Exploring the Embodied Mind: Functional Connectome Fingerprinting of Meditation Expertise

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Abbreviations: open presence (OP), open monitoring meditation (OM), loving-kindness and compassion meditation (LKC), back-to-back (B2B), resting-state (RS), mindfulness-based interventions (MBI), Visual (Vis), dorsal attention (DA), ventral attention (VA), salience network (SN), frontoparietal (FP), default-mode-network (DMN), Drexel defusion scale (DDS), Beck depression inventory (BDI), five facets mindfulness questionnaire (FFMQ), N,N-Dimethyltryptamine (DMT), Supplementary Materials (SM)

Abstract:

Short mindfulness-based interventions have gained traction in research due to their positive impact on well-being, cognition, and clinical symptoms across various settings. However, these short-term trainings are viewed as preliminary steps within a more extensive transformative path, presumably leading to long-lasting trait changes. Despite this, little is still known about the brain correlates of meditation traits. To address this gap, we investigated the neural correlates of meditation expertise in long-term Buddhist practitioners, comparing the large-scale brain functional connectivity of 28 expert meditators with 47 matched novices. Our hypothesis posited that meditation expertise would be associated with specific and enduring patterns of functional connectivity present during both meditative (open monitoring/open presence and loving-kindness compassion meditations) and non-meditative resting states, as measured by connectivity gradients. Our finding revealed a trend toward the overall contraction in the gradient cognitive hierarchy in experts versus novices during open presence meditation. The signature of expertise was further characterized by an increased integration of large-scale brain networks, including the somatomotor, dorsal and ventral attention, limbic and frontoparietal networks, which correlated with a higher ability to create psychological distance with thoughts and emotions. Applying a support vector classifier to states not included in training, we successfully decoded expertise as a trait, demonstrating that its non-state-dependent nature. Such heightened integration of bodily maps with affective and attentional networks in meditation experts could point toward a signature of the embodied cognition cultivated in these contemplative practices.

INTRODUCTION:

Short 8-week mindfulness-based interventions (MBIs) are routinely used in various clinical and educational settings. Meta-analyses indicate that they positively impact well-being and cognition, and decrease clinical symptoms, in particular in mood disorders (1,2). MBI can induce functional changes in the neural processes underlying affect and attention (3,4) which are not always associated with structural changes (5), the latter being reported following longer meditation training (6). According to traditional meditation theories, these short-term training effects are only preliminary steps within a longer and more transformative path leading to long-lasting trait changes in cognition and self-related processes, and which require the combined practice of a variety of meditative techniques (7). Theoretical models of meditation have examined the psychological processes of such meditation practices, grouping them into attentional, constructive, and deconstructive families (7). The attentional family trains attention and meta-awareness and is exemplified by focused attention (FA) meditation, or open monitoring (OM) meditation (8). The constructive family, exemplified by compassion and loving-kindness meditation (LKC), trains perspective taking and cognitive reappraisal capacities and aims at transforming maladaptive self-schema (9). The deconstructive family trains in self-inquiry and aims at recognizing the nature of maladaptive mental schemas (7,10) that cause suffering and prevent a long-lasting form of well-being from emerging; it has thus far received less research interest (11). Deconstructive practice aims in particular at recognizing the constructive and transient nature of basic cognitive structures such as time, space, and subject–object orientation. To explore and gain such insights about the nature of perception and the nature of the self, some Buddhist practitioners are trained in particular into non-dual mindfulness meditations (10), such as Open presence meditation (OP). OP meditation is said to induce a minimal phenomenal state of consciousness where the intentional structure involving the duality between object and

subject is attenuated, as captured by the notion of non-duality (10,12). OP meditation is typically practiced with attentional and constructive practices involving mental imagery and compassion meditations. The alterations of these self-related and affective and attention processes throughout these various practices is said to have long-term impact on cognition as a trait (8) captured here by the notion of "meditation expertise". This developmental trajectory suggests that the baseline brain functional profile of experts will gradually tend to overlap with the dynamical profile of these meditative states themselves. Despite the potential therapeutic and scientific interest in characterizing long-term meditation expertise, little is still known about its neurophysiological mechanisms (13,14). The purpose of the present study is to investigate the neural correlates of meditation expertise in a sample of long-term Buddhist meditators, as measured by changes in the organization of intrinsic connectivity networks in the brain. We hypothesize that any long-lasting, trait-like changes in experts should correlate with specific changes compared to novices in large-scale brain functions detectable both during meditative states as well as at rest during non-meditative states.

To investigate the effect of long-term meditation practice on the intrinsic functional organization of the cerebral cortex (15), we employed a data-driven technique that captures its organization along continuous gradients, also known as connectivity gradients (16,17). This technique can reveal multiple dimensions of cortical organization, with the first dimension describing the cognitive hierarchy (15), starting from sensory cortex and ending with transmodal regions such as the default-mode network (DMN). The second gradient separates visual regions from the other networks (16), and the third gradient spans the multiple-demand network and the networks at opposite end (18). This network is composed of the inferior frontal sulcus, regions of the dorsolateral prefrontal cortex, the anterior insula,

the dorsal anterior cingulate, the pre-supplementary motor area, and the intraparietal sulcus. Previous studies have demonstrated that these gradients can be influenced by various factors, including disorders such as depression (19) and autistic spectrum disorder (20), as well as cognitive and psycho-affective training (21). Interestingly, psychedelics, such as psilocybin (22) and N,N-Dimethyltryptamine (DMT) (23) can induce ego dissolution and are correlated to a collapse of the cognitive hierarchy as measured by the first gradient. Given that both psychedelics and non-dual meditation are said to lessen self-related processes, we predicted that non-dual meditation would be associated with a similar compression of the cognitive hierarchy, as Timmerman and colleagues (23) reported, albeit weaker in its effects. Given the paucity of data in the literature on meditation expertise and novelty of the gradient connectivity method, further developing a specific functional hypothesis is challenging. However, one can identify brain networks candidates which may be impacted within the connectome. Meditation has been associated with brain structural and functional changes mainly in frontal and limbic networks (6,24) with the insula and anterior cingulate cortex, part of the salience network (SN), being the regions most sensitive to meditation training according to a meta-analysis (25). Studies on meditation traits and functional connectivity (26,27) or differences between long-term meditation practitioners and novices (13,14,28) have also shown that individuals with meditation experience exhibit reduced connectivity between the DMN and fontoparietal network/SN, while connectivity between the SN and FPN increases. Yet, these effects remain inconsistent across studies, as meditation training has also been linked to increased connectivity between the DMN and FPN/SN (29,30). A recent study reported effects of various forms of meditation training on the connectome consisting of increased functional segregation of regions, including parietal and posterior insular regions, following training in attentional family meditation, indicating that these networks are functionally different from the rest of the cortex. Conversely, perspective

training (i.e. constructive family) resulted in increased functional integration of these regions with other brain networks (21).

Investigating expert meditators could thus help develop hypotheses or theoretical understanding about the long-term developmental trajectory of meditation and minimal phenomenal states of consciousness.

METHODS:

Participants

Participants were recruited for the Brain and Mindfulness ERC-funded project, which includes a cross-sectional observational neuroscientific study on the effect of mindfulness meditation on experiential, cognitive and affective processes conducted in Lyon, France, from 2015 to 2018. Participants included novice and long-term meditation practitioners (referred to as 'experts'), who were recruited through multiple screening stages (for details, see the Brain & Mindfulness Project Manual (31)). 75 cognitively normal participants aged 35-66 (SD 7.7) including 28 expert meditators and 47 control participants (referred to as 'novices') matched on age and gender ($p>0.5$, see Table 1) were included in this study. Novices attended a one-weekend meditation training program prior to any measurement to get familiarized with the meditation techniques. Inclusion and exclusion criteria have been previously reported (31) (see (SM)). Finally, subjects had to be affiliated to a social security system. All participants received information on the experimental procedures during a screening session, and provided informed written consent. The study was approved by the regional ethics committee on Human Research (CPP Sud-Est IV, 2015-A01472-47). After excluding participants who exhibited more than 0.3mm/degree movement to control for

potential motion effects (2 experts and 3 novices), the analysis was conducted with a reduced sample size of 70 participants (32).

Paradigm

All participants attended a single fMRI session in which we first acquired their structural image. We then acquired functional scans, starting with a resting state (RS). We also acquired meditative states of LKC meditation. In addition, for novices, we acquired states of OM meditation, and for experts we acquired states of OP meditation (see SM for a description of the meditation practices). All states lasted 10 minutes. The order of acquisition of the two meditative states was random. For the present study, we used three psychometric scales, which are Drexel defusion scale (DDS) (33), Five facets mindfulness questionnaire (FFMQ) (34), and Beck depression inventory (BDI) (35) (for details, see SM).

Data acquisition and preprocessing

Data was collected on a 3T Siemens Prisma scanner. Functional data was acquired with EPI (TR=2100ms, TE=30ms, 39 slices, voxel size 2.8x2.8x3.1mm3). Structural scans were T1w (1mm iso), T2w (1mm iso) and T2*w (1mm iso). Preprocessing used fMRIprep v1.2.6 (36). This included motion correction, co-registration, normalization to MNI space, CompCor for physiological noise removal, ICA-AROMA denoising, and FreeSurfer surface reconstruction (see SM for details).

Connectome gradient construction

The construction of the functional connectome gradient followed the procedures detailed in Hong et al. (2019) (20) and in the SM.

3D gradient metrics

To investigate multidimensional differences in cortical organization, we focused on the first three components, which explained over 50% of total variance. We combined these gradients

by forming a 3D space (21,37), where each gradient constitutes an axis of this space described in Figure 1A.

Statistical analyses

We compared gradient component scores between experts and controls using surface-based linear models in SurfStat (http://www. math.mcgill.ca/keith/surfstat/). Surface findings were corrected for family-wise errors using random field theory ($pFWE < 0.05$). To show group differences in dispersion metrics, we used multivariate non-parametric two-sample testing (38). Post-hoc tests were computed using Studentized bootstrap-t tests with 10.000 repetitions (39). We trained classifiers on dispersion metrics to predict expertise using scikit-learn (40) with modified-huber loss and 5-fold cross-validation repeated 5000 times. We used area under the curve rather than accuracy to avoid bias from unbalanced samples. To disentangle collinear demographic factors, we used a back-to-back regression (B2B) (41), finding DDS score had a significant contribution to dispersion measures (details in SM).

RESULTS:

RESTING STATE ANALYSIS

We hypothesized that the large-scale fMRI connectomics measures would be modulated by trait-like effects of expertise not only during meditative states but also at rest during non-meditative states. To test this hypothesis, we first studied the RS, which is often viewed as a baseline, and its study is a standard approach to characterize expertise or traits (4,13,14) (see Figure 2A). The density of eccentricity map values for both groups (Figure 1F) illustrates how, globally, experts' vertices were embedded closer to the connectome centroid, resulting in more integrated vertices for experts. As a similar pattern was reported in the psychedelic literature, we explored whether the average eccentricity of experts was different from that of

novices, but the result was not significant (t(68)=0.35; p=0.16; [95% CI: -0.13,0.81]). These findings indicate that expertise affects the functional connectivity of the brain, resulting in changes in eccentricity that likely signify differences in information processing and integration.

To further functionally specify the group difference in eccentricity, we explored the multidimensional differences within the cognitive hierarchy, and between and within standard brain networks, as recently proposed (21,37) (Figure 2A). Using a multivariate non-parametric approach (38), we found an overall trend difference between groups between these various dispersion metrics (rv=0.055, p=0.066). We then investigated the group effect on each of these dispersion metrics as described in Figure 2A, as an exploratory analysis. These findings indicate that experts' dispersion metrics during the RS were lower compared to novices in specific networks. However, as experts are expected to exhibit a trait and possibly a trait by state effect during RS, these differences may not reflect the sole signature of expertise.

To address this concern, we repeated these analyses for LKC and OP/OM meditative states, in order to identify common characteristics among these states that could be considered as an effect of expertise. First, and following our hypothesis based on ego dissolution during psychedelics, we tested whether there was a global reduction of eccentricity. We computed a mixed ANOVA between groups and states to test for differences of mean eccentricity. There was a state effect (F(2,136)=4.78, p=0.009), but contrary to our hypothesis, no interaction effect [F(2,136)=0.83, p=0.43] and only a trend effect for the groups (F(1,68)=2.54, p=0.1). Regarding the group effect, we still performed an exploratory analysis as one of our hypotheses was that experts' connectome could show decreased eccentricity, mainly during

OP, as in psychedelics study (22,23), albeit much weaker. This prediction was confirmed only during OP state which showed lower mean eccentricity for experts compared to novices ($t(68)=0.5$; $p=0.048$; [95% CI: 0.01,1.04]), while the LKC state showed the lowest difference between groups ($t(68)=0.15$; $p=0.55$; [95% CI: -0.37,0.66]).

Similarly to RS, we computed the large-scale networks' dispersion metrics for these meditative states, revealing different contrasts (Figure 2). These findings indicate an expertise-effect during OM/OP meditation but not LKC meditation, which only partially overlapped with the pattern found during RS. This suggests that the effect of expertise on large-scale networks may vary depending on the cognitive state or task and that segregation of networks, as captured by gradient dispersion, may reflect global modes of function.

SVC EXPERTISE ANALYSIS

Our analyses revealed that each state showed a somewhat different signature of expertise, making it difficult to characterize its enduring dynamical characteristics. Although the so-called RS, where the participant is asked not to engage in any specific cognitive activity, is a gold standard approach to measure it, its instruction turns out to be ambiguous for many expert meditators. This instruction can typically be understood, on the one hand, as an invitation to spontaneously engage in OP meditation, a style of non-dual meditation, or on the other hand, as an invitation to actively try not to meditate by spontaneously following thoughts, such as during mind wandering.

To tackle this issue, we used a machine learning approach. We trained a support vector classifier (SVC) on a subset of a given state to distinguish experts from novices, and then tested its ability to both decode the same state and to generalize to the other states. Our

rationale was that if the expertise effect was an enduring dynamical characteristic present in every state, the SVC should be able to generalize to the other states as well. Specifically, the state with the least amount of noise around the effect of expertise should be the most susceptible to generalize when tested on another state (Figure 2E). We were able to decode expertise only for the OP state, but we were not able to generalize its classification on the RS nor on the LKC state. Next, to reduce the contribution of the trait-by-state effect, and to make the effect of expertise more salient, we averaged all three states together, and again trained the classifier using the average pattern. As expected, the model demonstrated significant expertise decoding ability when trained on the average state and subsequently tested on the remaining test set. Interestingly, unlike its performance when trained on OP, the model was also able to generalize its classification ability when tested on different states, specifically RS and OP. In the line with the previous results (Figure 2C), the decoder was not able to distinguish experts from novices during LKC.

AVERAGED STATE DISPERSION ANALYSIS

To further characterize the averaged state that best captured the fingerprint of meditation expertise, we examined the dispersion metrics of this averaged state using both a 3D space exploratory analysis (Figure 3A) and a surface-based analysis (Figure 3B). We also computed a surface-based analysis of the averaged state's eccentricity. All clusters showed reduced eccentricity for experts when compared to novices (Table 3). To investigate the behavioral relevance of these group differences, we then studied the individual contribution of various features, including sex, age, group, hours of meditation practice in life, and trait psychometric measures (DDS, BDI, FFMQ) to decode the dispersion metrics. To do so, we fitted a B2B model to control for the co-variance between features while optimizing the linear combination of dispersion metrics to detect the encoding information (Figure 3C). The output

of this model is a set of beta coefficients, one for each feature. Here, only the DDS, a scale reflecting a person's capacity to cognitively defuse thoughts, and emotions, yielded a significant contribution to the decoding (β=0.31; p=0.043). We then applied the same B2B model to each dispersion metric individually, meaning that we used all previous features to predict dispersion metrics. We only present the results for DDS, as it was the only scale to demonstrate a significant relationship (Figure 3D). Here, our goal was to identify which dispersion metrics predicted by the set of features exhibited a significant contribution from the DDS. Importantly, the only associations were negative correlations, where a higher DDS score was associated with a lower dispersion metric, consistent with the fingerprint found in Figure 3A. However, contrary to Figure 3A, a higher DDS score was not associated with a change of dispersion within networks. To summarize, our analysis suggested that the capacity to put psychological distance between thoughts and emotions was associated with reduced network dispersion between and across specific networks, largely overlapping with the expert-related trait signature (Figure 3A), indicating a potential link between trait-like measures and neural activity during meditation. Tese findings shed light on the neural mechanisms underlying expertise effects in meditation and highlight the importance of considering state-averaging approaches in future studies.

DISCUSSION:

In this study, we first measured the vertex-wise eccentricity of the diffusion map embedding gradient, which reflects the functional integration (low eccentricity) and segregation (high eccentricity) along a scalar value (21,37,42). We found a higher integration for experts during OP (Figure 2D) and as a trend during RS (Figure 2D) in the overall mean eccentricity values. In line with these findings, previous studies have observed increased integration in long-term meditation practitioners' brains using different methodologies, such as graph analysis (43)

and diffusion-weighted imaging (44–46). Additionally, using diffusion map embedding, similar but much more pronounced patterns of increased integration have been identified in studies investigating the acute effects of psychedelics (22,23). This consistency across different research approaches provides some support to our initial hypothesis of a compression of the cognitive hierarchy associated with the lessening of self-related/discursive processes during non-dual meditation akin to OP meditation. This observed increase in brain integration has been proposed to be a consequence of a heightened state of brain entropy, which has been observed both in psychedelic experiences (47) and during meditation (48). For instance, the REBUS model theorizes that this heightened brain entropy state is associated with "a relaxation of the precision weighting of priors that coincide with liberation of bottom-up signaling" (49). This means that the brain becomes less reliant on its pre-existing expectations or beliefs and pays more attention to the incoming sensory information. This mechanism also aligns with the description provided within the free energy principle framework (50) of the deconstructive meditation family (51) as cultivated in OM meditation and non-dual meditative states such as OP. Hence, our study provides some support with these current theories, which should guide the future empirical studies of these non-dual meditations.

Next, we showed specific group-related dispersion metrics effects (Figure 2B) which were not identical across the three states, suggesting both a group-by-state effect and a state independent trait effect (Figure 2A,C). To be able to identify a state independent trait measure, we used a SVC to decode expertise and to test whether its training generalized to other states. First, we managed to decode the group only when it was trained and tested on the OP state, suggesting that this state was functionally the most different between groups. Yet, this pattern did not generalize as a trait, meaning that the SVC weights likely captured

also a trait-by-state effect. Next, we repeated the same procedure on the average of the three states, as the trait effect has been characterized by low-variability functional connectivity (52). If OP-related group differences was reflecting only a state effect, the predictability should decrease, because noise was added during the averaging. If, instead, the average of the three states was reducing noise by repeating a trait-like feature, then the predictability and its ability to generalize to other states should increase. We found some evidence for the latter (Figure 2E), suggesting that the average eccentricity was the best characterization of a trait-like effect in our sample.

Subsequent analyses specified the specific fingerprint of meditation expertise. Experts exhibited reduced average eccentricity in dorsal attention (DA) and limbic networks, and, at tendency, in the SM cortex suggesting that these networks were more integrated within the cognitive hierarchy for experts, allowing for enhanced information exchange with other networks (21,37). In line with these findings, our surface-based analysis revealed clusters exhibiting solely decreased eccentricity among the expert group (Figure 3B) in the parahippocampal gyrus, premotor gyrus, and supplementary motor area, thereby confirming the results obtained from the average eccentricity analysis described above. Experts also demonstrated a more reduced within-network dispersion in the DA and VA networks compared to novices, as previously reported in the literature on meditation traits (14,26,27), suggesting an enhanced spread of information within these networks, as their voxels exhibit stronger connectivity. Finally, for experts only, the limbic network displayed increased connectivity with the SM, VA, and FP networks, the SM cortex exhibited stronger connectivity with the DA network, while the VA network demonstrated enhanced connectivity with the FP network. Numerous brain imaging studies on meditation have similarly highlighted the role of these attention and affective brain networks during meditation practices (for reviews see Tang et al. (24), Lutz et al. (53), and Sezer et al. (54)).

The functional coupling of these networks with the SM network in meditation is more rarely reported (55), even if it is consistent with the embodied nature of this practice (56,57). This finding pointed toward an important functional modulation of the SM cortex in meditation practice, which have often not been utilized as seeds or networks of interest in previous ICA studies.

We reported that several metrics capturing the meditation expertise fingerprint were correlated with the ability to create psychological distance between thoughts and emotions, as measured by the DDS. These correlations were assessed while considering the co-variation of all metrics included in the demographic table (Table 1), including expertise. Specifically, and in line with the trait fingerprint, a higher DDS score was associated with reduced averaged eccentricity in the SM cortex and limbic network. Additionally, the DDS negatively correlated with dispersion between the DA network and SM cortex, as well as between the limbic network and the SM and VA networks. These correlations between a higher DDS score and more integrated limbic, SM and VA networks, may explain how experts manage to modify their emotional processing. For example, Zorn and colleagues showed on the same sample of participants that these experts were more able to reduce and to decouple the unpleasantness of a painful stimulus from its intensity than novices (58). Moreover, they also showed that the DDS was a core mechanism to explain the stronger sensory-affective uncoupling of pain found in experts (59).

Finally, consistent findings in the study of meditation traits involve connectivity modifications between the FP and DMN, with both increased and decreased connectivity reported in the literature (13,14,26,27,29,30,60–62). However, our expertise fingerprint was

not associated with such differences, despite a negative correlation between the DDS and dispersion between the FP network and the DMN. Several factors may explain these discrepancies (see Sezer et al. (54) for discussion).

Our study had several limitations. The cross-sectional nature of the study limits our ability to establish causal relationships between variables. Although efforts were made to control for potential confounding variables by matching experts and novices for age, sex, and education, there may still be unaccounted factors that could explain the observed differences. In addition, our study was mainly exploratory as we used diffusion embedding to study the effect of long-term meditation practice on the brain, thus our findings will require replication by future studies.

In conclusion, our study investigated the effects of long-term meditation practice on brain functional architecture and connectivity patterns, focusing on the development of shared characteristics associated with expertise in meditation. We identified large-scale networks associated with meditation expertise, which were not limited to specific meditative states, and which shed new light on the neural mechanisms of cognitive defusion as measured by DDS.

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Gaël Chetelat: Supervision. **Sébastien Czajko**: Methodology, Validation, Formal analysis, Data curation, Writing, Visualization. **Loïc Daumail**: Formal analysis. **Antoine Lutz**: Methodology, Conceptualization, Supervision, Writing – editing, Funding acquisition. **Daniel Margulies**: Methodology, Supervision. **Ronan Perry**: Methodology, Validation. Formal

analysis. **Joshua Volgestein:** Methodology, Supervision **Jelle Zorn**: Conceptualization, Methodology, Investigation. Data Collection

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TABLE 1

	Novices	Experts	p
n	47	28	
Sex	24M/23F	16M/12F	0.91
Age	51.9 (7.5)	51.8 (8.0)	0.95
Education	3.6 (2.0)	3.2 (2.4)	0.52
DDS	29.0 (6.7)	39.0 (6.6)	<0.001
FFMQ	128.8 (20.4)	158.0 (18.2)	<0.001
BDI	5.4 (4.6)	3.4 (4.3)	0.074
Hours	26 (17)	39k (18k)	<0.001

Table 1: Demographics comparison between experts and novices. Continuous variables are presented as mean (standard deviation) and their p-values were calculated using t-test. For sex, the p-value was calculated using a chi-squared test. DDS: Drexel Defusion Scale. FFMQ: Five Facets Mindfulness Questionnaire. BDI: Beck Depression Inventory.

TABLE 2

Cluster region	*p*FDR	*kE*	*Tmax*	*x*	*y*	*z*
L visual association	**<0.001**	**967**	**3.4**	**-28**	**-75**	**-15**
R visual association	**<0.001**	**576**	**3.6**	**39**	**-85**	**13**
R temporal pole	**<0.001**	**206**	**-3.7**	**48**	**13**	**-37**
R dorsal PCC	**<0.003**	**127**	**-3.4**	**13**	**-30**	**44**
R supramarginal	**0.005**	**106**	**-2.8**	**55**	**-32**	**30**
R visuomotor	**0.014**	**114**	**-3.8**	**12**	**-53**	**71**

Table 2: Surface-based analysis of the RS's eccentricity. All eccentricity cluster were lower for experts than for novices, except for the bilateral visual cortex. PCC: Posterior Cingulate Cortex.

TABLE 3

Cluster region	*p*FDR	*kE*	*Tmax*	*x*	*y*	*z*
L superior temporal	**<0.001**	**854**	**-4.00**	**-50**	**0**	**-6**
R parahippocampal	**<0.001**	**774**	**-3.93**	**32**	**-11**	**-39**
R visuomotor	**<0.001**	**379**	**-3.9**	**37**	**-47**	**50**
R premotor + SMA	**<0.001**	**219**	**-3.5**	**5**	**13**	**71**
L supramarginal	**<0.001**	**148**	**-3.3**	**-48**	**-40**	**46**
L premotor + SMA	**0.001**	**105**	**-2.8**	**-32**	**-1**	**52**
L angular	**0.002**	**128**	**-3.4**	**-31**	**-50**	**38**
L visuomotor	**0.002**	**105**	**-3.3**	**-9**	**-46**	**41**
R dorsal PCC	**0.004**	**95**	**-3.9**	**-10**	**-12**	**43**
L ventral ACC	**0.015**	**106**	**-3.2**	**-10**	**-12**	**43**
L medial temporal	**0.027**	**85**	**-3.2**	**-45**	**-52**	**12**

Table 3: Surface-based analysis of the averaged states' eccentricity. All eccentricity cluster were lower for experts than for novices. SMA: Supplementary motor area. PCC: Posterior Cingulate Cortex. ACC: Anterior Cingulate Cortex.

Figure 1

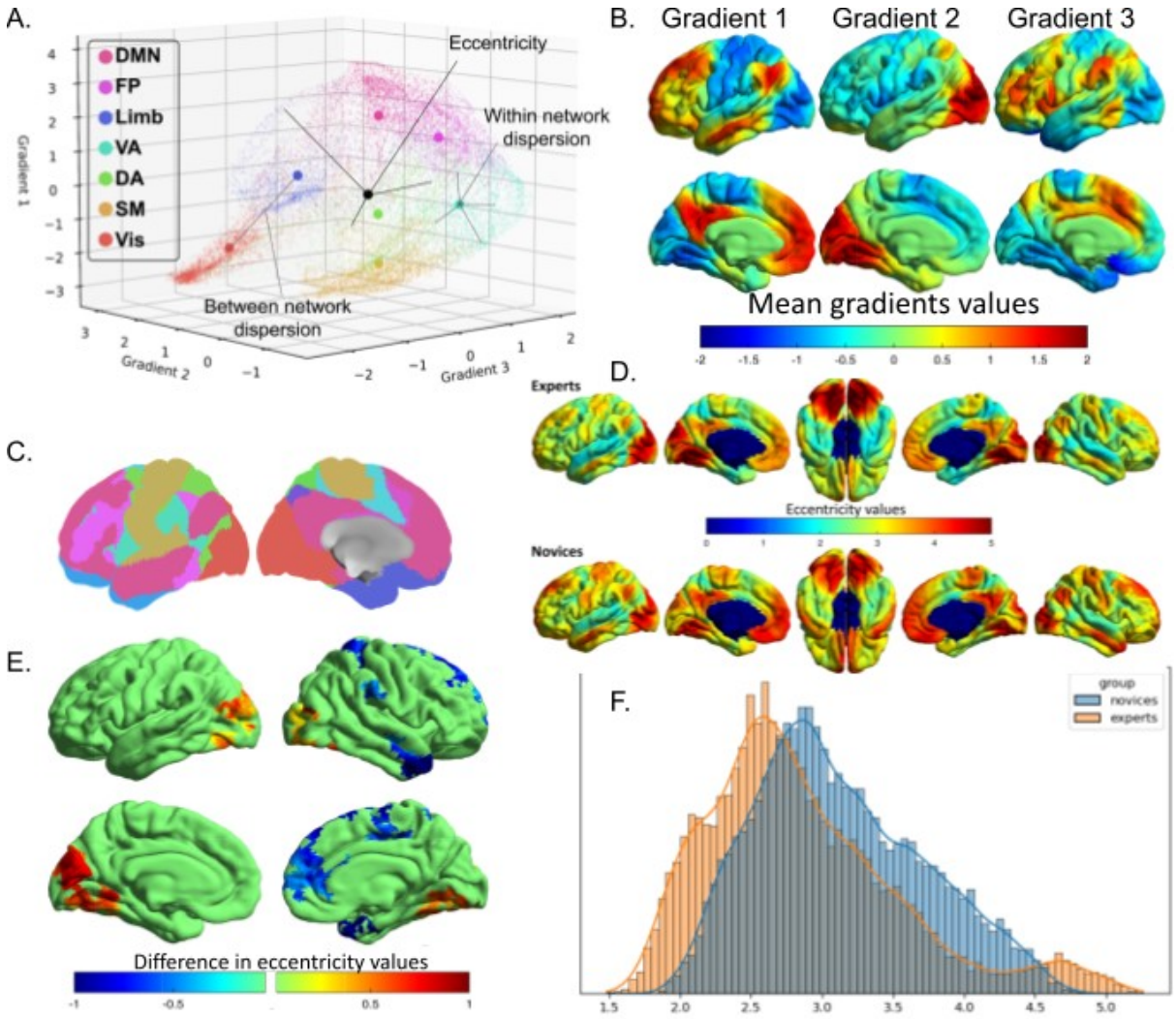

Figure 1 Effect of long-term meditation practice on eccentricity maps: (A) Visualization of dispersion metrics within the three-gradient space. The eccentricity value of a vertex corresponds to the Euclidean distance from the barycenter (depicted by a black dot) of the 3D space. For each individual 3D map, we computed an eccentricity map defined by the Euclidean distance from each vertex to the individual barycenter of the 3D space (21,37). These maps reflect the integration (low eccentricity) and segregation (high eccentricity) within the connectome for each voxel of each participant. We then quantified the dispersion metrics, which represents the segregation of large-scale networks (21). The within-network dispersion is calculated as the sum squared Euclidean distance of network vertices to the network barycenter. Between-networks dispersion is quantified as the Euclidean distance between network barycenters (21). (B) The first gradient (left) denotes the cognitive hierarchy of the brain, ranging from the unimodal cortex to the DMN. The second gradient (middle) differentiates the visual cortex from other networks, while the third gradient (right) segregates the limbic network. (C) Visualization of the cortical parcellation (63) used in (A). The color code corresponds to the one in Figure 1A (D) The eccentricity map describes a continuous coordinate system, where a lower value signifies that the vertex is closer to the barycenter of the 3D space. Sensory regions, including the visual and somatomotor cortex, and the DMN tend to be the least integrated regions. Although the average maps of experts and novices are similar overall, it is evident that eccentricity values are visually lower for experts than novices, except within the visual

cortex. (E) Surface-wide statistical comparisons between novices and experts are presented, with increases/decreases in experts shown in red/blue. Findings were obtained using surface-based linear models implemented in SurfStat during RS. They show statistically significant differences in eccentricity values between experts and novices particularly in the bilateral visual cortex and within the right hemisphere of the brain. Specifically, experts had decreased eccentricity in the right temporal pole, dorsal posterior cingulate cortex, supramarginal gyrus and visuomotor cortex (Table 2). On the other hand, only one bilateral cluster within the visual association cortex showed increased eccentricity for experts. This finding indicates that the visual cortex's cluster is more segregated in experts than in novices, whereas all the other clusters were more integrated. (F) A global histogram analysis confirms that, overall, eccentricity values are qualitatively lower for experts than for novices, except for vertices belonging to the visual cortex.

Figure 2

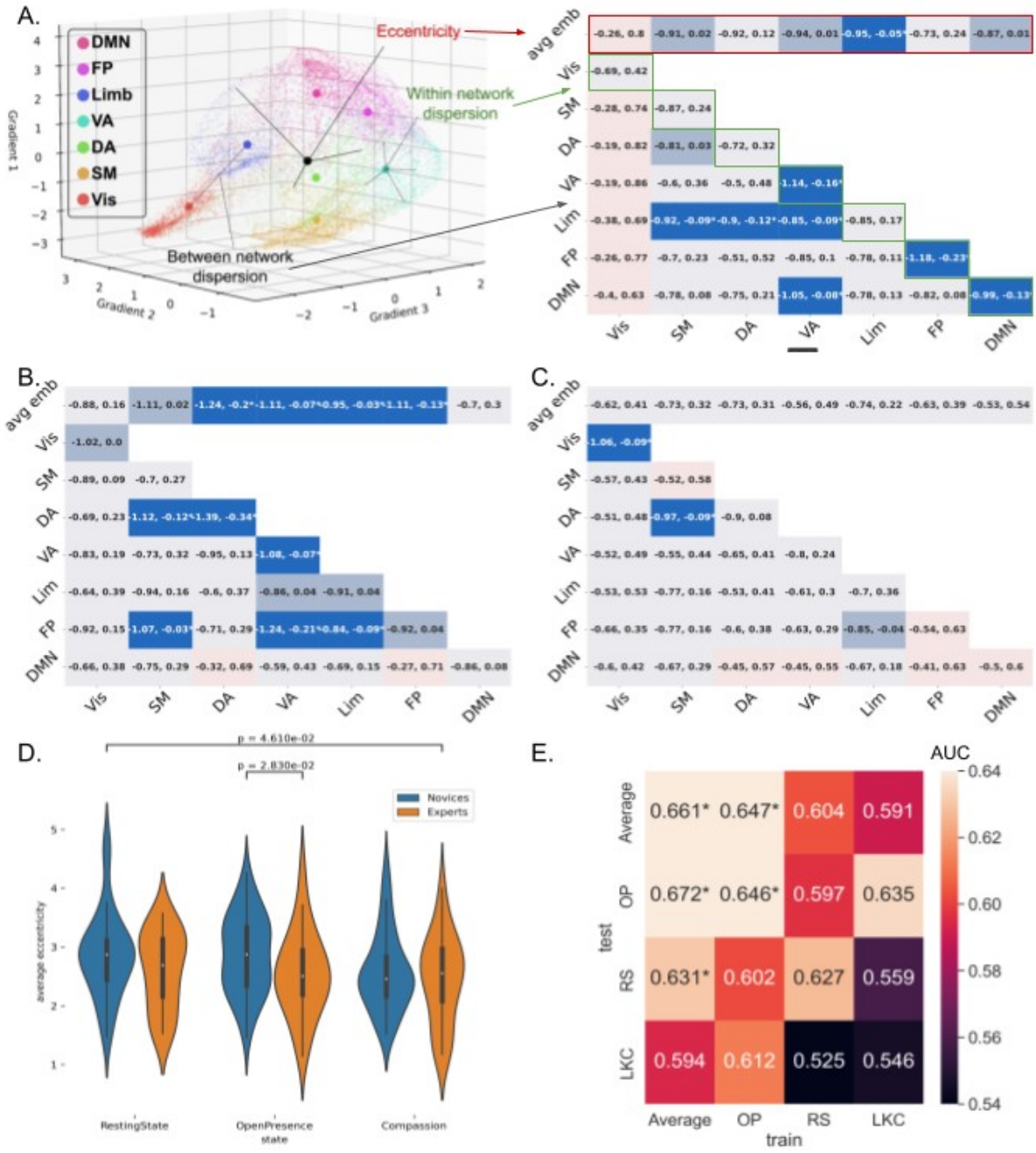

Figure 2 Comparison of networks' dispersion between experts and novices during several mental states: (A) Visual explanation of the dispersion metrics using the RS as an example. The first row of each matrix shows the average vertex-wise eccentricity of each network, referred to as the average embedding (21). The remaining dispersion metrics display the within-network dispersion (diagonal in green) and the between-network dispersion (the remaining squares). Significance was tested using bootstrap-t tests (39), and 95% confidence intervals are plotted in each box. The color blue (respectively red) indicates that the average eccentricity value was lower (respectively higher) for experts than novices. Bright-colored boxes indicate significant tests ($p<0.05$), medium-colored boxes indicate a trend ($0.1>p>0.05$), while light-colored boxes indicate non-significant tests ($p>0.1$). The tests are not corrected for multiple comparisons. The results indicate that the several dispersion metrics decreases in experts compared to novices during the RS, which was expected based on

previous analyses (Figure 1), except for the visual cortex, which is not significant here. Here, a higher between-network dispersion reflects a weaker connectivity between two networks and a higher within network dispersion, a lower connectivity between the voxels of a given network. We performed a brain parcellation in large-scale networks (63), commonly utilized in conjunction with diffusion map embedding (16,20). Using Studentized bootstrap tests (see details in SM), we found that, overall, the dispersion of the visual network did not increase for experts within the 3D space during the RS, as we would have expected from the surface-based analysis. However, the dispersion of the limbic network decreased ($t=0.51$; $p=0.045$), and marginally decreased for the somatomotor ($t=0.45$; $p=0.069$), ventral attention ($t=0.46$; $p=0.064$), and DMN networks ($t=0.44$; $p=0.073$). Furthermore, the dispersion within the ventral attention ($t=0.63$; $p=0.015$), frontoparietal ($t=0.68$; $p=0.007$), and default-mode ($t=0.55$; $p=0.022$) networks also decreased. We observed a decrease of dispersion between the limbic network on one side and the somatomotor ($t=0.51$; $p=0.031$), dorsal attention ($t=0.52$; $p=0.025$), and ventral attention ($t=0.49$; $p=0.035$) on the other side, and between the ventral attention and the DMN ($t=0.55$; $p=0.03$). (B) Dispersion metrics during open presence. Similarly to the resting state, all significant results show a decreased dispersion for experts. However, the results are not identical between the two states, which suggests a modulation of the states by expertise. Specifically, the average eccentricity of the dorsal attention ($t=0.69$; $p=0.007$), ventral attention ($t=0.57$; $p=0.027$), limbic ($t=0.5$; $p=0.048$), and frontoparietal ($t=0.61$; $p=0.018$) networks decreased within the 3D space, and marginally for the somatomotor ($t=0.52$; $p=0.056$) cortex for the experts compared to the novices. The eccentricity also decreased within the dorsal ($t=0.82$; $p=0.002$) and ventral attention ($t=0.55$; $p=0.033$) networks. We also observed a decrease of dispersion between the frontoparietal network on one side and the somatomotor ($t=0.52$; $p=0.049$), ventral attention ($t=0.71$; $p=0.007$) and limbic network ($t=0.49$; $p=0.032$) on the other side and between the somatomor cortex and the dorsal attention network ($t=0.59$; $p=0.018$) for experts. (C) Dispersion metrics during loving-kindness compassion. This state appears to be more similar for both groups than the other states. (D) Mixed-ANOVA analysis between group and state of the average eccentricity. Only the state effect was significant. Post-hoc tests reported on the figure are not corrected for multiple comparisons. (E) A stochastic gradient descent classifier was trained on the dispersion metrics (A-C) to decode expertise. The training was performed on a subsample of the three states or the average of the three states. The classifier was tested on the same metrics of the remaining sample, either from the same state or from a different state, using AUC. Results showed that the RS state cannot be used to significantly decode the effect of expertise. The SVC was able to decode expertise when trained and tested on OP ($p=0.027$). However, it was not able to generalize to the other states. Only the average of the three states was able to decode expertise ($p=0.021$) and to generalize to the OP ($p=0.02$) and RS ($p=0.046$) states. These results suggest that the average of the three states was the best way to capture an effect of expertise that would be present across all states. Additionally, the results confirm that the compassion state was very similar between experts and novices, as it was not possible to decode expertise in this state or when trained on it. There was no group difference during LKC ($rv=0.30$, $p=0.21$) confirming the finding with the multivariate approach. We confirmed this negative finding on the individual dispersion measures, which showed minimal variation between experts and novices, converging with the previous analysis. By contrast, there was an overall group difference on the dispersion measures ($rv=0.079$, $p=0.024$) during OP/OM states. This global effect was driven again by reduced dispersion, yet with a somewhat distinct pattern from RS.

Figure 3

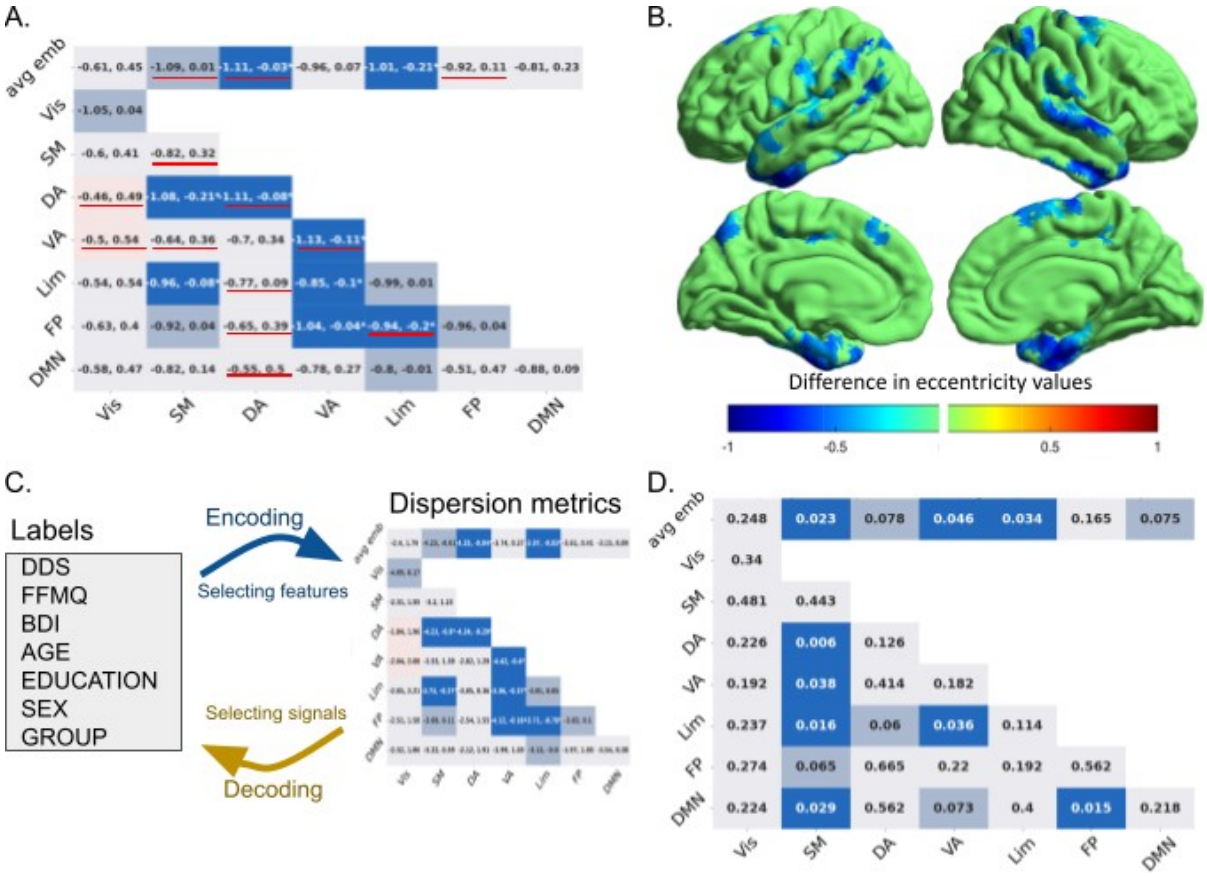

Figure 3 Expertise and traits effect on networks' dispersion: (A) Dispersion metrics after averaging RS, OP and LKC gradients. Colors are explained in Figure 2A. The red underlines indicate which dispersion metrics contribute significantly to the decoding of expertise (Figure 2E). Again, the results suggest that the dispersion of many networks decrease in experts compared to novices. This effect should reflect the expertise effect on the brain's dispersion metrics and be less influenced by state modulation. We found a significant decrease average eccentricity for the experts of the dorsal attention using a Studentized bootstrap (t=0.54; p=0.046), limbic (t=0.61; p=0.017) networks, close to significance for the somatomotor (t=0.51; p=0.058) network and within the dorsal (t=0.57; p=0.029) and ventral attention (t=0.6; p=0.02) networks. Additionally, we observed a decrease in dispersion between the limbic network and the somatomotor (t=0.52; p=0.038), ventral attention (t=0.48; p=0.039), and fronto-parietal (t=0.56; p=0.021) networks, as well as between the ventral attention and the fronto-parietal (t=0.51; p=0.037) networks, and between the dorsal attention network and the somatomotor cortex (t=0.62; p=0.012). (B) Surface-wide statistical comparisons between novices and experts after averaging RS, OP and LKC eccentricity maps. Many clusters mainly belonging to the sensorimotor (SM), dorsal attention (DA), ventral attention (VA), and limbic (Lim) networks show less dispersed vertices for experts than for novices. (C) The B2B regression method was computed, using the indicated labels as features and dispersion metrics as signals. An encoder was used on top of a decoder to determine the importance of features despite their shared covariance. The DDS was

found to be the only significant feature (β=0.31; p=0.043). (D) The dispersion metrics were used to predict DDS scores using B2B on each metric. The color code is the same as in Figure 2A with the difference that blue corresponds to an anti-correlation and red to a correlation between the DDS and the corresponding dispersion metric. The results show that the DDS can predict mainly the same metrics that are significant in Figure 3A. A higher DDS trait score is associated with less dispersion in these metrics. More specifically, a higher DDS score was associated with lower average eccentricity in SM (β=0.13; p=0.023), VA (β=0.09; p=0.046) and limbic (β=0.11; p=0.034) networks. A higher DDS score was also associated with less dispersion between the SM network on one side and the DA (β=0.21; p=0.006), VA (β=0.1; p=0.038), limbic networks (β=0.15; p=0.016), and DMN (β=0.11; p=0.029) on the other side, and between the limbic and the VA networks (β=0.11; p=0.036), and between the FP network and the DMN (β=0.15; p=0.015).