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Striatal functional connectivity associated with Sahaja Yoga meditation

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Neuroscience research has associated meditation practice with effects on cognitive, motivational and emotional processes. These processes are mediated by several brain circuits, including the striatum and its associated cortical connections. The aim of this study was to focus on the striatum and test how its functional connectivity is affected in long-term practitioners of Sahaja Yoga Meditation. We studied differences between resting and meditation states in a group of 23 Sahaja Yoga Meditation experts. We also compared the resting state between meditation experts and a control group of 23 non-meditating participants. Functional connectivity contrasts between conditions and groups were performed using seeds in the dorsal and ventral striatum (caudate, putamen and nucleus accumbens). During meditation, compared to the resting state, meditators showed altered connectivity between the striatum and parietal, sensorimotor and cerebellar regions. Resting state in meditators relative to that of controls showed reduced functional connectivity between the left accumbens and the mid cingulate, which was correlated with reduced Simon Task interference reaction time effect in meditators. In conclusion, the striatum may play a pivotal role in the practice of Sahaja Yoga Meditation by altering attention and self-referencing, and by modulating bodily sensations. Furthermore, meditation practice could produce long-term changes in striatal connectivity.

The practice of meditation is frequently associated with subjective experiences of calmness and equanimity, and changes in cognition, attention, emotion and motivation. The term meditation has been described as a group of cognitive and emotional regulatory practices affecting a wide range of mental processes[1,2]. Particularly, Sahaja Yoga Meditation (SYM) allows meditators to perceive the state of a subjective subtle body which includes different centres or chakras. Through active focusing of their attention on these centres, the meditators achieve a state of thoughtless awareness or mental silence[3–5]. In this deep meditative state, individuals have very few or no thoughts while maintaining full awareness of their surroundings and inner selves. Reduction or elimination of thoughts is the key goal of meditation as originally conceived in the East[6]. Mental silence is a state of high efficiency, combining calmness with alertness, where the meditators are fully present[4,7]. A major goal of many studies in the past twenty years has been to identify brain anatomy and brain function correlates of meditation and its positive effects on cognition and emotion that could help to understand and further develop equanimity. Indeed, brain imaging studies have shown functional, structural[8,9] (but see[10]), and connectivity changes associated with meditation[11,12]. Effects of Meditation have been reported for several networks, including the default mode network (DMN), the salience network and the central executive network (CEN)[1,13–15].

The striatum (caudate, putamen and nucleus accumbens) has been shown to subserve motor, cognitive and motivational processes[16–25], and their alterations[20,26–33]. Furthermore, several fMRI studies have found the striatum to be involved in meditation[11,34–38]. Lazar et al.[39] and Tang et al.[40] reported increased activity in the caudate and putamen, which have been related to the maintenance and onset of the meditation state (MS)[39,40], respectively, as well as to attention and self-regulation, and to enhanced reward activity during the MS[41–44]. Other neuroimaging studies on meditation have related reduced caudate and putamen function to less

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susceptibility to reward incentives in mindfulness meditators during reward anticipation and outcome[34,45]. In SYM, striatal activation and associated medial prefrontal cortex connectivity effects have been related to mental silence experienced in the meditative practice[11], which suggested that the experience of the depth of mental silence could be related to cortico-striatal circuitry regulating top-down attention and emotional control[11].

However, the striatum has been usually absent from theoretical proposals and models of the neural correlates of meditation[14,46]. Only recent seed-based connectivity analyses have shown effects of meditation directly from striatal structures. Santarnecchi et al.[47] described reduced functional connectivity (FC) during resting state (RS) after mindfulness-based stress reduction meditation training between the anterior putamen and anterior cingulate cortex, and reduced cerebellum connectivity with posterior putamen during meditation. These authors associated mindfulness practice with a readjustment of the dorsal striatum, particularly affecting pain and attention modulation[47]. In another study, open monitoring meditation and focused attention meditation showed reduced FC between the striatum and the posterior cingulate cortex; additionally, open monitoring meditation has exhibited reduced ventral striatum FC with the visual cortex and retrosplenial cortex, related to attention and memory function, while focused attention meditation showed the opposite effects[48].

Our goal in this study was to provide a detailed striatum connectivity analysis using an early FC survey of striatal circuitry in humans[48–50] during MS compared to RS, to identify SYM related connectivity attributes (state effects); as well as comparing RS between SYM experts and non-meditators, as a test to contrast potential long-term MS effects on regular day-to-day striatal connectivity (trait effects). Given the impact of meditation effects on mental processes subserved by the striatum, and prior evidence of striatal functional connectivity changes associated with other meditation techniques[47,48] and with the state of MS in SYM[11], we hypothesized that SYM would have effects on FC between the striatum and frontal, parietal and cerebellar cortices during the MS and the RS. Particularly, we expected that the striatum´s pattern of connectivity would be related to the previously observed patterns of functional changes and effects of meditation on brain regions of the DMN, SMN and the CEN. Furthermore, given the association between meditation and improved behavioural self-control and cognitive control functions[51], including findings of better interference inhibition skills in long-term meditators of SYM[11,12], and the association between fronto-striatal connections and inhibitory control[52–54], we also tested for associations between FC changes induced by meditation with behavioural measures of impulsivity and cognitive measures of cognitive control in a Go-no-go task of motor inhibition and a Simon task of interference inhibition.

Results
The comparison between MS and RS in meditators revealed significant FC differences for the seeds in the ventral striatum inferior/nucleus accumbens (VSi), ventral striatum superior/ventral caudate (VSs), dorsal caudate (DC), and ventral rostral putamen (VRP). FC analyses also revealed significant differences between SYM experts and controls during the RS in the VSi and dorsal rostral putamen (DRP) seeds, as a measure of trait-like brain alterations related to long-term meditation practice. Additionally, as previously reported by Barrós-Loscertales et al., neuropsychological measures (Go/No-Go and Simon tasks, see methods section) revealed, for SYM practitioners relative to non-meditators, significant reduced interference reaction time effect (RT) in the Simon task [t(41) = 2.33; p = 0.04] and increased self-control as measured in the Barrat Impulsivity Scale (BIS-11) [t(44) = 5.81; p = 0.02][12].

Differences between MS and RS within meditators
Ventral striatum
A main effect for both left and right seeds in the VSi was reduced FC during MS relative to RS in the primary sensory and motor cortex, premotor, supplementary motor area (SMA) and paracentral lobule (see Fig. 1; Table 1).

The right VSs showed a significant increase of FC during MS compared to RS with the left and right anterior lobes of the cerebellum and parts of the pons (see Fig. 2; Table 1).

Dorsal caudate
MS compared to RS showed a significant increase in FC for left and right DC seeds with the superior parietal lobe, the angular gyrus and parts of the superior occipital lobe (see Fig. 3; Table 1).

Ventral rostral putamen
The right VRP seed demonstrated significantly reduced FC with the left inferior parietal lobe during MS when compared with RS (see Fig. 4; Table 1).

Differences between meditators and controls during RS
Ventral striatum
Left VSi seed showed significant reduced FC for meditators, relative to non-meditators, in the mid-cingulate (see Fig. 5; Table 2). Furthermore, reduced FC was significantly positively correlated with the reduced Simon interference RT effect in the meditators (z = 2.1; p = 0.04).

Dorsal rostral putamen
In the left DRP seed, meditators relative to non-meditators had significant reduced FC with right cerebellum, declive and temporal lobe, fusiform gyrus (see Fig. 6; Table 2); as well as increased FC with right medial and superior frontal gyrus and a smaller portion of the same regions on the left side of the brain (see Fig. 6; Table 2).
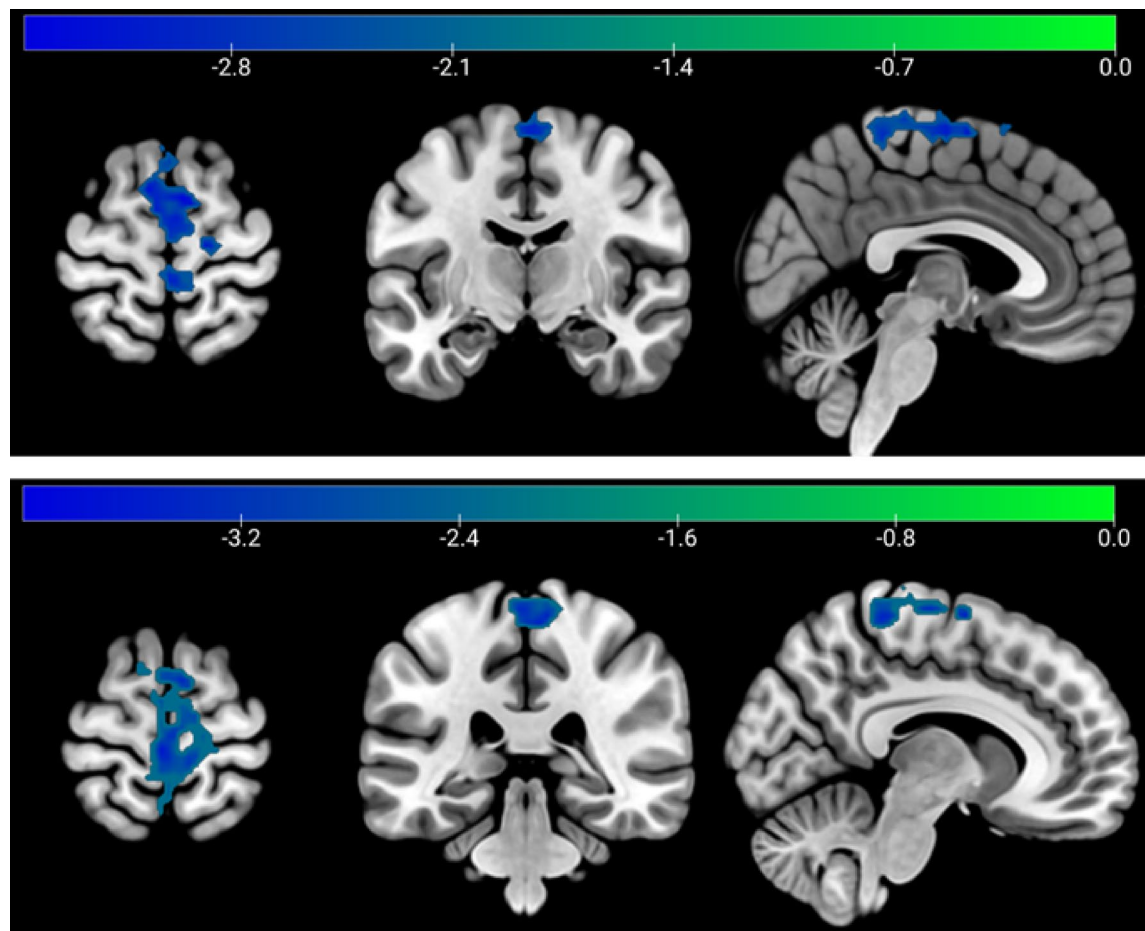
Fig. 1. MS Comparison with RS in meditators: VSi seeds showed reduced FC with somatosensory, motor, premotor and paracentral lobule cortical regions (left VSi (top, MNI coordinates: 3-11 66) and right VSi (bottom, MNI coordinates: 8-34 68)).

Seed	Result	Hemisphere	Cluster size (voxels)	Peak T-value*	Peak MNI coordinates (X Y Z)
Right VSi	Sensorimotor cortex, SMA, premotor, paracentral lobule	Bilateral	284	− 4.09	6 0 66
Left VSi	Premotor, SMA, premotor Paracentral lobule	Bilateral	236	− 3.50	− 12 6 69
Right VSs	Cerebellum Pons	Bilateral	156	3.79	− 18 − 42 − 39
Right DC	Parietal lobe, angular gyrus	Right	282	3.71	36 − 69 48
Left DC	Parietal lobe, angular gyrus	Right	318	4.22	18 − 87 42
Right VRP	Parietal lobe, supramarginal gyrus	Left	181	− 4.44	− 48 − 36 45

Table 1. FC differences between MS and RS in expert meditators. * Positive and negative T-values indicate the positive or negative FC between Seed and Result regions during meditation.

Discussion

This study shows that SYM changes striatal FC with cortical and subcortical regions during the meditation state (during MS versus rest), as well as potential long-term meditation alterations on RS striatal connectivity. We observed that during the MS, multiple areas of the striatum showed FC changes with regions from distinct brain networks involved in previous meditation studies such as CEN, DMN and sensorimotor network (SMN). Additionally, we observed that the RS of meditators relative to non-meditators showed reduced FC between striatal nuclei and cerebellum, while displaying increased FC with the anterior DMN and reduced FC with the mid-cingulate cortex, suggesting carry-over lasting effects of meditation onto day-to-day brain function in expert SYM practitioners. Therefore, the striatal connectivity with the cortex and the cerebellum is changed during meditation (as a state) and altered as a consequence of this practice (as a trait).
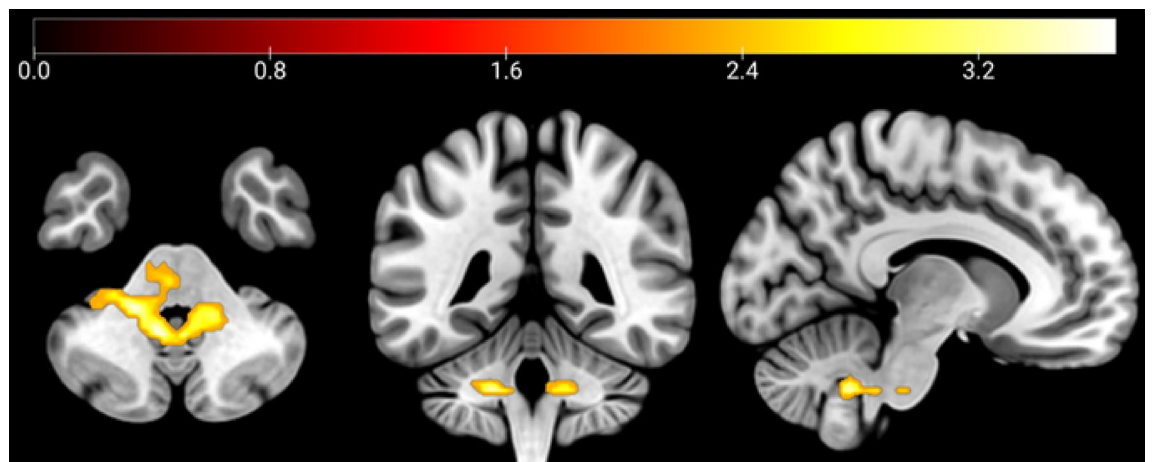
Fig. 2. MS Comparison with RS in meditators: Right VSs seed showed increased FC with cerebellar and pons (MNI coordinates: -8 -43 -38).
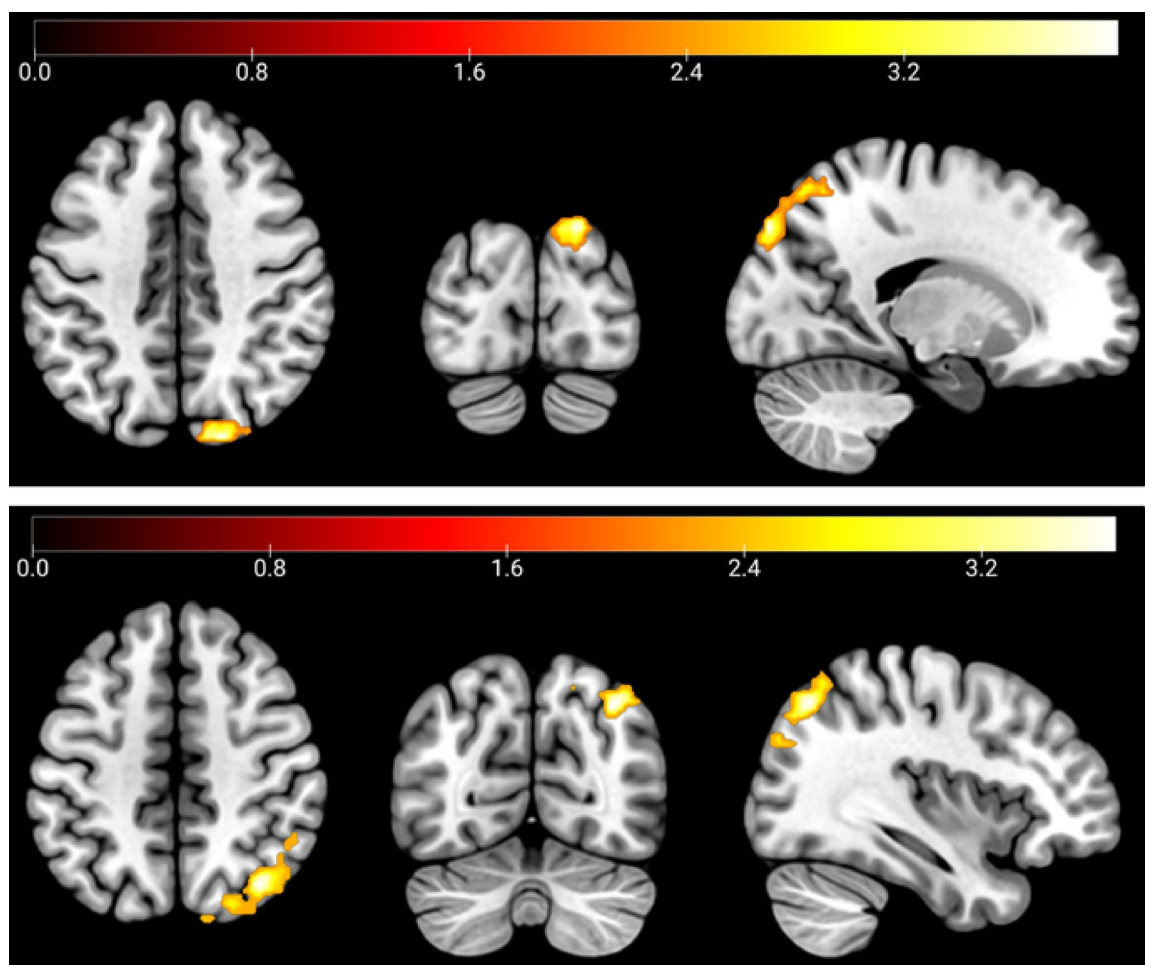

Fig. 3. MS Comparison with RS in meditators: Left DC seed showed positive FC with the medial superior parietal lobe and occipital lobe (top, MNI coordinates: 18-87 42). Right DC seed showed positive FC with the angular gyrus in addition to parts of the superior parietal area (bottom, MNI coordinates: 35-68 47).
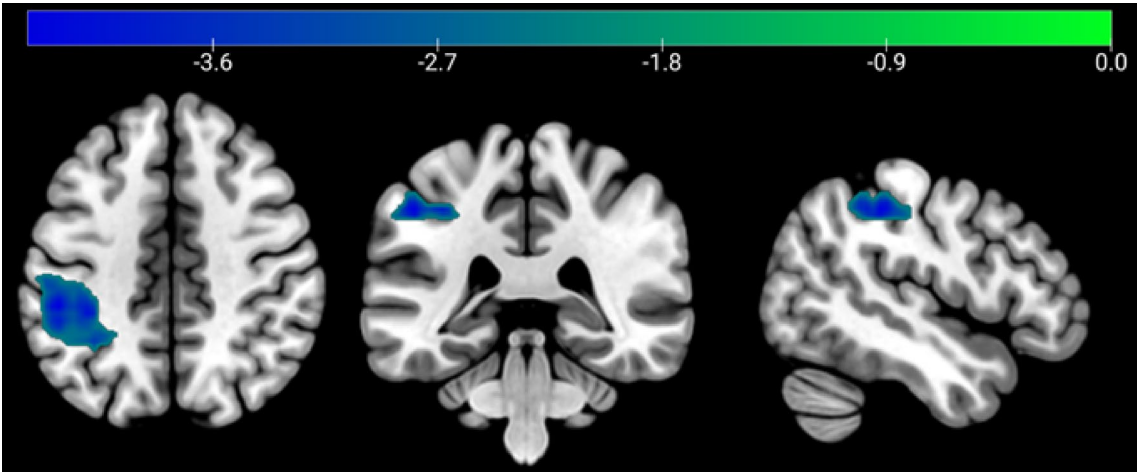
Fig. 4. MS Comparison with RS in meditators: Right VRP seed showed negative FC with a parietal lobe cluster in the supramarginal gyrus (MNI coordinates: -48 -37 45).
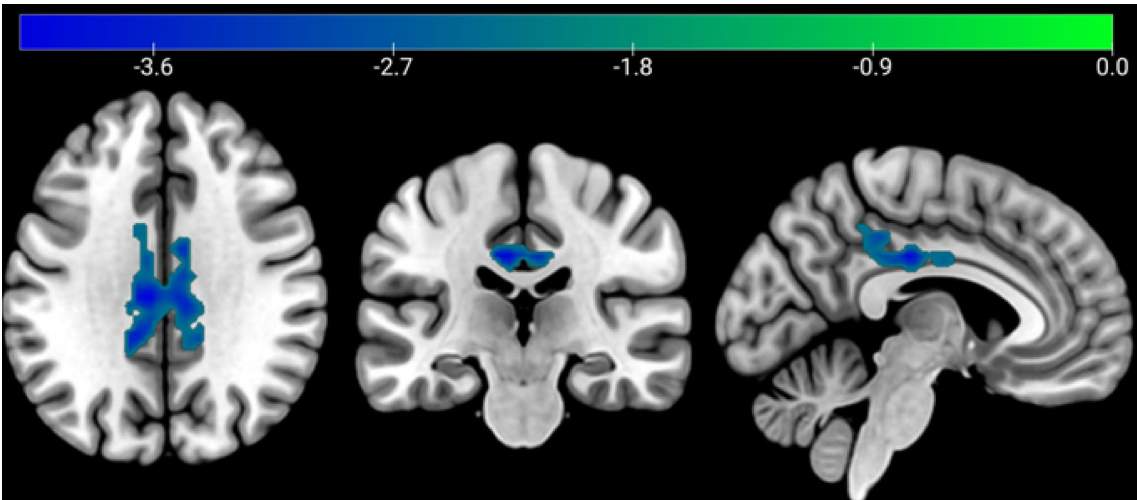

Fig. 5. RS comparison between meditators and controls: Left VSi seed showed negative FC with the Mid-cingulate cortex (MNI coordinates: -6 -24 33).

Seed	Result	Hemisphere	Cluster size (voxels)	Peak T-value*	Peak MNI coordinates (X Y Z)
Left VSi	Mid-cingulate cortex	Bilateral	218	− 4.15	− 6 − 24 33
Left DRP	Cerebellum, declive	Right	164	− 3.74	27 − 66 − 18
	Dorsomedial prefrontal cortex, BA9	Right	170	4.57	18 45 33

Table 2. FC differences between expert meditators and controls during rest. *Positive or negative T-values indicate positive or negative FC between Seed and Result regions for meditators compared to Controls during Rest.

Meditators strengthened attentional orientation during meditation

Interestingly, when comparing MS with RS in meditators, we observed increased FC of the DC with the medial and lateral parietal regions. Previous meditation research has highlighted the role of caudate as a neural hub, showing larger caudate connectivity to a wide range of brain regions and associating it to different brain circuits and multiple cognitive abilities[55,56]. However, considering that DC is thought to be a central node between frontal and parietal regions[57], as well as functionally connected to the CEN[58], this result of increased FC connectivity with lateral parietal regions is consistent with previously observed increased CEN intra-network connectivity for different meditation techniques[59–61]. Especially, lateral portions of the parietal cortex are considered active
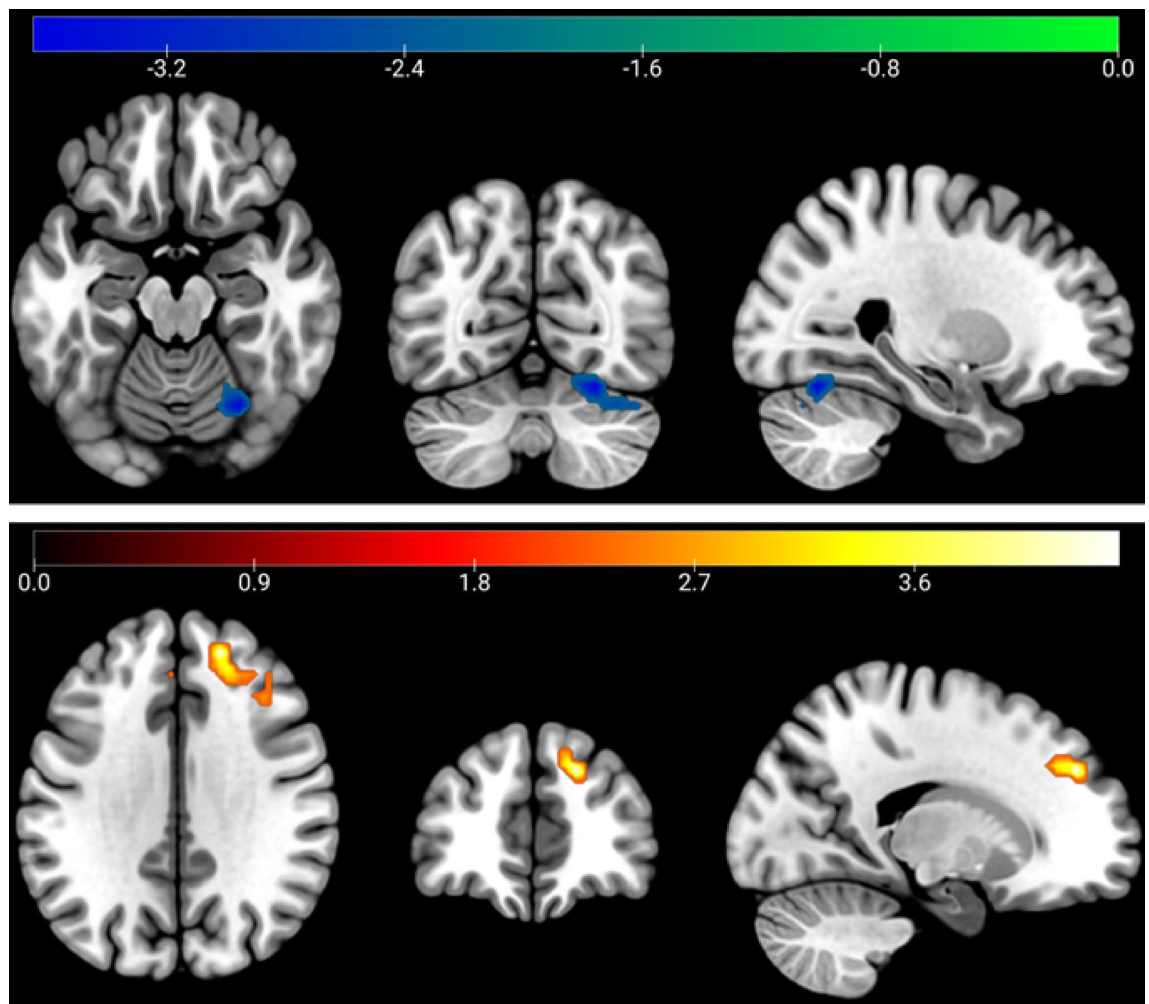
Fig. 6. RS Comparison Between meditators and controls: Left DRP seed showed negative FC with the cerebellum (top, MNI coordinates: 26-66 -18), and positive FC with the dorsomedial/ prefrontal cortex (bottom, MNI coordinates: 18 45 33).

during goal-directed tasks[62,63] and during attentional processes needed for meditation. Thus, if we describe SYM as a conscious and attentional search of mental silence, through focusing on the different centres or chakras, the effect of SYM on the DC increased connectivity with these parietal regions suggests an effect during meditation on attentional orientation[38,64]. Therefore, increasing fronto-parietal activity during goal-oriented events but reducing it during non-targeted ones, favouring the suppression of potential interference from salient, conscious, but non-goal-oriented stimuli[63].

Striatal connectivity alterations relate to better cognitive control

When comparing the RS of SYM experts to that of non-meditators we observed a pattern of reduced connectivity between the VSi and the mid-cingulate. These regions have been associated with attention, reward and pain processes[65], which have been shown to be affected by mindfulness meditation[2,44,66,67]. Previous studies have shown increased connectivity between ventral striatum (nucleus accumbens) and posterior mid-cingulate at pain onset in control conditions (as compared to reward and sleep interruptions)[68]. Interestingly, the VSi-mid cingulate connectivity pattern observed here was higher in non-meditators and related to increased interference RT effect in the Simon task. Meditators, relative to non-meditators, showed decreased Simon task interference RT effect, which is the key behavioural measure in this task. The finding suggests better cognitive control and better ability to inhibit interference/distraction. This is likely due to trait-like effects of years of meditation practice, which may serve as a probe of self-control training during the meditation, which led to Tang et al.[69] to suggest meditation as a self-control training for addiction treatment by the role of the prefrontal and cingulate cortex[12], as well as the striatum.

Meditation related striato-cerebellar connectivity alterations may influence sensory-thalamic processing

Other effects, like the VSi negative FC with sensorimotor regions and increased FC between VSs with the cerebellum/pons during meditation could be understood from a physiological perspective. The cerebellum outputs contain excitatory projections to the thalamus. From the thalamus, excitatory outputs arrive at the striatum and the sensorimotor cortex, modulating their function. This modulation from the thalamus is regulated by the globus pallidus internal (GPi) through GABAergic projections. Previous research has shown that meditation affects the regulation of the basal ganglia (GPi), leading to a reduction in thalamic outputs to the cortex. Consequently, the cortex exhibits reduced activity. We speculate that our finding supports a physiological environment in which external stimuli are suppressed[70], which also may be associated with previous effects showing an increased dopamine release in the striatum[71] and increased GABA levels in the thalamus[72,73] during meditation and after yoga practices, respectively.

At the functional level, previous studies on SYM[74] and other meditation techniques[75–77] have reported increased anterior insula activity during meditation, which was associated with the state of mental silence. Furthermore, previous FC research on anterior cingulate cortex connectivity in SYM practitioners showed increased insular and reduced thalamic connectivity[11], which could be related to the effect of the reception of multisensory and motivational inputs, from sensory afferents and VS/VTA respectively[78]. Thus, as we have suggested in our previous works[11,79] we may be observing an effect where the processing of salient stimuli and external sensory stimuli becomes less relevant compared to the emotional and reward cues, presumably during the state of mental silence. In this sense, the thalamus is also a central node affected by striatal and cerebellar connectivity or coactivation[80]. Compared to the RS of controls, the DRP showed reduced connectivity with cerebellar regions for the RS of the meditators. The activation of these regions has been observed during meditation onset[35,81]. Particularly, Santarnecchi et al.[47] showed the modulatory effects of the cerebellum during meditation by a decrease in inhibitory outputs and excitatory inputs to the motor partition of the putamen. Our pattern of FC with the cerebellum involves more anterior portions of the putamen which may be related to executive functioning. We therefore speculate that the coactivation between the striatum and the cerebellum may influence the thalamus in meditation.

The role of the putamen during the MS and the RS

Additionally, when comparing MS and RS in meditators, we observed a pattern of reduced VRP connectivity with inferior parietal regions, which are part of the DMN. Meditation research has reported reduced posterior DMN activation during meditation[15,37,82–84] as well as decreased posterior DMN intra-connectivity[12,14,59,85]. These effects have been associated with meditative experiences affecting self-related processing and (less) mind wandering[37] and have been suggested to mediate the space- and timelessness experienced during meditation[59,86]. On the other hand, DRP presented a pattern of increased connectivity with medial frontal regions of the DMN during the RS in SYM practitioners relative to controls. Medial prefrontal regions extending to the superior frontal cortex are usually deactivated during the practice of meditation[14,76,81]. We observed increased connectivity between the DRP to these medial prefrontal regions in meditators during RS when compared to controls. Interestingly, this result suggests that the increased connectivity of the putamen with anterior DMN nodes in expert meditators may be in synchrony with lateral frontal regions of the CEN, whose activity has been associated with a change from evaluative to non-evaluative self-monitoring during meditation onset[82]. Also, DRP increased connectivity with dorsomedial PFC may be related to increased processing of online experience[81] as a reflection of increased activation in DMN alongside non-dual related experiences[14]. VRP showed a pattern of reduced connectivity with the inferior parietal region which may be related to the experiential focus on the present moment of the meditator during meditation. Therefore, different portions of the putamen may be related to previously reported regions involving psychological processes related to meditation as a trait and as a state. Taken together, these results of putamen FC agree with the pattern of reduced activation and intra-connectivity in the posterior portion of the DMN and extended regions, and increased anterior DMN activation associated with the meditation practice[14], which may be connected to the putamen as a neural hub[87].

As we stated in the introduction, the striatum has been generally excluded from neurobehavioral models of meditation. In this sense, its inclusion in a hypothetical model of meditation would involve its connectivity with different cortical networks and the cerebellum as a meditation related alteration. Current results and previous analysis of expert SYM meditators[11,12] suggest that daily meditation practice may subserve diverse patterns of cortical connectivity, such as the FC within and between the DMN nodes (e.g., anterior and posterior DMN partitions) and other cortical networks during and after meditation practice[14]. Our study suggests that the striatal nuclei´s functional organization may be subserving psychological processes that are altered during meditation (Fig. 7): Inhibitory control, attentional orientation, self-referencing and sensory processing; as it has been proposed for self-control in meditation-based addiction treatments[69]. Therefore, we suggest the striatum should be included in current meditation models and empirical testing. For example, other models may be supported by the observed FC of the striatum, in which the cortex and the cerebellum may be subserving the deconstruction of predictive error processing as a theoretical model for meditation effects[88–90]. Similarly, future empirical studies may explore the role of meditation effects on cortico-striatal connectivity in everyday-habits[91], learning specializations or planning[92] as well as subjective and neurophenomenological states[12,92,93].

Our study is not without limitations. It is still an open question whether a meditator may actually enter a semi-meditative state during the RS acquisition or whether meditation effects are trait in addition to state effects. For example, Fujino et al.[48] observed that some connectivity changes were sustained from the meditation to the RS. However, the pattern of FC cannot be attributed to meditation or RS since comparing between group effects does not fully allow for causal inference. Thus, longitudinal studies on state and trait related resting and meditation effects need to be studied in randomised controlled designs.
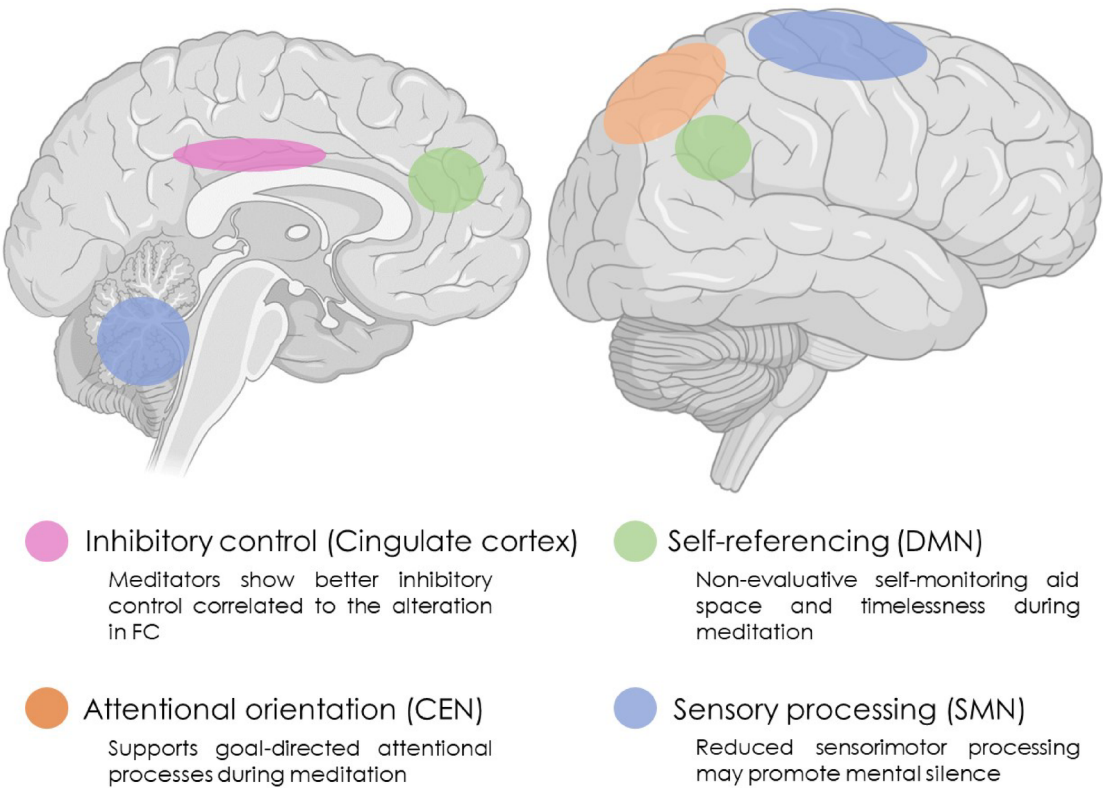
Inhibitory control (Cingulate cortex)
Meditators show better inhibitory control correlated to the alteration in FC

Self-referencing (DMN)
Non-evaluative self-monitoring aid space and timelessness during meditation

Attentional orientation (CEN)
Supports goal-directed attentional processes during meditation

Sensory processing (SMN)
Reduced sensorimotor processing may promote mental silence

Fig. 7. Overview of the alterations of striatal nuclei´s functional organization related to long-term SYM practice.

	Meditators Mean (SD)	Controls Mean (SD)	*p*-value
Age (years)	46.5 (11.4)	46.9 (10.9)	0.89
Education degree, 0 to 6	3.78 (1.2)	4.04 (1.36)	0.50
Height (cm)	167.0 (8.8)	167.2 (7.6)	0.93
Weight (kg)	69.5 (14.6)	71.7 (14.5)	0.60
Body-mass index	24.9 (4.5)	25.5 (3.9)	0.60
Meditation practice (years)	14.1 (6.1)		
Daily meditation practice (minutes)	84.7 (32.2)		

Table 3. Demographic characteristics of the groups and meditation practice related information.

Methods
Participants
Forty-six right-handed, white Caucasian, healthy volunteers participated in the study, 23 SYM experts (17 females) and 23 non-meditators (17 females). Groups were matched on age, gender and level of studies (see Table 3). Volunteers had no physical or mental illness, no history of neurological disorders, no addiction to nicotine, alcohol or other drugs. Different functional and structural aspects of this dataset were analysed in previous studies[5,11,12,94]. The current analyses focus on the strategic comparison of FC of the striatum in the RS and MS in meditators and the comparison between meditators and non-meditators during the RS. Our previous studies analysed the differences in structural imaging[5,94] and in FC during MS and RS separately[11,12] between those two samples based on a different hypothesis.

Meditators were recruited from a local Tenerife SYM group in addition to SYM practitioners attending a seminar of SYM in Tenerife in January 2014. Controls were recruited through local and social networks advertisements. Controls were not practicing any type of meditation or yoga when participating in the study. All participants filled in different questionnaires to evaluate their individual health status, education and age. Meditators additionally filled in a questionnaire to register their experience in SYM, including years of practice and average time dedicated to meditation per day (see Table 3). Three controls reported a minimum meditation experience of less than 6 months' practice before the study. The rest of participants in the control group had no meditation experience. All participants signed informed written consent. The Ethics Committee

of the University of La Laguna approved this study. All experiments were performed in accordance with relevant named guidelines and regulations.

Behavioural and neuropsychological measures of impulsiveness

Equivalent to Barrós-Loscertales et al.[12], given the association between meditation and improved measures of impulsiveness[40,95], differences between expert meditators and non-meditators in behavioural and neuropsychological measures of impulsiveness and its relationship with SYM striatal FC effects were assessed. Thus, the participants were asked to fill in the BIS-11, a self-report questionnaire containing 30 questions which requires participants to answer in terms of frequency (e.g., from "rarely/never" to "almost always"). The items are scored from 1 to 4, yielding a total score and six first-order factors: attentional impulsivity, motor impulsivity, self-control, cognitive complexity, perseverance, and cognitive instability[96].

Two digitalized tasks of cognitive control, motor and interference inhibition (i.e., the go–no-go task and the Simon task), respectively, taken from the adult version of the Maudsley Attention and Response task battery[97,98] were included in the neuropsychological evaluation.

Go/No-Go task

A measure of motor response inhibition, the Go/No-Go task requires a motor response to go stimuli and response inhibition to no-go stimuli. Participants responded with their dominant hand. In 73.4% of trials, a spaceship (go stimulus) pointing right appeared in the centre of the screen, and the participants must press the right arrow key as fast as possible. In 26.6% of trials, a blue planet (no-go stimulus) appeared in the centre of the screen instead of a spaceship, and the participants must inhibit their response. The go and no-go stimuli were displayed for 300 ms, followed by a blank screen for 1 s. There were 150 trials in total (110 go trials, 40 no-go trials). The dependent variable was the probability of correct inhibition to no-go stimuli.

Simon task

This task measures stimulus–response conflict resolution/interference inhibition and selective attention. In this task, arrows pointing left or right appeared on the left- or right-hand side of the screen on a black background. During the task, participants must press the keyboard´s arrow key corresponding to the direction of the arrow in the screen as fast as possible. In 72.73% of trials, the arrow points to the same side of the screen that it appears on and are hence congruent; the remaining 27.27% trials are incongruent trials (e.g., the arrow points to the opposite side of the screen it appears on). Response conflict arises between the iconic information (i.e., a left-hand keyboard response to a left- pointing screen arrow) and the predominant, incompatible spatial information (i.e., the screen´s arrow appears on the opposite side of the screen it is pointing toward). This conflict is typically reflected in slower RT to incongruent relative to congruent trials, and the difference between these trials (RT incongruent – RT congruent) is called the Simon RT effect[99].

Yellow arrows were displayed on black backgrounds and then followed by a blank screen with an inter-stimulus interval of 1400 ms. There were 220 trials in total, 160 congruent trials (80 left tip arrows, 80 right tip arrows) and 60 incongruent trials. The dependent variable is the Simon RT effect (i.e., RT incongruent – RT congruent, the Simon RT effect).

MRI acquisition and RS protocol

Axially oriented functional images were obtained by a 3T Sigma HD MR scanner (GE Healthcare, Waukesha, WI, USA) using an echo-planar-imaging gradient-echo sequence and an 8-channel head coil (TR = 2000 ms, TE = 21.6 ms, flip angle = 90°, matrix size = 64 × 64 pixels, 37 slices, 4 × 4 mm in plane resolution, spacing between slices = 4 mm, slice thickness = 4 mm, interleaved acquisition). High-resolution sagittal oriented anatomical images were also collected for anatomical reference, acquired for 12 min and 44 s, for this purpose a 3D fast spoiled-gradient-recalled pulse sequence was obtained with the following parameters: TR = 8.761 ms, TE = 1.736 ms, flip angle = 12°, matrix size = 256 × 256 pixels, 0.98 × 0.98 mm in plane resolution, spacing between slices = 1 mm, slice thickness = 1 mm. The participant's head was stabilized with foam pads. The slices were aligned to the anterior commissure—posterior commissure line and covered the whole brain.

Functional scanning was preceded by 18 s of dummy scans to ensure tissue steady-state magnetization. Then, the scanning sequence was as follows: (1) Resting state: 6 min (180 volumes). (2) Acquisition of anatomical images: 12 min and 44 s, with instructions to initiate meditation at the beginning of this period. (3) Meditation state (meditation group): 6 min (180 volumes). This sequence lasts a total of 24 min and 44 s, leveraging the 12 min and 44 s required for the T1 acquisition to allow the meditators to deepen their meditation. As a result, at the start of the dedicated meditation state period, participants should ideally already be in a state of deep meditation. All three phases were conducted with eyes closed and without the presence of music.

Instructions to participants

For the meditation scan, experts were instructed to close their eyes and to go into meditation, trying to achieve the state of mental silence. For the RS functional scan, all participants were explicitly instructed to close their eyes, relax, lie still, allow their mind to wander and not to fall asleep. Moreover, expert meditators were explicitly instructed not to meditate during the resting scan.

After de scanner session all volunteers reported through questioners the degree of achievement of MS and RS inside the scanner. Meditators reported their performance during the scanning acquisition of their perception of mental silence in a scale of 1 (not achieving mental silence) to 5 (performing a good meditation with mental silence most of the time). The average of the mental silence scores was 3.09 and, moreover, these scores correlated with the usual/at home perception of mental silence reported by participants (r (22) = 0.67, $p < 0.001$).
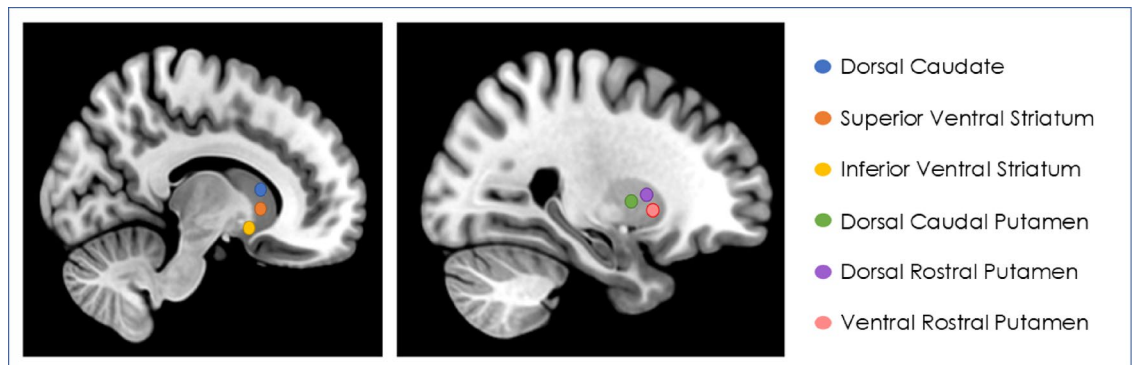
Fig. 8. Visual representation of the striatal regions of interest.

Data preprocessing

All the images were preprocessed using the Data Processing Assistant for Resting-State fMRI Advanced Edition (DPARSF-A) toolbox version 3.2, which is part of the Data Processing and Analysis of Brain Imaging (DPABI) toolbox version 1.2 [100]. Preprocessing steps included: (1) slice time correction by shifting the signal measured in each slice relative to the acquisition of the slice at the mid-point of each TR; (2) realignment using a least squares approach and a 6 parameter (rigid body) spatial transformation; (3) co-registering individual structural images to the mean functional image of each subject; (4) T1 images were segmented into grey matter, white matter and cerebrospinal fluid using the diffeomorphic anatomical registration through exponentiated lie algebra (DARTEL)[100]; (5) spatial normalization of functional volumes by using the parameters extracted from the anatomical segmentation procedure in each subject and resampling voxel size to $3 \times 3 \times 3$ mm^3; (6) spatial smoothing with a 4-mm full-width-at-half-maximum Gaussian kernel; (7) nuisance regression, including principal components (PC) extracted from subject-specific white matter and cerebrospinal fluid masks (5 PC parameters) using a component based noise correction method[101], as well as Friston 24-parameter model (6 head motion parameters, 6 head motion parameters one time point before, and the 12 corresponding squared items)[102]. The component-based noise correction method procedure here consisted of detrending, variance (i.e., white matter and cerebral spinal fluid) normalization and PC analysis according to Behzadi[101] (8) band-pass temporal filtering (0.01–0.1 Hz).

To quantify head motion, the frame-wise displacement (FD) of time series was computed based on Jenkinson et al.[103] as suggested by Yan et al.[104]. The mean FD was controlled as a covariate of no interest in statistical analyses in order to reduce the potential effect of head motion. Following the criteria mentioned by the DPARSF developers[104], one control and one meditator subjects were excluded because their head motion was beyond 2.0 mm and/or 2.0º.

The selection of seed regions

We used a priori defined regions of interest (ROIs) as seed regions, subdividing the striatal subregions in MNI space following Di Martino et al.[49]: Ventral striatum inferior/nucleus accumbens, ventral striatum superior/ventral caudate, dorsal caudate, dorsal caudal putamen (DCP), dorsal rostral putamen, and ventral rostral putamen (Fig. 8). One set of spherical seeds with radius 3.5 mm was created for each hemisphere, generating a total of 12 ROIs.

FC analyses

The analysis was carried out using functions in DPABI toolbox version 5.1 [100]. For FC, voxel-wise FC was calculated based on the predefined seed regions. Specifically, the mean time series were firstly computed for each participant by averaging the time series of all the voxels within the seed region, and then Pearson's correlation between the mean time series of the seed region and time series of all other voxels within the whole brain was computed. The individual level correlation map (*r*-map) was obtained for each subject, and subsequently, all *r*-maps were converted into *z*-maps with application of Fisher's *r*-to-*z* transformation to obtain approximately normally distributed values for further statistical analyses.

We contrasted the RS and MS FC maps within meditators using the "y_TTestPaired_Image" function, from DPABI[104], to determine condition differences (Meditation vs. Resting in meditators) for each of the selected seed regions. Also, we compared RS FC maps between meditators and controls using the "y_TTest2_Image" function, in DPABI[104], to determine if there were group differences (Meditators vs. controls during Resting) in FC between each of the selected seed regions and other regions in the brain. In the independent t-tests, we controlled for age and gender. The resulting connectivity maps between meditators and controls were corrected for multiple comparisons using the "y_GRF_Threshold" function in DPABI[104] based on Gaussian Random Field Theory (GRF), with a threshold of $|Z| > 2.3$ (cluster-wise $p < 0.05$, GRF corrected).

Data availability

Data is available upon request to the corresponding author.

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Author contributions

OPD: design, analysis, interpretation of the data, draft and supervision of the work. SEHA: design, acquisition and supervision of the work. LLB: interpretation of the data, draft and supervision of the work. YX: analysis and supervision of the work. JLGM: acquisition and supervision of the work. KR and ABL: interpretation of the data, draft and supervision of the work. All authors have approved the submitted version and have agreed both to be personally accountable for the author's own contributions and to ensure that questions related to the accuracy or integrity of any part of the work, even ones in which the author was not personally involved, are appropriately investigated, resolved, and the resolution documented in the literature.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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