators, non-meditators, the main effect (TANOVA without L2 normalisation), and the post hoc *t*-test (TANOVA with L2 normalisation). The blue reflects subtraction of the non-meditator group data from the meditation group data (in red). Note that the blue patches in the non-meditator group indicate regions that show no gamma power above the 1/f activity. **b** Violin plots demonstrating the distribution of values for the RMS analyses of gamma power for both meditators (left) and non-meditators (right), with the eyes open condition depicted in red, and eyes closed condition in blue

same pattern as the TANOVA without L2 normalisation. The effect size for the difference in theta power RMS was large ($p < 0.001$, $\eta p^2 = 0.145$), indicating a large between-group difference in global power. The effect size for the RMS test was larger than the effect size of the TANOVA with L2 normalisation ($p < 0.001$, $\eta p^2 = 0.038$). These combined results demonstrate the primary effect is that meditators show not only a higher global theta power, but also a shifted distribution of activity with meditators showing more theta power in right posterior regions, and less theta power over fronto-central regions (with a smaller effect size). The meditators also showed more theta power over orbito-frontal regions, and less theta power over right frontal regions. These results complement and add to the findings from the non-normalised TANOVA and the RMS test, demonstrating that experienced meditators not only show globally higher power of their theta oscillations, but also suggest the engagement of a different pattern of brain regions generating theta activity. However, we caution against over-interpretation of the involvement of particular regions, as our statistical tests only indicate a group difference, and do not provide statistically significant results for specific electrodes. These results are further depicted in Fig. 1a, and in Table 2.

Similarly, for alpha power, both the RMS and TANOVA with L2 normalisation analyses were significant (Tables 2, 3, and 4; all $p < 0.05$). The t-map of meditator activity minus control activity for alpha power after L2 normalisation was characterised by positive values in left frontal regions (t-max 4.041 at F5, where the meditator group showed larger alpha power values) and negative values over posterior regions (t-min -3.318 at OZ, where the meditator group showed smaller alpha power values). Interestingly, these results indicate a different pattern within the topographical distribution of neural activity to the non-normalised TANOVA reported in our primary analysis, which was indicated by a maximal difference over central posterior regions (t-max 5.367 at PZ), and also indicated that meditators showed higher alpha power at all electrodes. Exploration of the L2 normalised TANOVA and RMS tests provided an explanation for this finding. Firstly, the between-group effect size for the RMS analyses was small to medium ($p = 0.029$, $\eta p^2 = 0.057$), showing higher global alpha power values in the meditator group, with a larger effect size than the TANOVA with L2 normalisation ($p < 0.001$, $\eta p^2 = 0.040$). This higher power of global alpha in the meditation group drove the finding of higher posterior alpha power in the meditator group within

Table 2 Statistical results for tests of overall effect for oscillatory power and 1/f components

Variable	Effect/interaction	TANOVA without L2 normalisation (testing for overall effect including both amplitude and distribution effects)	TANOVA with L2 normalisation (testing for distribution effects independent of overall amplitude differences)	*RMS statistics*
Theta power (a.u.)	Main effect	$p < 0.001$, BH-p = 0.003**, $\eta p^2 = 0.139$	$p < 0.001$, BFincl = 7.164e + 13, $\eta p^2 = 0.038$	$p < 0.001$, BFincl = 52.911, $\eta p^2 = 0.145$
	Condition	$p = 0.110$, BH-p = 0.198, $\eta p^2 = 0.029$	$p < 0.001$, $\eta p^2 = 0.045$	$p = 0.313$, BFexcl = 3.650, $\eta p^2 = 0.014$
	Interaction	$p = 0.071$, BH-p = 0.142, $\eta p^2 = 0.036$	$p < 0.001$, $\eta p^2 = 0.05$,	$p = 0.160$, BFexcl = 1.794, $\eta p^2 = 0.025$
Alpha power (a.u.)	Main effect	$p = 0.006$, BH-p = 0.014*, $\eta p^2 = 0.066$	$p < 0.001$, BFincl = 2.661e + 18, $\eta p^2 = 0.040$	$p = 0.029$, BFincl = 1.462, $\eta p^2 = 0.057$
	Condition	$p < 0.001$, BH-p = 0.003**, $\eta p^2 = 0.532$	$p < 0.001$, $\eta p^2 = 0.240$	$p < 0.001$, BFincl = 8.183e + 16, $\eta p^2 = 0.591$
	Interaction	$p = 0.122$, BH-p = 0.2, $\eta p^2 = 0.057$	$p = 0.131$, $\eta p^2 = 0.027$	$p = 0.203$, BFexcl = 0.679, $\eta p^2 = 0.048$
Beta power (a.u.)	Main effect	$p = 0.169$, BH-p = 0.254, $\eta p^2 = 0.030$	$p = 0.061$, $\eta p^2 = 0.026$	$p = 0.288$, BFexcl = 1.991, $\eta p^2 = 0.016$
	Condition	$p < 0.001$, BH-p = 0.003**, $\eta p^2 = 0.499$	$p < 0.001$, $\eta p^2 = 0.203$	$p < 0.001$, BFincl = 3.148e + 14, $\eta p^2 = 0.636$
	Interaction	$p = 0.389$, BH-p = 0.467, $\eta p^2 = 0.022$	$p = 0.062$, $\eta p^2 = 0.032$	$p = 0.947$, BFexcl = 4.212, $\eta p^2 < 0.001$
Gamma power (a.u.)	Main effect	$p < 0.001$, BH-p = 0.003**, $\eta p^2 = 0.191$	$p < 0.001$, BFincl = 2.034e + 25, $\eta p^2 = 0.087$	$p < 0.001$, BFincl = 77,313.447, $\eta p^2 = 0.258$
	Condition	$p = 0.004$, BH-p = 0.01*, $\eta p^2 = 0.052$	$p = 0.002$, $\eta p^2 = 0.042$	$p < 0.001$, BFincl = 4715.458, $\eta p^2 = 0.234$
	Interaction	$p = 0.231$, BH-p = 0.32, $\eta p^2 = 0.015$	$p = 0.033$, $\eta p^2 = 0.028$	$p = 0.136$, BFexcl = 1.033, $\eta p^2 = 0.031$
Slope	Main effect	$p = 0.61$, BH-p = 0.66, $\eta p^2 = 0.005$	$p = 0.09$, $\eta p^2 = 0.018$	$p = 0.684$, BFexcl = 2.453, $\eta p^2 = 0.002$
	Condition	$p < 0.001$, BH-p = 0.003**, $\eta p^2 = 0.393$	$p = 0.294$, $\eta p^2 = 0.013$	$p < 0.001$, BFincl = 6.326e + 15, $\eta p^2 = 0.585$
	Interaction	$p = 0.715$, BH-p = 0.715, $\eta p^2 = 0.008$	$p = 0.270$, $\eta p^2 = 0.013$	$p = 0.929$, BFexcl = 4.226, $\eta p^2 < 0.001$
Intercept	Main effect	$p = 0.378$, BH-p = 0.467, $\eta p^2 = 0.009$	$p = 0.046$, $\eta p^2 = 0.020$	$p = 0.415$, BFexcl = 1.816, $\eta p^2 = 0.007$
	Condition	$p < 0.001$, BH-p = 0.003**, $\eta p^2 = 0.643$	$p = 0.025$, $\eta p^2 = 0.022$	$p < 0.001$, BFincl = 3.142e + 24, $\eta p^2 = 0.736$
	Interaction	$p = 0.623$, BH-p = 0.66 $\eta p^2, = 0.010$	$p = 0.016$, $\eta p^2 = 0.023$	$p = 0.804$, BFexcl = 4.292, $\eta p^2 = 0.003$

Main effect compares meditators and non-meditators. Condition compares eyes closed vs eyes open conditions. Interaction compares the group (meditators and non-meditators) and condition (eyes closed and eyes open). ηp^2, partial eta squared; *a.u.*, arbitrary units resulting from Morlet wavelet transform measures of power after the subtraction of the eBOSC modelled 1/f non-oscillatory activity. Adjusted *p*-values are specified by BH-p, and uncorrected *p*-values are also reported. *BF*, Bayes factors. $BF_{01} > 1$ favours the model of the null hypothesis. BF_{01} (BFexcl) is reported for non-significant findings whilst BF_{10} (BFincl) is reported for significant findings. For the TANOVA with L2 normalisation, the BFincl value reflects a test of the interaction between Group and Electrode. *RMS*, root mean square. All significance levels (α) set at 0.05. *$p < 0.05$. **$p < 0.01$. ***$p < 0.001$

our primary non-normalised TANOVA, where alpha power values across all electrodes (including the posterior electrodes) were higher in the meditation group. However, the normalized TANOVA demonstrated that the distribution of alpha power also differed between the groups, after controlling for global amplitude. Within the meditator group, higher levels of frontal alpha power were present relative to overall alpha power compared to the non-meditator group. As such, when the global power differences were normalised (controlled for) and compared with the L2 normalised TANOVA, such that alpha power values over each brain region were tested relative to global alpha power within the individual, relative posterior alpha power in meditators was lower than the control group's relative posterior alpha power.

Table 3 Statistical results for the RMS analyses of theta, alpha, and gamma power

RMS analyses of theta, alpha, and gamma power

	Condition	Meditators Mdn (MAD)	Non-meditators Mdn (MAD)	Statistics
Theta power (a.u)	Eyes closed	755,755.3 (357,971.1)	416,944.7 (345,125.5)	$p < 0.001$, BFincl = 52.911, $\eta p^2 = 0.145$
	Eyes open	333,974.4 (344,038.9)	387,094.6 (167,288.2)	
Alpha power (a.u)	Eyes closed	2,380,160.7 (641,271.7)	1,332,889.2 (1,062,783.4)	$p = 0.029$, BFincl = 1.462, $\eta p^2 = 0.057$
	Eyes open	483,201.4 (298,702.5)	445,314.1 (157,038.5)	
Gamma power (a.u)	Eyes closed	9701.58 (3664.48)	5718.17 (2916.30)	$p < 0.001$, BFincl = 77,313.447, $\eta p^2 = 0.258$
	Eyes open	7667.52 (3123.46)	3817.31 (1294.39)	

RMS analyses are a measure of amplitude. *ηp²*, partial eta squared; *BF*, Bayes factors. $BF_{01} > 1$ favours the model of the null hypothesis. BF_{01} (BFexcl) is reported for non-significant findings whilst BF_{10} (BFincl) is reported for significant findings. Median and MAD were obtained from analyses conducted in R. All significance levels (α) set at 0.05. $^{*}p < 0.05$. $^{**}p < 0.01$. $^{***}p < 0.001$. *a.u*, arbitrary units resulting from Morlet wavelet transform measures of power after the subtraction of the eBOSC modelled 1/f non-oscillatory activity. *RMS*, root mean square; *MAD*, median absolute deviation; *Mdn*, median

Table 4 Statistical results for the TANOVA with L2 normalisation of theta, alpha, and gamma power

TANOVA with L2 normalisation of theta, alpha, and gamma power

	t-max	t-min	Statistics
Theta power (a.u)	5.971 at P6	−3.541 at FC2	$p < 0.001^{***}$, BFincl = 7.164e + 13, $\eta p^2 = 0.038$
Alpha power (a.u)	4.041 at F5	−3.318 at OZ	$p < 0.001^{***}$, BFincl = 2.661e + 18, $\eta p^2 = 0.040$
Gamma power (a.u)	6.076 at F2	0.531 at CZ	$p < 0.001^{***}$, BFincl = 2.034e + 25, $\eta p^2 = 0.087$

TANOVA with L2 normalisation is an overall measure of the distribution of neural activity. T-min values indicate where meditators showed more negative values than non-meditators, and the t-max values indicate where meditators showed more positive values than non-meditators. *ηp²*, partial eta squared; *BF*, Bayes factors. $BF_{01} > 1$ favours the model of the null hypothesis. BF_{01} (BFexcl) is reported for non-significant findings whilst BF_{10} (BFincl) is reported for significant findings. BFincl for oscillatory power has been produced by L2 normalisation of the data prior to testing the interaction between group and electrode in JASP, and the BF value for this interaction between group and electrodes reflects the equivalent of the normalised TANOVA. All significance levels (α) set at 0.05. $^{*}p < 0.05$. $^{**}p < 0.01$. $^{***}p < 0.001$. *a.u*, arbitrary units resulting from Morlet wavelet transform measures of power after the subtraction of the eBOSC modelled 1/f non-oscillatory activity

As such, the results of the L2 normalised TANOVA suggest the meditator group demonstrated an altered distribution of alpha power, with more frontal alpha produced relative to central and posterior alpha power in comparison to the control group (which showed a larger bias towards higher power in posterior regions), in addition to the increase in global alpha power, in the meditation group. Having noted these details, it is worth mentioning that the meditation group still showed higher normalized alpha power over central parietal regions. Additionally, as per our theta results, we caution against over-interpretation of the involvement of particular regions, as our statistical tests only indicate a group difference, and do not provide statistically significant results for specific electrodes. These results are depicted in Fig. 2a, and in Table 2.

For gamma power, both the RMS and TANOVA with L2 normalisation analyses were significant (Tables 2, 3, and 4; all $p < 0.001$). The t-map of meditator activity minus control activity for gamma power after L2 normalisation demonstrated positive values over fronto-central regions (t-max 6.076 at F2, where the meditator group showed higher gamma power) and negative values over central regions (t-min 0.531 at CZ, where the meditator group showed lower gamma power values) (Fig. 3), reflecting the same pattern as our primary analysis of the TANOVA without L2 normalisation. A medium to large effect size was found for RMS analysis of gamma power ($p < 0.001$, $\eta p^2 = 0.258$), which tested for global differences in gamma power. This effect size for the RMS test was larger than the effect size of the TANOVA with L2 normalisation ($p < 0.001$, $\eta p^2 = 0.087$). The combined results from the non-normalised and normalised TANOVA suggest that meditators demonstrate overall higher gamma power in combination with a shifted distribution of gamma activity, with meditators showing more gamma in frontal regions relative to their global gamma power. These results are depicted in Fig. 3a, and in Table 2.

In the present study, there was also a significant main effect found for the percentage of EEG trace showing theta oscillations, with meditators demonstrating a greater percentage of the EEG trace showing oscillations within the theta frequency compared to non-meditators (value = 5.11, $p = 0.026$). These results are explored further in the Supplementary Information.

Discussion

The present study aimed to determine if MM is associated with differences in resting-state EEG oscillatory power after controlling for 1/f activity, and whether MM is associated with differences in the slope and intercept of 1/f non-oscillatory EEG activity.

Meditators demonstrated significantly higher oscillatory power than non-meditators for theta, alpha, and gamma oscillations. The differences were driven by differences in both the distribution of activity across brain regions and variations in the global strength of these oscillations. In particular, meditators demonstrated higher theta power as well as a shifted distribution of theta activity, with meditators demonstrating higher theta power in posterior regions relative to their global theta power. For alpha power, the meditator group demonstrated an altered distribution of activity, with higher alpha power over frontal regions (relative to the global alpha power), as well as higher global alpha power. Meditators also demonstrated an overall higher gamma power, as well as a shifted distribution of gamma power, with meditators showing higher gamma power in frontal regions relative to their global gamma power.

In line with these findings, Bayesian analyses demonstrate strong support for the alternative hypothesis for group differences in both the global power and distribution of theta, alpha, and gamma power. No interaction effects were observed between groups and eyes-open vs eyes-closed EEG conditions, indicating that the effects of MM were present and consistent regardless of whether participants had their eyes open or closed. No differences were found between meditators and non-meditators for the 1/f components slope and intercept, or for beta oscillatory activity.

The results of the present study suggest that MM is associated with differences in oscillatory neural activity within specific frequency bands, and the use of resting-state EEG data indicates that these differences reflect trait differences, rather than simply meditation state-related differences. Furthermore, given that theta, alpha, and gamma are associated with specific cognitive functions, with larger power values typically being related to enhanced cognitive performance, the higher oscillatory power or altered distribution of oscillatory neural activity (as measured by EEG) may be one mechanism through which MM leads to benefits in cognition, attention, and general well-being.

Meditators demonstrated greater global theta power in comparison to non-meditators. These results mostly align with previous findings that found an association between increased theta power and meditation (Aftanas & Golocheikine, 2002; Cahn & Polich, 2006; Dunn et al., 1999; Howells et al., 2012; Lagopoulos et al., 2009; Lomas et al., 2015; Tanaka et al., 2014). In particular, the findings of the present study are consistent with findings reported by Wong et al. (2015), whereby practiced meditators demonstrated higher theta power whilst at rest when compared to non-meditators. Importantly, the present study indicates that differences in theta activity remain significant after accounting for the potentially confounding effects of 1/f activity. These findings are of particular interest, as 1/f activity is most prominent for lower frequency ranges and thus more likely to influence the measurement of theta oscillations than other frequencies (Voytek & Knight, 2015). Additionally, given the association between theta and attentional processes (see Klimesch et al., 2005; Sauseng et al., 2010), greater theta power may be one way through which MM leads to improvements in attention and general cognitive functioning.

For alpha power, the significant differences between meditators and non-meditators were driven by differences both in the distribution of neural activity and in global alpha power. More specifically, the topographical distribution differences were characterised by higher frontal alpha power in the meditator group (relative to global alpha power), suggesting frontal regions generated relatively greater alpha activity in meditators, in comparison to the primarily posterior alpha distribution in non-meditators. In contrast to this result, previous research has demonstrated greater alpha power in mindfulness meditators that is specific to posterior regions (Lagopoulos et al., 2009), both when comparing to a concentrative meditation practice, and separately to a relaxation condition (Dunn et al., 1999). However, this previous research did not account for the contribution of 1/f activity to measurements of alpha power, and implemented single-electrode analyses which are unable to differentiate between differences in global alpha power and differences in the distribution of alpha power across the scalp. With regard to the interpretation of our alpha power results, broadly, alpha activity is thought to reflect attentional related changes, the processing of irrelevant/distracting information, and the active inhibition of processing within specific brain regions (Foxe & Snyder, 2011; Rihs et al., 2009; Wang et al., 2020). Although speculative, it may be that non-meditators only inhibit posterior (visual processing related) regions whilst at rest, but continue to process memories and thoughts, and engage other attentional mechanisms, generating activity in frontal regions. Alternatively, as meditation involves focused training in attending to the sensations of the present moment, meditators may engage inhibitory mechanisms within their frontal regions, as during rest there are limited changes in sensory experience to process, and as such, the processing of non-sensory experience (for example, memories, thoughts, and attentional processes) may be reduced for practiced meditators in comparison to non-meditators.

In line with previous studies investigating gamma activity (both at rest and during tasks or meditation), the present study demonstrated that meditation experience is associated with enhanced resting gamma power (Berkovich-Ohana et al., 2011; Braboszcz et al., 2017; Hauswald et al., 2015; Lutz et al., 2004). Gamma activity is linked to cognitive and attentional functions, with higher gamma power correlating with enhanced perceptual clarity (Kambara et al., 2017; Lee et al., 2018; Pritchett et al., 2015). There is also evidence implicating gamma activity in the role of neuroplastic changes via repetition, suggesting that increases in gamma power are positively correlated with practice (Lee et al., 2018). Greater gamma power and an altered distribution of gamma activity in the meditation group may therefore reflect a neurophysiological mechanism through which MM leads to benefits associated with cognition, attention, and well-being, potentially reflecting the product of prolonged training of attentional processes — through a MM practice.

There is some evidence that beta power increases during active meditation as compared to when at rest (Dunn et al., 1999; Faber et al., 2015). In contrast, the current study reflects the first examination of beta power during resting EEG in long-term meditators as compared to a meditation-naïve group. The absence of group differences in beta power is of particular importance as it indicates that meditation was not simply associated with an overall increase in oscillatory power, but rather a selective increase in oscillatory power within certain frequency ranges. Additionally, most past research examining beta activity has not compared a meditation-naïve group compared with more well-practiced meditators, and instead performed comparisons between resting-state EEG and EEG recorded during active meditation practice. Nonetheless, these methods only allow examination of the electrophysiological changes associated with the practice of meditation (i.e. state-dependent changes in oscillatory activity). In contrast, by comparing resting-state EEG between experienced meditators and those without a history of meditation, the current study provides valuable information regarding persistent electrophysiological changes associated with long-term meditation practice (i.e. trait-dependent changes in oscillatory activity). As general functions of beta activity include alertness, attentional arousal, and anticipatory attentional processing (Kamiński et al., 2012), it is also possible that differences between groups in these functions are found only in a state-related context, rather than during resting-state EEG (as measured by the present study). Given the limited evidence exploring beta activity and mindfulness meditators at rest, further research is needed to consolidate the findings of the present study.

Overall, these accumulative findings regarding oscillatory activity provide strong evidence that long-term meditators display specific alterations in the distribution and amplitude of theta, alpha, and gamma oscillations. Whilst extensive research has focused on exploring oscillatory dynamics which underlie the meditative state, the present study demonstrates that long-term MM practice is associated with persistent changes in resting-state oscillatory activity, thereby signifying a potential neurophysiological mechanism for the long-lasting trait changes in attention and cognitive processes associated with meditation practice. As such, the current study provides a critical contribution to our understanding of the neural mechanisms related to mindfulness meditation. In addition, rather than just an overall difference in the strength of oscillations, the present study highlights that differences in the topographical distribution of activity (reflecting altered engagement of brain regions) for these oscillations drive these results, indicating that meditation may lead to differential engagement of neural activity.

The differences observed in the topographical distribution of oscillations and/or amplitude of different oscillatory patterns may be a result of the modulation of neural activity by meditators, dependent on the requirements at hand. Modulation of neural signals contributes to healthy cognition (Armbruster-Genç et al., 2016) by helping us adapt in times of uncertainty (Kosciessa et al., 2021), and adapt to our environment (Kloosterman et al., 2020). Previous research has demonstrated that experienced meditators display a greater ability for the modulation of oscillations, specifically for theta and alpha bands (Tanaka et al., 2014; Wang et al., 2020). Wang et al. (2020) found meditators demonstrated a greater ability to modulate alpha distribution between low-task demands and high-task demands — which may require more neural resources. In line with these past findings, the present study may not necessarily reflect that meditation consistently results in larger oscillatory power across theta, alpha, gamma, and beta power. It may be that meditators are able to modulate neural activity with either increases or decreases in favour of task-relevant processing regions, leading to a larger range for modulation, and a MM-related increase in one's ability to respond to their environment. Changes that result from meditation may therefore reflect enhancement not of one specific neural process, but of the modulation of a range of oscillatory activity which support cognitive, emotional, or attentional processing. However, we note that that our recent "highly comparative" analysis that assessed a massive number of statistical properties of the EEG time series showed that features related to the stationarity of the EEG data (the consistency of statistical properties across different periods within the EEG data) provided more successful classification of meditators than oscillatory measures (Bailey et al., 2024). Band power measures assessed in that study did not account for 1/f activity, and only assessed band power within the top eight principal components of the EEG data, and within a small number of single electrodes. As such, the current study more comprehensively characterises differences in oscillatory activity between meditators and non-meditators (Bailey et al., 2024).

Our findings may provide further insight when viewed within the conceptual framework of the free energy principle (FEP). The FEP suggests that the brain maximises efficiency through proactive and anticipatory modelling of its environment, and thereby minimises “free-energy” arising from prediction errors and the likelihood of “surprise” (Friston, 2013). Through construction of hierarchical predictive models that have been selected through processes analogous to Bayesian probabilistic reasoning (e.g. based on model fit and prior beliefs), the brain (and nervous system) functions by minimizing prediction error (the mismatch between its prior model and incoming sensory information). Within this free-energy minimization framework, models constructed by the brain can be updated to better fit the world (perceptual inference) or update the world (through motor control of the body’s musculature) to better fit the brain’s prior model (active inference). We propose two theoretical perspectives for how mindfulness may affect parameters of the predictive coding framework that align with our results. Firstly, the increase in theta and gamma power shown in our results might reflect “fact-free learning”. Fact-free learning has been suggested to occur in the brain, whereby the brain constructs better models that have greater explanatory power through iterative adjustments of existing priors, without additional sensory information (priors) or active inference (taking action to ensure sensory information aligns with the brain’s model) (Friston et al., 2017). Secondly, meditators might show a reduction in counterfactual processing, which may align with the shift towards alpha power with a more frontal distribution in meditators, where counterfactual processing taking place in the higher regions of the predictive coding hierarchy (reflected by the frontal regions) might be inhibited. “Counterfactual” processing refers to the modelling (or internal simulation) of sensory states that an individual may observe if they were to perform or participate in actions under a particular set of model parameters (e.g. possible outcomes) (Corcoran et al., 2020). This allows for the evaluation of the expected prediction error (free energy) from a variety of actions under alternative contexts before making a decision and taking action. Laukkonen and Slagter (2021) suggest that meditation may reduce “counterfactual” temporally deep cognition and reduce predictive abstraction through being in the “here and now”, leading to greater flexibility in daily life. We note that these two explanations could be seen as conflicting, and furthermore that the finding of increased theta and gamma power concurrent with increased alpha power (which is thought to reflect an inhibition of activity within a brain region) might also be seen to be a conflicting finding. Further research is required to determine the functional relevance and the physiological explanation of these findings.

Previous research has suggested that differences in the 1/f slope may reflect differences in the E/I balance in the brain (Donoghue et al., 2020; Voytek & Knight, 2015). In relation to meditation, one study has reported differences between meditators and novices in the 1/f slope, with experienced meditators demonstrating a more negative (steeper) slope during meditation relative to rest, and novice meditators presenting the opposite pattern — a flatter slope during meditation relative to rest (Rodriguez-Larios et al., 2021). Rodriguez-Larios et al. (2021) have suggested these findings may be due to the fact that novices found the meditation condition more cognitively demanding than rest (leading to a flatter slope and a higher E/I ratio), whilst the opposite was true for more experienced meditators (leading to a steeper 1/f slope and lower E/I ratio).

Contrary to our hypotheses and prior research, no differences were found between meditators and non-meditators for 1/f slope or intercept in the present study. This result suggests that whilst differences in oscillatory activity are present, meditation is not associated with differences in neural activity produced by altered E/I balances related to neuroplastic change (primarily modulated by GABAergic and glutamatergic neurotransmitters). These findings are particularly interesting given that 1/f activity has also been found to be functionally relevant for perceptual processing (such as perceptual decision-making) and visuomotor performance (Immink et al., 2021), and may also be more reflective of cognitive performance in comparison to the measure of oscillatory activity (Peterson et al., 2023). The null findings and large BF01 values of the present study indicate that differences in the E/I balance of the brain at rest are unlikely to be related to long-term meditation practice, and may not be the explanatory mechanism for improved attention, mental health, and well-being from MM. It is worth noting however, that because our study focused on healthy participants, the current results cannot rule out the possibility that meditation may lead to improvements in E/I balances found in clinical populations where E/I balances may be atypical prior to a meditation intervention (Peterson et al., 2023). Rather, it may be that the E/I balance is not altered by meditation when it is already functioning adequately in healthy controls. In addition, this null finding also provides important validation for previous studies demonstrating that MM is associated with differences in oscillatory power. Given that 1/f activity can significantly influence the measurement of oscillatory power if not properly controlled, we can be confident that the observed differences in theta, alpha, and gamma power in the present study do indeed reflect changes in long-term MM rather than simply reflecting 1/f changes.

Limitations and Future Directions

Although significant differences were found between meditators and non-meditators for theta, alpha, and gamma activity, the findings of the present study were cross-sectional; and therefore, causal relationships cannot be established. Additionally, while the meditator and non-meditator groups in the current study were matched on key demographic variables which may influence oscillatory activity (such as age and gender), it is also possible that individuals who practice meditation have different lifestyle habits or participate in other activities not accounted for that may influence changes in neural activity (e.g. diet, exercise or physical activity, sleep quality, and substance use; see Cramer et al., 2017). Future research could control for this by exploring what other lifestyle habits participants may be involved in and performing between-/within-group comparisons to determine if significant differences are present. Future research would also benefit from testing causal relationships through longitudinal studies which would include an active control condition or sham meditation condition to provide strong conclusions about the causal role of meditation in the observed effects. However, we note that these studies are exceedingly difficult to achieve in practice given the "long-term" nature of meditation practice, which included a minimum of 6 months of meditation practice in the current study.

Additionally, our results may be specific to the conditions of the present study, which recruited healthy participants across a broad age range, and who practiced MM (with recruitment not constrained to specific sub-types of a MM practice, i.e. MM practice included both focused attention and open monitoring meditation practices). Further research should be conducted to explore whether these trait changes are consistent with different populations, such as different age groups, varying levels of experience, or different meditation practices. In particular, it may be interesting for future research to explore potential differences between open monitoring and focused attention meditation practices.

As meditation practices are a subjective endeavour, the number of hours an individual has invested in meditation may not necessarily equate to how advanced someone is in their practice. The inclusion criteria of our study required experienced meditators to have a minimum of 6 months of consistent practice — however, one meditator had 48 years of experience. Even though the number of years individuals practice for may be considered a subjective account for being an experienced meditator, certain benefits may be associated with the length of time spent meditating. Our study did confirm that the groups differed significantly in trait mindfulness as measured by the FFMQ, which was expected given that this measure may be influenced by previous meditation experience (Pang & Ruch, 2019). To further explore this issue, future research would benefit from recruiting participants specifically from distinct categories of experience (for example, novice, somewhat experienced, and very experienced meditators), or a larger sample size that could provide sufficient statistical power to robustly assess correlations between experience and oscillatory power.

In addition, a potential limitation was that participants completed a cognitive task prior to the recording of their resting EEG. Previous research has demonstrated that recent motor tasks can alter resting functional connectivity, so it is possible the cognitive task may have influenced their neural activity (Sami et al., 2014; Tung et al., 2013). However, because the meditation and non-meditation groups were matched in terms of the completion of cognitive tasks prior to the resting recordings, the neural activity of both groups would have been influenced in the same manner by the cognitive task. As such, while the completion of the cognitive task prior to the resting recordings may have influenced the neural activity we measured, it does not reflect a confound to our results.

A further potential limitation of the current research is that it focused solely on measuring neural oscillations from experienced meditators. Future research might benefit from combining multimodal imaging techniques as well as behavioural measures of cognition to provide a holistic understanding of the effects of mindfulness meditation, including how differences in neural oscillations might affect well-being and cognitive performance. Future research might also benefit from undertaking source localization analyses (guided by magnetic resonance imaging scans to provide high-accuracy results) and examining measures of functional connectivity between brain regions to further elucidate potential neural mechanisms underlying the effects of mindfulness meditation. However, we note that this is beyond the scope of the present study.

Finally, whilst participants were under explicit instruction to refrain from meditating during the resting EEG recordings, and to rest without any deliberate control over their mental contents, we cannot verify that they followed this instruction and were not meditating. Even if participants were following these instructions, it may be that a meditative state of mind is a long-term meditator's typical baseline resting state, which presents the possibility that different mental states were measured between the two groups. Nonetheless, whilst this may be a critique of the current study, we note that it is a limitation that is impossible to address, since beyond a participant's self-report, there is no way to verify whether a participant is in the state of rest or meditation. Additionally, even if the meditator's baseline resting state is more similar to a meditative state than a typical non-meditator's resting state, we propose that our results are still informative about neural oscillations in long-term meditators during "resting" periods, as this limitation indirectly suggests that a meditator's resting state throughout the day contains brain activity that is more similar to the meditative state. Moreover, one of the primary motivations for adopting a MM practice is that beneficial physical and psychological effects persist outside of meditation practice itself, hence the need for studies examining the neural correlates of MM in a resting state reflected by the present study.

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Author Contribution Brittany McQueen: investigation, methodology, formal analysis, writing — original draft. Oscar W Murphy: supervision, writing — review and editing. Paul B Fitzgerald: supervision, writing — review and editing, resources. Neil W Bailey: conceptualization, methodology, investigation, writing — review and editing, supervision, software, formal analysis, data curation, project administration, resources.

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Data Availability Data included in this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of Interest In the last 3 years, PBF has received equipment for research from Neurosoft, Nexstim, and Brainsway Ltd. He has served on scientific advisory boards for Magstim and LivaNova and received speaker fees from Otsuka. He has also acted as a founder and board member for TMS Clinics Australia and Resonance Therapeutics. PBF is supported by a National Health and Medical Research Council of Australia Investigator grant (1193596). The other authors declare that they have no conflicts of interest.

Ethics Approval Ethics approval was provided by the Ethics Committees of Monash University and Alfred Hospital. All participants provided written informed consent prior to participation in the study.

Use of Artificial Intelligence Artificial intelligence was not used for any aspect of this study.

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