

Distinct patterns of directed brain connectivity in focused attention, open monitoring and loving kindness meditation: An EEG Granger causality study with long-term meditators

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Abstract

The present study applied spectral Granger causality analysis to electroencephalographic (EEG) recordings obtained during Focused Attention Meditation (FAM), Open Monitoring Meditation (OMM), and Loving Kindness Meditation (LKM) in highly experienced meditators. The aim of the investigation was to characterize distinct connectivity signatures associated with each meditation style by examining the strength, frequency, and direction of inter-regional interactions. These differences were expected to specify the neural connectivity profiles of the cognitive and affective state of each meditative practice.

Multivariate Granger causality (GC) was computed from high-resolution EEG signals recorded from long-term meditators ($n = 22$) in four conditions: rest, FAM, OMM, and LKM. GC was analyzed in the frequency domain for key electrode clusters (anterior and posterior) in the two hemispheres to compare frequency-specific directed connectivity between rest and each meditation type.

Main results demonstrated that each meditation state produced highly specific alterations in directed influences relative to rest. In FAM, there was significant reduction in posterior-to-anterior GC in the alpha and beta bands, and decreased multi-spectral inter-hemispheric frontal GC implying attenuated bottom-up sensory and associative inputs. In OMM, multi-spectral GC was significantly increased from the left hemisphere to the right posterior cluster implying expanded awareness in the right posterior regions through enhanced top-down modulation by the left-hemisphere. The distinctive features of LKM profile were the inter-hemispheric symmetry, the posterior-anterior bi-directionality, and the specific beta-band engagement, implying a co-activation of systems that support an emotionally balanced stance, equanimity and pro-social attitude.

These novel findings demonstrate that the direction and frequency specificity of information flows provide complementary insights into neural processes underlying distinct meditative states.

Key words: EEG, Granger causality, directed connectivity, long-term meditation, brain states, meditation types, FAM, OMM, LKM

INTRODUCTION

Contemporary neuroscience increasingly recognizes that meditation does not modulate isolated brain regions in a uniform manner but rather orchestrates dynamic interactions within and between large-scale brain networks. Among these, the Default Mode Network (DMN), fronto-parietal control networks, attentional networks, and salience network (Uddin et al., 2019) involved in self-referential processing, attentional control, and emotion regulation are recognized as critical in meditation (Mantini et al., 2007; Berkovich-Ohana et al., 2014; Panda et al., 2016; Lomas et al., 2015; Shen et al., 2020). Meditative states represent a particular class of non-ordinary (contemplative) brain states (Raffone et al., 2019; Panda et al., 2016, 2023; Kumar et al., 2024) that may require a unique functional architecture across networks (Yordanova et al., 2020). However, since different meditative practices emphasize distinct cognitive and affective processes such as sustained attention, meta-awareness, emotional regulation, and prosocial affect (Cahn and Polich, 2006; Lutz et al., 2008; Malinowski, 2013; Raffone et al., 2019), they also may involve dissociable frequency-specific neural circuits (Fox et al., 2014, 2016).

In *Focused Attention Meditation* (FAM), practitioners actively sustain attention on a chosen object while inhibiting distractions. This practice has been associated with increased connectivity within the frontoparietal control network and dorsal attention network, supporting top-down attentional regulation and cognitive control (Tang et al., 2015; Fox et al., 2016). Electroencephalographic (EEG) studies have shown elevated frontal midline theta and beta coherence, especially between frontal and parietal regions, related to enhanced executive processing and sustained attentional effort (Cahn et al., 2010; Lomas et al., 2015; Yordanova et al., 2021).

In contrast, *Open Monitoring Meditation* (OMM) cultivates non-reactive awareness of moment-to-moment experience without focusing on a particular object. This style has been linked to more distributed and flexible brain dynamics, including decreased coupling between the striatum and posterior DMN regions such as the posterior cingulate cortex, in line with the diminished self-referential processing and increased cognitive flexibility (Lutz et al., 2008; Brewer & Garrison, 2014). EEG and MEG studies report increased gamma-band synchrony in right fronto-parietal networks during OMM, reflecting heightened sensory awareness and adaptive monitoring (Lutz et al., 2004).

Loving-Kindness Meditation (LKM) focuses on cultivating prosocial emotions like compassion and empathy and has been shown to increase connectivity between medial prefrontal and inferior frontal cortices, as well as posterior DMN hubs (Garrison et al., 2014; Mascaro et al., 2013). Long-term LKM practice is also associated with enhanced integration across the DMN, salience, and social cognition networks, in line with the emotional and interpersonal dimensions of this practice (Valk et al., 2017).

While these findings have implicated the involvement of specific neural circuits during different meditative states, less is known about the directionality and frequency-specificity of directed interactions. Most neuroimaging and electrophysiological studies to date have relied on measures of undirected functional connectivity (e.g., correlation, coherence), which reflect synchronous inter-regional co-activations. Effective connectivity approaches - such as Granger causality (GC) - allow inferences about the directionality of influence among neural sources (Barnett & Seth, 2014; Friston et al., 2013; Seth et al., 2015). They may provide insight into how top-down (e.g., prefrontal-to-sensory) or bottom-up (e.g., sensory-to-frontal) interactions are modulated by meditative state. This is particularly important given that

distinct meditation styles may rely differentially on anticipatory control versus receptive awareness. Moreover, directed neural communication may be spectrally structured depending on the functional engagement. Extensive previous research has reported associations between frequency-specific oscillations (theta, alpha, beta) and cognitive functions such as memory, external and internal attention, monitoring and cognitive control (Klimesch, 1999; Engel & Fries, 2010; Cavanagh & Frank, 2014; Palva & Palva, 2007; 2012; Daitch et al., 2013; Cohen, 2011; Duprez et al., 2020). Empirical studies also suggest that posterior-to-anterior signalling predominates in the alpha–beta range, whereas anterior-to-posterior signalling is typically carried by theta and alpha rhythms (Hillebrand et al., 2016; Wang et al., 2019). Therefore, the frequency content of directed interactions may contribute to specifying the neuro-functional profile of meditative states.

The present study aims to characterize directed connectivity patterns associated with different meditative states. For that aim spectral Granger causality analysis was applied to high-density EEG recordings obtained during FAM, OMM, and LKM in highly experienced meditators. We hypothesize that each meditation style will exhibit a distinct pattern of large-scale profiles characterized by specific directional pathways and dominant frequency bands. These differences are expected to reflect the cognitive and affective emphasis of each meditative practice. From the perspective of large-scale networks functionality, FAM can be expected to enhance anterior→posterior directed connectivity mainly in theta and low-alpha bands, in relation to active top-down control from frontal to sensory and associative cortices, accompanied by reduced posterior→anterior GC in alpha/beta, reflecting strengthened sensory gating (Cavanagh & Frank, 2014; Jensen & Mazaheri, 2010; Sadaghiani & Kleinschmidt, 2016). OMM may increase posterior→anterior directed connectivity across a wider spectral bandwidth (theta–alpha–beta), a pattern where information from multiple sensory/interoceptive/associative sources contributes to flexible open monitoring in frontal integrative regions (Rao et al., 2018; Hillebrand et al., 2016). LKM, on the other hand, may promote distributed cross-regional interactions in accordance with a balanced integration of top-down emotional regulation and bottom-up affective resonance (Klimecki et al., 2014; Lutz et al., 2008; Singer & Klimecki, 2014). It is important to note that such mechanistic predictions based on established network functionality can be violated by (1) neuroplastic alterations of large-scale networks in expert meditators (Shen et al., 2020; Fox et al., 2016; Tang et al., 2015), and (2) the complexity of neurophysiological processes that affect spectral GC measures, as outlined below.

Granger causality quantifies the degree to which past activity in one signal improves the prediction of future activity in another, thereby capturing the directionality of interactions (Granger, 1969). When extended to the frequency domain, GC decomposes these directed dependencies across spectral components, revealing at which specific frequency the source signal contributes significantly to the dynamics of the target signal (Geweke, 1982; Barnett & Seth, 2014, 2015). However, the neurophysiologic grounds of directed communication cannot be definitely concluded from GC peaks. Conceptual models (Vinck et al., 2023, 2025) demonstrate that spectral GC signatures are embedded within a larger communication repertoire in the brain encompassing: (1) communication-through-coherence, where synchrony facilitates selective routing in distributed frequency-specific oscillatory networks; (2) communication-through-resonance, depending on the intrinsic resonant properties and recurrent amplification in target regions; and (3) coherence-through-communication, where synchrony emerges as a by-product capturing predominantly power modulations in the driving area. Because spectral GC is computed on the total power spectrum, GC changes and peaks may reflect modulations of the broadband or aperiodic (non-oscillatory) components of

the background activity (Roberts et al., 2025; Gelens et al., 2024; Vinck et al., 2025). Frequency shifts in the driving region, in combination with intrinsic resonant features of the receiver, also modify GC peaks (Dowdall et al., 2023). In addition, nonlinear transients may convey computationally relevant information that can affect the linear spectral GC measures (Vinck et al., 2023, 2025). Hence, in contrast to information-theoretic metrics (e.g., Potash et al., 2025), spectral EEG GC may not establish firm physiological causation of information transfer but rather specifies frequency-resolved predictive statistical asymmetry. Although the precise neurophysiological functionality behind spectral GC may not be identified due to the complex interplay between rhythmic oscillatory, aperiodic, and intrinsic network-level mechanisms (Vinck et al., 2023, 2025), GC peaks still signal meaningful adaptations and reorganizations in the neural architecture supporting cortical communication (Friston et al., 2013; Seth et al., 2015). This allows inference to experimentally verified region-frequency-function associations. In the present study, the precise neural origins of GC modulations in specific meditation styles were not explored (c.f., Potash et al., 2025). Rather, spectral GC was applied to characterize the frequency-resolved profiles of directed connectivity of FAM, OMM, and LKM meditation states prompting neuro-functional implications based on the cognitive demands of each style.

METHODS

Participants

The group of long-term meditators (LTM) consisted of twenty-two healthy volunteers (mean age = 44.2 years, age range 26-70 years, 4 females). A priori G*Power analysis (Faul et al., 2007) suggested a total sample size of 21 participants for a repeated measurement design and an effect size of $f = 0.75$, estimated with alpha error probability of 0.05, power of 0.95, and one group. It is to be noted that most of the studies of expert meditators rely on small samples (e.g., Chételat et al., 2017 with $n = 6$; Nicolardi et al., 2024 with $n = 12$; Ken Tanaka et al., 2022 with $n = 21$) or single-case designs (Chowdhury et al., 2023) reflecting the practical limits of recruiting such unique samples (decades of practice, rare availability), yet yielding strong effects due to highly specialized expertise. All participants were right-handed and did not report any history of movement disorders, neurological, psychiatric or somatic diseases. These participants were monks, nuns and novice practitioners residing at Amaravati Buddhist Monastery, in Southern England, and at Santacittarama Monastery, in Central Italy. Practices at both monasteries are aligned with the Tai Forest Theravada Buddhist tradition which is now established, widely acknowledged and influential in the West. Participants practiced FAM, OMM and LKM meditation forms in a balanced way in this tradition, often in integrated sessions, including silent meditation retreats (3 months per year). Meditation expertise is measured in hours taking into account both practice in the monastic tradition and practice before monastic life. As suggested by the abbots of the monasteries, we estimated participants with an average of 100 hours of practice per month during monastic life, with a balance of FAM, OMM and LKM facets of meditation. The lifetime duration of meditation practice of the participants was estimated as a mean value = 19358 hours (SE=3164), range 900-50600 hours.

The study had prior approval by the dedicated Research Ethics Committee at Sapienza University of Rome, Italy. All participants gave informed consent before participation according to the Declaration of Helsinki.

Experimental design

Participants had to perform a non-meditative rest condition and three meditation conditions: FAM, OMM and LKM. The switching between conditions was cued by voice. The instructions for the four conditions, which were written together with the abbot of Amaravati Monastery, the internationally recognized teacher Ajahn Amaro, were as follows: Rest: “Rest in a non-meditative relaxed state, without falling in sleep, while allowing any spontaneous thoughts and feelings to arise and unfold in the field of experience”. Focused attention meditation: “Sustain the focus of attention on breath sensations, such as at the nostrils, noticing readily and with acceptance any arising distraction, such as on thoughts or stimuli, and in case of detected distraction, return readily and gently to focus attention on the breath sensations”. Open monitoring (awareness) meditation: “With an open receptive awareness, observe the contents of experience as they arise, change and fade from moment to moment, without restrictions or judgments – such contents including breath and body sensations, sensations arising from contact with external stimuli, feelings and thoughts”. Loving kindness meditation: “Generate and sustain metta, acceptance and friendliness towards yourself and the experience in the present moment, as well as towards any being, in any state or condition”.

Procedure

EEG recordings. EEG was recorded with eyes closed in blocks of duration of approximately 2.5-3 minutes each, while the above mentioned conditions were repeated two times. In such a way, four blocks were repeated twice in the following order: REST, FAM, OMM, LKM. For analysis, trials from each block/per condition were used thus capturing brain states at distributed time points. Although the conditions were not fully randomized, the repetitive presentation of different meditative states across blocks during the entire session was designed to minimize order effects linked to fatigue and habituation. Thus, there were approximately 5-6 minutes (2 blocks x 2.5-3minutes) of total recording time for each condition, consistent with established experimental protocols for transient (short-lived) meditative state manipulation (e.g., Lutz et al., 2004; Perlman et al., 2010). State fidelity was verified by collecting brief structured subjective self-reports immediately after session. Participants were asked to evaluate their success in rapid entry into the instructed state, achieving the intended state-specific mode, stability of state maintenance, and control over distractions. All participants reported consistently high levels of success across these dimensions. No sessions or participants were excluded on the basis of insufficient state engagement. EEG was acquired by a mobile wireless system produced by Cognionics (<https://www.cognionics.net/mobile-128>) using an electrode cap with 64 active Ag/AgCl electrodes located in accordance with the extended international 10/10 system and referenced to linked mastoids. Electrode impedances were kept below 10 kOhm. EEG signals were collected at a sampling rate of 500 Hz. For control of ocular artefacts, vertical and horizontal electro-oculogram (EOG) was also recorded. The experiment was conducted at the two monasteries in a quiet, dark room suitable for meditation and recording EEG. All participants were tested with the same experimental design.

EEG pre-processing. EEG pre-processing was performed by means of Brain Vision Analyzer 2.2 (Brain Products GmbH, Germany). EEG analysis of Granger causality were conducted by means of software developed on Matlab R2013b (The Math Works Inc.). EEG traces were visually inspected to reject epochs with noise or non-physiological artefacts. Bad channels were interpolated according to Hjorth (1975). All EEG traces were EOG corrected by means of independent component analysis (ICA, Makeig et al., 1997). EEG data were down-sampled to reduce off-line the recording frequency of 500 Hz to 250 Hz for data pre-processing.

To achieve a reference-free evaluation, all data analyses were performed after current source density (CSD) transform of the signals (Perrin et al., 1989; Nunez et al., 1997). The exact mathematical procedure is presented in detail in Perrin et al. (1989). The algorithm applies the spherical Laplace operator to the potential distribution on the surface of the head. The CSD transform replaces the potential at each electrode with the current source density of the electrical field calculated from all neighbour electrodes, thus eliminating the reference potential. When applied with dense electrode arrays (48–256 electrodes, 64 in the present study), this procedure provides excellent estimates of the bioelectric activity of the cortical surface (Nunez & Pilgreen, 1991). In the present analyses, to improve spatial resolution and reduce the volume conduction between electrodes, CSD was applied following with the parameters: order of splines = 10, maximal degree of Legendre polynomials = 4, and regularization parameter $\lambda = 1\text{E-}7$. Edge electrodes were excluded from all analyses, resulting in a reduced but consistent channel set across participants. To ensure channel quality, a small number of channels were interpolated where necessary. Specifically, one channel was interpolated for one participant, and two to three channels were interpolated for three participants. All subsequent analyses were performed on CSD-transformed data from 50 electrodes. EEG recordings from all conditions were segmented into equal-sized, non-overlapping epochs of 4.096 s duration. During preprocessing, approximately 5–15% of epochs per participant were excluded due to artifact control, resulting in an average of 58 ± 20 accepted epochs per participant/condition. There were no statistically significant differences in the number of accepted epochs between groups for any condition (REST, FAM, OMM, LKM).

Analysis of Granger causality in the frequency domain

To support the applied methodology, the formalism of Granger causality in the frequency domains is briefly presented in the following section. One of the main reasons that Granger causality has generated so much interest in neuroscience is the fact that it can be reformulated to estimate the connectivity between neural sources in specific frequency bands (Geweke, 1982, 1984). In order to calculate spectral GC it is not correct to apply band-pass filters to the data and then apply Granger causality. Instead, a Fourier transform is applied to the time lagged regression coefficients and then the frequency specific Granger causality is calculated according to the formula:

$$f_{Y \rightarrow X}(\omega) = \ln \frac{S_{xx}(\omega)}{H_{xx}(\omega) \Gamma H_{xx}^*(\omega)}$$

Here S represents the cross-power spectral density, H is the transformed (following Geweke, 1982) transfer function, with the star denoting the complex conjugate, and Γ is the residual covariance matrix. The full derivation of the frequency domain Granger causality is presented in detail in Chen et al. (2006) and Barnett & Seth (2014).

GC computation pre-processing. Granger causality was analyzed using the publicly available MATLAB package (MVGC Matlab toolbox, Barnett & Seth, 2014). We paid particular attention to pre-processing steps given the sensitivity of GC to standard manipulations (Bressler & Seth, 2011; Seth, 2010). Analysis of Granger causality requires the analyzed signals to be stationary and not collinear (Seth, 2010). To avoid problems associated with these properties, the following additional pre-processing steps were undertaken.

First, as outlined before, a Laplacian filter (CSD) was applied to remove correlations in nearby electrodes, thereby also reducing the collinearity between signals. Second, following the requirements (Barnett & Seth, 2011, 2014), to remove mains-electricity line-noise (50 Hz) as well as its harmonic at 100 Hz which may lead to nonstationarity, notch filters (49–51 Hz and 99–101 Hz) were applied to the raw data. No other filtering was carried out. Also, since the length of the initially selected epochs in the data (4.096 s, 250 Hz) has been demonstrated to exhibit nonstationary features (e.g., Barrett et al., 2012), these epochs were additionally processed. They were divided into stationary non-overlapping segments of 1.024-s length. This length also was chosen to approach a balance between stationarity (shorter time series are more likely to be stationary) and model fit (longer time series support better parameter estimation for locally valid linear autoregressive models). This segmentation increased reliability by leading to a mean of 232 ± 40 artefact-free EEG epochs per subject/per condition. After this step, the GC estimation still took an intractable amount of time. Therefore, to ensure reasonable amount of computation time and a reasonable model order for autoregressive modelling (Seth, 2010; Brovelli et al., 2004), as an additional step for GC computation the selected artefact-free epochs were further down-sampled by taking every fourth point from each time series. This effectively reduced the sampling rate by a factor of 4 (62.5 Hz, Nyquist frequency of 31.25 Hz) while preserving high frequencies and minimizing autoregressive model order for stable GC estimation. In this way, each epoch used for final analyses had a length of 1.024 s comprising 64 data points.

The third pre-processing step was to compute sensor-based regions of interest or electrode clusters (C) covering the left and right anterior and posterior cortical regions, for which specific connectivity patterns in meditation have been reported (Yordanova et al., 2020). We performed clustering as demonstrated in Fig. 1. The clustering scheme involved averaging the signals from the following electrodes: C1 (left anterior) = [F7, F5, F3, F1, FC5, FC3, FC1, C5, C3, C1]; C2 (right anterior) = [F8, F6, F4, F2, FC6, FC4, FC2, C6, C4, C2]; C3 (left posterior) = [CP5, CP3, CP1, P7, P5, P3, P1, PO7, PO3, O1]; C4 (right posterior) = [CP6, CP4, CP2, P8, P6, P4, P2, PO8, PO4, O2]. The creation of these clusters (1) considered the potential roles of anterior (frontal) and posterior (parietal and parieto-occipital) cortices in conscious state regulation and awareness (Ihalainen et al., 2021; Panda et al., 2023b; Llinás et al., 1998; Gaillard et al., 2009; Yordanova et al., 2017) and broadly approximated the nodes of major cognitive control networks implicated in meditation (Shen et al., 2020), (2) aimed at increasing the signal-to-noise ratio by attenuating channel-specific noise thereby reducing spurious directed dependencies (Haufe et al., 2013; Barnett & Seth, 2014) and increasing the stability of autoregressive model fitting, and (3) provided methodological consistency with our previous research of undirected connectivity (Yordanova et al., 2020; 2021).

After the spatially averaged single-trial EEG of each defined cluster were computed, to avoid further confounds due to nonstationarity, a linear detrend was applied (Bernasconi & König, 1999; Hesse et al., 2003). Single-trial time-series corresponding to C1, C2, C3 and C4 were extracted for each subject and each condition and were used in subsequent analyses.

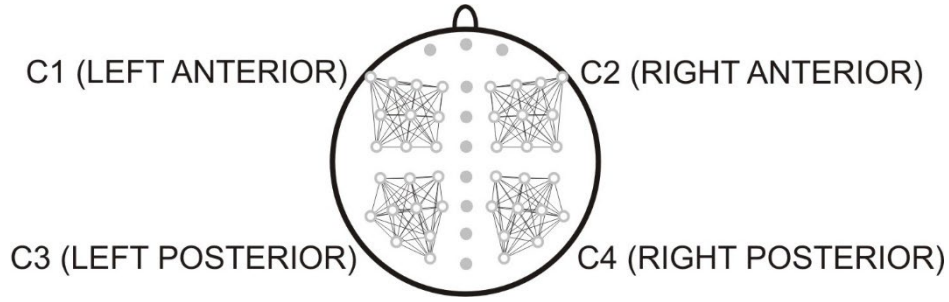


Figure 1. Schematic presentation of topographic clusters used for analysis: C1 (left anterior) = [F7, F5, F3, F1, FC5, FC3, FC1, C5, C3, C1]; C2 (right anterior) = [F8, F6, F4, F2, FC6, FC4, FC2, C6, C4, C2]; C3 (left posterior) = [CP5, CP3, CP1, P7, P5, P3, P1, PO7, PO3, O1]; C4 (right posterior) = [CP6, CP4, CP2, P8, P6, P4, P2, PO8, PO4, O2].

Computation of GC. Computation of Granger causality was performed using the available MATLAB package MVGC Matlab toolbox (Barnett & Seth, 2014). This software was first applied to estimate the model order. For each single EEG epoch of the data, the recommended model order was computed as defined by the Akaike information criterion (AIC, Akaike, 1974; McQuarrie & Tsai, 1998). The 95th percentile of the values obtained was 10 (corresponding to 160 ms) and was used as model order throughout the GC analysis. The need of model order selection is to balance the number of parameters (as determined by the maximum order - lag) so as to achieve the best model fit to data while avoiding overfitting a finite data sequence. The next step was to maximise the likelihood function for the respective models. The MVGC toolbox facilities were used to obviate the need to estimate the reduced model parameters separately from the data. Specifically, to yield estimates asymptotically equivalent to the maximal likelihood estimate, ordinary least squares (OLS) were used (Hamilton, 1994). The estimated regression coefficients in the time domain were then transformed to an auto-covariance sequence through the Yule-Walker equations (Barnett & Sett, 2014), which was used to compute GC in the time domain. Finally, this sequence was used to calculate the Granger causalities in the frequency domain.

Statistical analysis

In order to compare the Granger causalities across frequencies between REST and FAM, OMM, and LKM, the following steps were followed: (1) After computing GC in the frequency domain, first, the Granger spectrum for each subject, each condition, each single trial, and each between-cluster pair was discretized into 1 Hz bins. (2) Then, to compare the GC between REST and FAM, REST and OMM, and REST and LKM, all GC values within each 1Hz frequency bin for each trial/condition/pair in each group were concatenated and subjected to a non-parametric pair-wise Kruskal-Wallis test. Since this type of analysis involves multiple comparisons, the results were corrected with a false discovery rate (FDR) correction, as recommended for GC analysis in the frequency domain (Barnett & Seth, 2014). Because Granger causality was assessed in a frequency-resolved, nonparametric framework, reporting separate effect sizes for each frequency bin would strike an enormous complexity. Any attempt to summarize frequency-resolved Granger causality differences with a single effect-size value would require averaging across frequencies and thus obscure the spectral specificity that motivates frequency-domain GC analysis used here. For these reasons and also because effect magnitude can be inferred from the absolute GC spectra and the consistency of significant differences across frequencies bands, effect size values were not assessed.

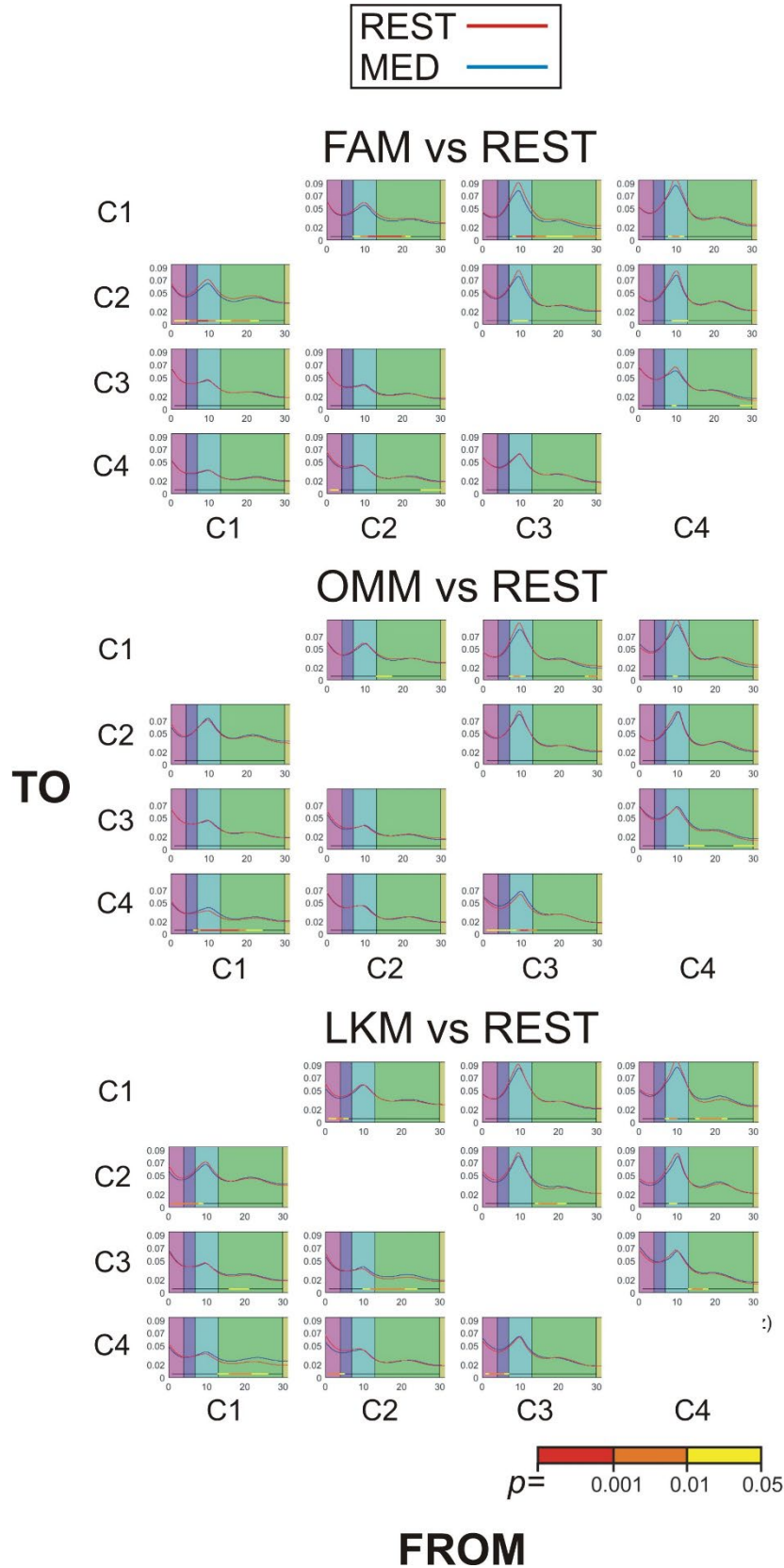


Figure 2. Frequency representation of Granger causality in long-term meditators: MEDITATION (MED) - blue line; REST - red line; FAM, Focused Attention Meditation; OMM, Open Monitoring Meditation; LKM, Loving Kindness Meditation. FROM and TO indicate the direction of interactions. Frequency-resolved statistical significance (FDR corrected) of between-group differences is presented for each pair of clusters in each condition.

RESULTS

Granger causality of experienced meditators was analyzed in the frequency domain with respect to delta, theta, alpha and beta frequency bands. Figure 2 depicts frequency-domain plots of GC for four clusters. A hertz-by-hertz FDR statistics applied to compare GC of each meditation state with GC during rest also is demonstrated in Fig. 2, and additionally summarized graphically in Fig. 3.

Observation of frequency-domain representations of GC in Fig. 2 during rest and different types of meditation revealed the presence of a dominating broad peak in LTM with a maximum in the alpha band (8-10 Hz) encompassing also frequencies from the lower (theta) and higher (beta) bands. The broad alpha peak in LTM was most prominent for directed transfer connections from posterior (C3 and C4) to anterior (C1 and C2) clusters. A broad higher-frequency beta peak also was observed for most of the between-cluster connections.

During FAM, multi-spectral (delta/theta, alpha and beta) GC decreased bi-directionally for inter-hemispheric anterior clusters. A suppression of mainly alpha directed influences was observed for both inter- and intra-hemispheric posterior-to-anterior connections (C3→C1, C2; C4→C1, C2). The posterior-to-anterior GC decrease was most expressed in the left hemisphere (C3→C1) including alpha and beta frequencies.

During OMM, the influences from the left hemisphere to the right posterior cluster (C4) was significantly enhanced for multi-spectral GC (theta, alpha and beta). This was verified by the significant OMM-related GC increases for C1→C4 and C3→C4 (Figs. 2 and 3). The influence from C4 was only enhanced to C3 in the beta band pointing to increased bi-directional communication between the posterior clusters of the two hemispheres. In parallel, a slight decrease of the dominant posterior→anterior alpha peak was detected for intra-hemispheric connections.

During LKM, the main pattern of changes was characterized by a bi-directional cross-hemisphere increase of GC between posterior and anterior clusters supported by beta networks. These effects are demonstrated in Figs. 2 and 3 by the C1→C4, C4→C1, C2→C3, and C3→C2 GC increases in the beta band. The directed interactions across posterior regions of the two hemispheres also increased in the slow (delta, theta) and fast (beta) frequency bands.

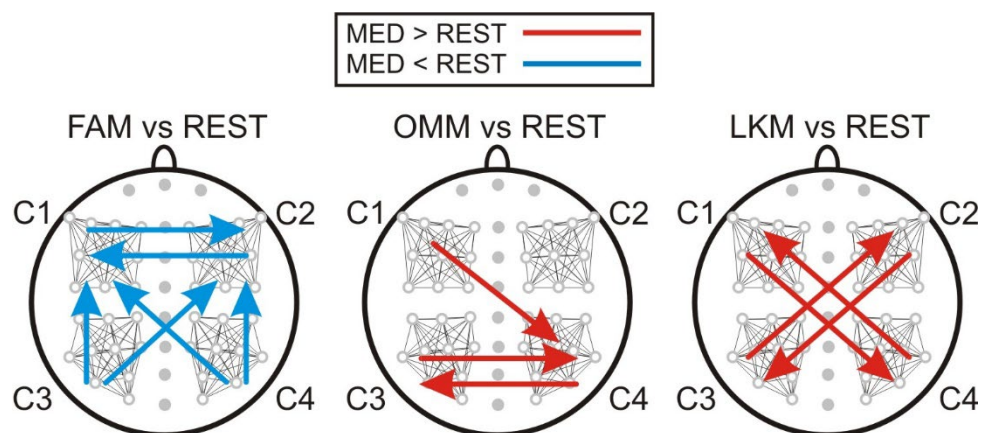


Figure 3. Schematic presentation of statistically significant differences between-conditions: MEDITATION (MED) > REST – red arrows; MED < REST – blue arrows (FDR corrected, $p \leq 0.05$) in Granger causality in the frequency domain. Clusters: C1, C2, C3, C4. Focused Attention Meditation (FAM), Open monitoring

Meditation (OMM), and Loving Kindness Meditation (LKM). Arrows indicate the direction of significantly different directed influences.

DISCUSSION

The present study employed EEG-based Granger causality to investigate whether distinct meditation styles – FAM, OMM, and LKM - are associated with differences in the strength, frequency, and direction of inter-regional interactions in highly experienced practitioners. It was hypothesized that the different activations and communications of large-scale brain networks in specific meditative states (Brewer et al., 2011; Tang et al., 2015; Fox et al., 2014; Yordanova et al., 2021) would be accompanied by distinctive patterns of directed connectivity.

The main results substantiated this hypothesis and demonstrated that each meditation state produced highly specific alterations in spectral patterns of directed connectivity relative to rest. However, as detailed below, our mechanistic hypotheses about the specific effects of FAM, OMM, and LKM on spectral GC were only partially confirmed. This may be due to the multitude of neurophysiologic mechanisms (oscillatory, aperiodic, or non-linear) affecting GC (Vinck et al., 2023; Chandia-Jorquera et al., 2025). It is also important to acknowledge that the reported here directionality and spatial distribution at the scalp reflect weighted mixtures of cortical generators at relatively broad sensor-level clusters. Even with the current-source-density (CSD/Laplacian) transformation used here, local scalp potentials represent combinations of multiple underlying sources that approximate cortical regions. Hence, the integrated source contribution might have additionally modulated the results deviating from hypotheses based on the topographies of specific large-scale networks.

To interpret meditation state-specific modulations of GC, we take into account possible neuroplastic effects of long-term meditation practice on directed connectivity. We consider our previous observations of altered GC in the same group of experienced meditators as compared to novices during rest (Kolev et al., in prep.). In that study, it was found that extensive meditation practice produced a pronounced increase of directed connectivity from posterior to anterior clusters in the two hemispheres. The enhanced GC was multi-spectral involving theta, alpha and beta frequency bands, with most prominent expression of GC alpha peak. These effects were interpreted as associated with (1) increased bottom-up (sensory and interoceptive) signalling, and (2) neuroplastic reorganization of main cognitive (fronto-parietal) networks as a result of meditation practice, whereby posterior areas might inform rather than be directed by frontal executive regions (Hillebrand et al., 2016; Wang et al., 2019). We proposed this was due to practice-induced stabilization of “multi-modal priority attentional maps” in the parietal cortex (Gottlieb et al., 2009; Humphreys et al., 2017) which might foster bottom-up attentional capture (Cabeza et al., 2008, 2012) and minimize frontal executive guidance in experienced meditators (Kolev et al., in prep.). In light of these findings, the significant reduction of posterior-to-anterior GC in the alpha and beta bands during FAM implies a suppression of bottom-up sensory and associative inputs (Hillebrand et al., 2016). By attenuating driving signalling from posterior areas the brain may reduce perceptual interference, thus enhancing internal focus stability. This is consistent with the cognitive demands of FAM, which emphasizes sustained, narrow attentional focus on a chosen object (e.g., the breath) while minimizing the influence of distractors (Cahn and Polich, 2006; Lutz et al., 2008; Malinowski et al., 2013). Since functional connectivity in theta and alpha bands in frontal areas is typically associated with executive regulation and cognitive control allocation (Cavanagh & Frank, 2014; Cohen, 2011; Clayton et al., 2015),

the reduction in multi-spectral GC across anterior clusters further suggests diminished demands for coordination of executive control networks and decreased need for cognitive flexibility or task switching during the maintenance of focused attention (Malinowski et al., 2013). Generally, the observed here overall reductions in directed connectivity during advanced FAM practice may reflect a shift from more distributed toward local, functionally specialized loops supporting the maintenance of a narrow attentional focus.

During OMM, experienced meditators showed significantly enhanced GC from the left-anterior to the right-posterior as well as from the left-to-right posterior electrode clusters across theta, alpha, and beta frequency bands. This pattern during OMM specifies the left hemisphere as a major multi-spectral leading source, and the right posterior cluster as a major receiving target. In interpreting the left-to-right directed influences, attentional fronto-parietal networks may be considered with regard to the regional (anterior/posterior) distribution of the currently defined clusters (Uddin et al., 2019). The bi-lateral dorsal attentional networks are associated with goal-directed sustained focus and top-down regulation of spatial and feature-based attention (Corbetta & Shulman, 2002; Szczepanski et al., 2013; Gross et al., 2004; Popov et al., 2017). In contrast, the right-lateralized ventral attentional network is known to support stimulus-driven reorienting, especially to salient, novel, or distracting stimuli. Its function is crucial for detecting mind-wandering, internal distractions, or unexpected sensory inputs (Corbetta & Shulman, 2002; Vossel et al., 2014; Uddin et al., 2019). The major operating rhythms of attentional networks encompass both slow and fast-frequency EEG ranges, in particular theta, alpha and beta frequency bands (Daitch et al., 2013; Sadaghiani & Kleinschmidt, 2016; Yordanova et al., 2017). In this perspective, the asymmetric left-to-right posterior connectivity observed during OMM may reflect the volitional influence on the ventral attention network promoting early detection and expanded conscious monitoring of all external and internal mental events, as well as flexible dynamic shifts in attention, as cultivated by OMM (Cahn & Polich, 2006; Lutz et al., 2008). Second, the increased receiving role of the right posterior cluster implies a specific functional involvement of these regions in OMM. Clinical evidence from patients with spatial neglect following right parietal damage verifies this region's role in maintaining perceptual awareness of the contralateral space (Vallar & Calzolari, 2018; Corbetta & Shulman, 2011; Yordanova et al., 2017). Also the right parietal cortex, particularly the inferior parietal lobule and temporo-parietal junction, is central to constructing the embodied sense of self in space and time, as these areas have been linked to core aspects of bodily self-consciousness, self-location, ownership, and agency (Blanke & Arzy, 2005; Blanke et al., 2015; Uddin et al., 2006; Convento et al., 2018; Ionta et al., 2014). The right temporo-parietal junction has also been implicated in interoceptive awareness (Critchley et al., 2004; Raimo et al., 2020). These previously established functional engagements suggest that the enhanced directed influences to the right posterior cluster studied here (broadly encompassing the relevant regions) may underlie the maintenance of augmented non-reactive external and internal awareness, consistent with mental experiences during OMM. Together, the GC effects imply the emergence of a specific neural communication architecture during OMM in meditation experts where enhanced influences of the left-hemisphere over right posterior regions possibly promote expanded monitoring, awareness and open receptivity.

According to the present results, there was a striking distinctive pattern of directed connectivity during LKM. The distinctive features of this profile were (1) the cross-hemispheric symmetry, (2) the posterior-anterior bi-directionality, and (3) the specific beta-band engagement. The increased posterior-anterior bi-directional connectivity generally confirms our hypothesis for LKM and suggests facilitated large-scale communication across

networks. LKM involves the intentional cultivation of affective states such as compassion, kindness, and warmth toward self and others. This process may engage both prefrontal regions implicated in emotion regulation and cognitive control (Ochsner & Gross, 2005), and posterior regions (e.g., temporo-parietal junction, posterior cingulate cortex) implicated in self-referential processing, perspective-taking, and social cognition (Decety & Lamm, 2007; Lutz et al., 2008). Indeed, neuroimaging studies have shown that LKM engages bilateral networks, including medial prefrontal cortex, insula, and temporo-parietal regions (Lutz et al., 2009; Mascaro et al., 2013). Hence, the LKM-related GC increase across anterior-posterior clusters may be tentatively associated with an intensified modulation of affective and self-related representations to support sustained compassionate mental states (Lutz et al., 2008). Second, the detected symmetry of the cross-hemispheric GC profile (left anterior - right posterior and right anterior - left posterior) may be referred to the known lateralization of affective processing (Davidson, 2004). The left frontal cortex is frequently associated with approach motivation and positive affect, whereas the right frontal cortex is linked to vigilance and withdrawal (Davidson, 1992, 2004). The co-activated cross-connectivity of these systems may underlie a balanced recruitment of emotional approach and avoidance. Such symmetry may be especially critical for the generation of positive stance, empathic resonance, and equanimity during LKM (Singer & Klimecki, 2014; Klimecki et al., 2014). Third, LKM manifested a specific engagement of directed beta connectivity, in contrast to the directed multi-spectral connectivity in FAM and OMM. Beta-band connectivity has been implicated in the maintenance of task goals and internal sets, and in the coordination of top-down attention (Buschman & Miller, 2007; Cavanagh et al., 2009; Fries, 2015; Gaillard et al., 2009; Engel & Fries, 2010; Spitzer & Haegens, 2017). Since in LKM, practitioners aim to sustain a positive intention toward self and others, the enhanced directed beta connectivity may reinforce a stabilized cognitive-affective mode where emotional intentions are integrated in a goal-directed representation of a compassionate mindset. This suggestion is supported by prior EEG studies of meditation showing enhanced beta coherence during concentrative and affective practices (Cahn et al., 2010). Together, the observed here specific GC features during LKM (i.e., cross-hemispheric, symmetric, bi-directional, anterior-posterior connections in the beta band) might highlight novel EEG correlates of positive emotional states in the brain.

One important issue that needs to be emphasized is that when the frequency characteristics of functional (undirected) connectivity were analyzed in the same sample of experienced meditators in the same meditative conditions – FAM, OMM, and LKM (Yordanova et al., 2020), connectivity patterns were revealed that were common for the three meditation styles. Specifically, common hubs were detected in the left posterior cortex supported by theta networks and in the right posterior cortex supported by alpha networks. Only a lateralization of undirected connectivity in the beta band distinguished the three meditation conditions. These previous observations of undirected connectivity are in contrast with current findings on directed connectivity indicating conspicuously distinctive profiles in the three meditation states as compared to rest. They confirm that the direction and frequency specificity of connectivity profiles carry relevant additional information about underlying neural architecture (Pullon et al., 2017; Hillebrand et al., 2016) that may provide complementary insights to understanding brain states. Specifically, according to the present results in FAM, advanced internal control of focused attention may not require enhanced guidance by anterior (prefrontal/frontal) control systems. Rather, it can be suggested to rely on reorganized posterior attentional maps leading to reduced interference from sensory, interoceptive and associative inputs. The currently found left-to-right directed connectivity in OMM suggests that previously identified consistent predominant engagement of the left hemisphere across

meditation states in long-term meditators (Fox et al., 2014; Marzetti et al., 2014; Guidotti et al., 2023; Yordanova et al., 2020, 2021; De Filippi et al., 2022; Raffone et al., 2019) may be essentially linked to the faculties of mindfulness (monitoring, awareness, and equanimity) penetrating in each style, which are especially emphasized in OMM (Malinowski et al., 2013; Raffone et al., 2019). Based on LKM results, it is intriguing to suggest that a refined advanced control over mental states (emotional, compassionate) mainly relies on fast-frequency activity, in contrast to the advanced control of attentional focus engaging mainly theta/alpha networks.

The present study has several limitations. First, the meditation states (FAM, OMM, LKM) were relatively short, and the order of conditions was not fully randomized. This may have limited the establishment and stabilization of specific mindsets; however, the extensive meditative expertise of the participants studied here (also supported by subjective reports) likely ensured a reliable transition into, and maintenance of, the different meditation styles. Second, distinct psychological descriptors of meditation-specific context (e.g., attentional focus aperture and strength, distraction control, predominant awareness content, empathic/pro-social or self-oriented attitudes) were not systematically assessed after each session. This precluded correlation analyses with directed connectivity measures that could have further supported interpretations. Future research adopting a stronger neurophenomenological approach may address these associations more directly. Third, the electrode clusters used in this study encompassed relatively broad cortical regions, limiting more precise correspondence with nodes of established large-scale cognitive networks (e.g., default mode, attentional, and fronto-parietal networks). Further studies applying information transfer measures to explicitly specified network models may help elucidate the neurophysiological origins of the directed connections observed across meditative states and their relationships to frequency-specific oscillatory dynamics within recognized large-scale networks.

Acknowledgments

We would like to express our gratitude and appreciation to the monks, nuns and novices of Amaravati and Santacittarama Buddhist Monasteries for their outstanding dedication and participation in our study. This work has been supported by a grant from BIAL Foundation (Portugal) for the project “Advancements on the aware mind-brain: New insights about the neural correlates of meditation states and traits” (Grant 272/70), and by the National Research Fund by the Ministry of Education and Science, Sofia, Bulgaria (Project KP-06-N73/2).

Data Availability Statement

The datasets used and analyzed during the current study are available from the corresponding author on reasonable request.

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