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Research Article

Nonlinear brain correlates of trait self-boundarylessness

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Abstract

Alterations of the sense of self induced by meditation include an increased sense of boundarylessness. In this study, we investigated behavioural and functional magnetic resonance imaging correlates of trait self-boundarylessness during resting state and the performance of two experimental tasks. We found that boundarylessness correlated with greater self-endorsement of words related to fluidity and with longer response times in a math task. Boundarylessness also correlated negatively with brain activity in the posterior cingulate cortex/precuneus during mind-wandering compared to a task targeting a minimal sense of self. Interestingly, boundarylessness showed quadratic relations to several measures. Participants reporting low or high boundarylessness, as compared to those in between, showed higher functional connectivity within the default mode network during rest, less brain activity in the medial prefrontal cortex during self-referential word processing, and less self-endorsement of words related to constancy. We relate these results to our previous findings of a quadratic relation between boundarylessness and the sense of perspectival ownership of experience. Additionally, an instruction to direct attention to the centre of experience elicited brain activation similar to that of meditation onset, including increases in anterior precentral gyrus and anterior insula and decreases in default mode network areas, for both non-meditators and experienced meditators.

Keywords: fMRI; DMN; self-boundaries; self-referential processing; minimal self; perspectival ownership of experience

Highlights

- Trait self-boundarylessness showed a U-shaped relation to resting-state default mode network connectivity.
- Trait self-boundarylessness showed an inverse U-shaped relation to medial prefrontal cortex activity during self-referential processing.
- Trait self-boundarylessness correlated with endorsing more words relating to fluidity as self-descriptive and with longer response times in a math task.
- An instruction to direct attention to the centre of experience elicited a brain activation pattern similar to that of meditation onset.

Introduction

The complex construct of the self has been usefully divided into two aspects: the narrative and minimal self (Gallagher 2000), following James (1890). The narrative self refers to a conceptual understanding of ourselves as temporally extended persons, while the minimal self has to do with a momentary sense of being separable from the surroundings. The most minimal kind of self is arguably the sense of perspectival ownership of experience (Albahari 2010), a first-person perspective that amounts to nothing more than the sense that experiences are presented to, or experienced by, a kind of centre, observer, or witness.

A central aspect of the experience of self refers to a sense of separateness, duality, or boundedness in relation to the world. This can appear in different ways, pertaining to, e.g., life history and identity, the spatial location of the self in relation to the surroundings, the extent of one's possibility to influence the course of events through agency, or the division between 'mine' and 'not mine' applied to physical or mental phenomena (Lindström et al. 2022). This ordinary sense of being a bounded self can be altered through meditation, and such changes may occur not only during the meditative practice itself but also gradually become part of the practitioner's everyday life—a trait-level alteration (Lindahl and Britton 2019, Raffone et al. 2019). The purpose of our study was to investigate brain correlates of trait-level sense of self-boundaries in participants with varying meditation experience during rest, a narrative self task, and a minimal self task focused on the sense of perspectival ownership of experience.

Previous brain imaging studies suggest that a decreased sense of self relates to decreased activity of the default mode network (DMN; e.g. Schoenberg et al. 2018) and increased connectivity between DMN and the fronto-parietal network (FPN, e.g. Josipovic

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et al. 2012). Decreased activity in the main DMN hubs posterior cingulate cortex (PCC), medial prefrontal cortex (mPFC), and inferior parietal lobes/temporo-parietal junction (IPLs/TPJ) is a common finding across various studies on meditation (Fox et al. 2016, Raffone et al. 2019) and also been found in studies of transient states of self-transcendence induced by hypnosis and psychedelic drugs (e.g. Demertzi et al. 2011, Carhart-Harris et al. 2012, 2016, Lipari et al. 2012; see Cardeña and Lindström 2021, for a review). Although not specifically targeting selflessness, several studies on meditators during rest have reported trait-level increases in within-network connectivity of the DMN and FPN and increased between-network connectivity for the DMN, FPN, and the salience network (SLN; e.g. Lutz, et al. 2004, Brewer et al. 2011, Jang et al. 2011, Hasenkamp and Barsalou 2012, Taylor et al. 2013, Bauer et al. 2019). However, findings on resting-state alterations in meditators diverge (Mooneyham et al. 2016), and it is important to consider the detailed phenomenology of the targeted states. For example, in focused attention meditation, self-related processing is actively suppressed and thus decreased DMN activity is an expected finding, while in open monitoring meditation the goal is not to suppress but to attend to the free movement of the mind, which may or may not include DMN activity (Lutz et al. 2015). Along these lines, Xu et al. (2014) found higher activity in the PCC during nondirective meditation compared to rest. Increased DMN connectivity has been linked to an increased sense of wakefulness during meditation and decreased anticorrelation between networks to attention systems being active also at rest (Britton et al. 2014).

In an illuminating magnetoencephalography study, Dor-Ziderman et al. (2013) investigated the neural correlates and phenomenology of narrative and minimal self and of selfless experience. This study reported that narrative self corresponded to gamma activity in the medial and (predominantly left) lateral frontal areas and thalamus and minimal self to beta activity in partly overlapping areas including the left ventral mPFC and thalamus and right premotor cortex and in the (predominantly right) IPL, PCC, precuneus, and insula. When meditators entered the selfless mode from the minimal mode, activity in the areas implicated in minimal self decreased. The level of decrease in the right IPL and left dorsomedial thalamus correlated with reports of lack of sense of ownership in the selfless state. In a follow-up case study, Dor-Ziderman et al. (2016) targeted the sense of boundarylessness in selfless experience, an experience described as lacking both ownership and centredness. The study found pronounced decreases in beta activity during experiences of boundarylessness in two major areas: the bilateral TPJ and medial parietal cortex. In addition, beta decreases were seen in the primary sensory and motor regions, insula, and right supplementary motor area (SMA). Likewise, Fingelkurts et al. (2022) found that a decrease in electroencephalography (EEG) synchrony in bilateral posterior DMN areas correlated with an experience of expanding self-boundaries. Similar results come from a functional magnetic resonance imaging (fMRI) study by Farb et al. (2007), who found activity in the mPFC in narrative self-processing and decreases in this area in minimal self, defined as present-moment experiencing. In addition, minimal self was associated with increased activity in the right prefrontal cortex, insula, secondary somatosensory cortex, and IPL.

The aforementioned studies thus point to an involvement of anterior and left-lateralized areas of the DMN (mPFC) in narrative self and an involvement of posterior and right-lateralized areas of the DMN (PCC/precuneus and IPL) in minimal self. However, other studies point to a more distributed set of brain regions involved in both these aspects of self. A recent meta-analysis of 125 studies on neural correlates of mental self-processing identified both anterior and posterior parts of DMN (mPFC, PCC, and TPJ) and several other areas (ACC, anterior insula, left thalamus, superior frontal gyrus, and right premotor cortex) as involved in the narrative self (Qin et al. 2020). An automated meta-analysis by Frewen et al. (2020) likewise found all the major hubs of the DMN (mPFC, PCC, and TPJ) and the ACC, frontal and temporal poles, and perirhinal cortex to be activated in verbal self-referential processing (SRP). In a study targeting minimal self, Fingelkurts et al. (2020) reported a decrease in functional connectivity, measured by EEG, in the mPFC in experienced meditators who were instructed to downregulate the sense of first-person perspective. Likewise in two previous studies (Fingelkurts et al. 2016a, 2016b), mPFC synchronicity increased with meditation training. The authors relate this increase to the sense of being a witnessing observer.

Despite these discrepancies, we conclude that the findings for both trait and state selflessness, pertaining to narrative and minimal self, relate strongly to alterations of DMN activity, mostly in a negative direction. Indeed, converging findings suggest that the DMN midline regions account for self-specificity at several levels, both explicit and implicit (Northoff 2016). The fact that the DMN is also the brain's default state, being active in the absence of tasks, can be seen as an indication that the self relates to a central and basal function of the brain (Northoff 2016). However, this is not universally consistent; in addition to the alterations seen as an effect of meditation, a recent cross-cultural investigation suggests that DMN connectivity and activity correlate negatively to collective and holistic thinking (Luo et al. 2022).

The present study

To target the neural correlates of trait self-boundarylessness both in rest and in relation to narrative and minimal self, we collected functional brain data in three contexts: a resting state, a standard SRP task using trait adjectives, and a novel 'checking-in' task intended to strengthen the sense of perspectival ownership of experience by asking participants to focus on their centre of experience and the sense of being an observer.

The fMRI data were correlated to a self-report measure of boundarylessness. As our previous qualitative analysis of interview data revealed a quadratic relation between this measure and descriptions of perspectival ownership of experience (Lindström et al. in preparation), we tested both linear and quadratic relations between boundarylessness and brain data and behavioural data using polynomial linear regression.

For the resting state, we expected DMN connectivity to correlate with boundarylessness. For the two experimental tasks, we hypothesized that the fMRI blood oxygenation level dependent (BOLD) signal activity in the main DMN hubs would correlate with boundarylessness. Thus, we selected the PCC/precuneus, mPFC, and left and right IPL as our a priori regions of interest (ROIs). Because of the role of the thalamus and insula in interoception, we also hypothesized that activity in these regions would correlate positively with boundarylessness in the checking-in task targeting minimal self. We further predicted that boundarylessness would correlate with a more positive and less static self-image, so that more positively valenced trait adjectives and adjectives relating to fluidity, but less negatively valenced words and words relating to constancy, would be endorsed as self-descriptive by more boundaryless participants.

The study was preregistered before fMRI data collection, however some interview and questionnaire data was collected before preregistration. (A further prediction mentioned in the preregistration was that SRP would have less emotional charge for more boundaryless participants, so that there would be a negative correlation between boundarylessness and response times and activity in the amygdala. However, this analysis could not be performed as the amygdala was lost due to an arrow field of view (see Fig. S2). In addition, we aimed to control for heart rate and breathing, but due to technical issues we were unable to obtain these measures for a majority of participants, meaning they could not be controlled for.)

Material and methods

Participants

Participants were recruited through the Lund University Department of Psychology website and an alumni network. We asked for both meditators and non-meditators interested in participating in a brain imaging study on self-consciousness and meditation. All participants signed an informed consent form and stated that they were not currently suffering from or under treatment for any severe mental illness, including depression, dissociation, or psychotic disorders. Participants were interviewed about their everyday self-experience, with a special focus on the sense of boundaries and perspectival ownership of experience. After the interviews they were asked about handedness and MR contraindications (claustrophobia and metal implants), and to estimate their meditation experience in terms of number of years, number of hours per week, and lifetime number of days on retreat, and then they completed a number of self-report scales, only one of which is used in the present study. Participation was compensated with cinema tickets or, if preferred, an equivalent monetary reimbursement. The study was approved by the Swedish Ethical Review Authority, #2020-00525.

Boundarylessness measure

Based on the results of interviews and questionnaires, reported elsewhere (Lindström et al. in preparation), we arrived at a self-rated measure of boundarylessness, which was used in this paper. This measure is an inversion of the Perceived Body Boundaries Scale (Dambrun 2016), a graphic, ungraded visual analogue scale with the end points ‘My body boundaries are almost imperceptible’ and ‘My body boundaries are extremely salient’. The marks made by participants on a 10-cm line were measured in millimetres, rendering an interval of 0–100, inverted so that 0 indicates the maximal sense of boundaries and 100 indicates the maximal boundarylessness. This rating was chosen as it showed excellent agreement with quantitative judgements of trait selflessness based on the phenomenological interviews made by two coders independently (Spearman’s $r = 0.92$ and 0.78, respectively), but with greater variance and reproducibility.

MRI tasks and procedure

Participants were screened for MR safety and informed about what to expect during MR scanning. They were fitted with hearing protection, a four-button keypad in their right hand to respond to tasks, and an emergency contact button in their left hand.

Data were acquired on an actively shielded 7 T Philips MR scanner (Achieva; Philips Healthcare, Best, Netherlands) with a two-channel transmit, 32-channel receive head coil (Nova Medical, Wilmington, MA, USA), and two dielectric pads (Multiwave Imaging, Marseille, France). The MR acquisition consisted of a high-resolution, T1-weighted anatomical image (voxel size $1 \times 1 \times 1\,mm^3$, echo time 1.97 ms, repetition time 5 ms, acquisition time 1.43 min, flip angle = 6 degrees, field of view = $199 \times 251 \times 200\,mm^3$). Three functional runs, one for resting state and one for each of two tasks, were obtained using a gradient echo planar image acquisition sequence with interleaved, oblique (orbitomeatal) axial slices with $2 \times 2 \times 2\,mm^3$ voxels and a 0.2-mm slice gap. Before each functional run, a field map was acquired to correct for inhomogeneities in the magnetic field, and five dummy scans were obtained to allow the MR signal to reach a steady state before data collection.

The first functional run was a resting-state scan lasting 10.43 minutes (350 TRs of 1.8 s each). Participants were instructed to keep their eyes closed and rest but not fall asleep and to not deliberately meditate. The field of view was $224 \times 232 \times 149\,mm^3$ comprising 68 slices.

The second functional run was a SRP task, administered through E-prime (Psychological Software Tools). During this task, adapted from Goldin et al. (2009), participants were administered a set of trait adjectives from the Affective Norms of Emotion Words database (Bradley and Lang 1999). The original 20 positive and 20 negative trait adjectives were translated to Swedish by the first author, slightly modified to make the words more relevant in Swedish, and divided into blocks of five words each, which were either all positive or all negative. To each block, one ‘fluid’ word and one ‘constant’ word judged to be of the same valence as the rest of the block were added (total 16 words relating to fluidity/solidity). Examples of such words were ‘beständig’ (durable; positive-constant), ‘dynamisk’ (dynamic; positive-fluid), ‘statisk’ (static; negative-constant), and ‘flyktig’ (volatile; negative-fluid). Half of the words, evenly distributed across positive and negative, were presented in uppercase, and the other half in lowercase letters. Each word was presented for 3 s, resulting in a total of 21 s per seven-word block. A fixation cross was presented for 4 s between each block. The blocks were presented three times, once in conjunction with each of three questions: ‘describes me?’ (Self condition), ‘is positive?’ (Valence condition), and ‘is uppercase?’ (Case condition). While Self was the condition of primary interest, Valence was included as a close control condition, and Case as a disparate control condition. Block order was the same across participants and was pseudo-randomized, so that no block type was presented two times in a row. The duration of this run was 10.48 minutes (540 TRs of 1.2 s each), and the field of view was $224 \times 232 \times 97\ mm^3$, comprising 44 dynamic slices.

The third functional run was designed to target the sense of perspectival ownership of experience (hereafter checking-in). This task was also presented through E-prime and consisted of simple math questions interspersed with presentations of shapes (circle, square, triangle, or arrow). Participants were instructed beforehand to ‘focus on the centre of your experience, the “experiencer” or “observer”’ whenever the arrow was presented. Again, while Arrow was the condition of interest, Symbol was a close control condition, and Math a disparate control condition. The duration of math blocks (three questions per block) and arrow blocks were fixed to 12 s, whereas the duration of the other symbols was jittered (randomized between two and eight TRs), so that the average was 12 s per block of two symbols. The order of the three conditions (Math, Arrow, and Symbol) was the same for all participants and was pseudo-randomized, so that no block type was presented more than twice in a row. The duration of this run was 12 minutes (600 TRs of 1.2 s each), and the field of view was $224 \times 232 \times 97\,mm^3$, comprising 44 dynamic slices.

All participants were familiarized with the two experimental tasks before scanning by means of a short demo version on a computer. After scanning, a brief recorded interview was conducted to assess the participants' experiences during the resting state and each of the two tasks.

MRI preprocessing and analysis

MR data were processed and analysed using SPM12 (https://www.fil.ion.ucl.ac.uk/spm) and the CONN toolbox for SPM, version 20.b (https://www.nitrc.org/projects/conn), in MATLAB, version R2021a (MathWorks Inc.). Further statistical analyses were done with jamovi 2.2 [jamovi. (Version 2.2) 2021], using the GAMLj module for regression models (Gallucci 2019), and data visualization was done using MRIcroGL 1.2 (https://www.nitrc.org/projects/mricrogl). Preprocessing (preregistered) consisted of realignment to the first slice, unwarping and susceptibility distortion correction using voxel-displacement maps, slice-timing correction to the middle slice, outlier volume scrubbing using ART as implemented in CONN, with 95 percentiles in normative sample for the resting state, and a threshold of <0.9 mm movement and $z<5$ global signal for the tasks, segmentation and normalization to Montreal Neurological Institute (MNI) space for functional and structural images separately, and smoothing with a 6-mm Gaussian kernel. The voxel size of $2\times2\times2$ mm^3 was not resampled during preprocessing.

For the resting state, mean connectivity was computed as means of the correlations of time series for each participant between each pair of DMN hubs, as defined by CONN (see Fig. S1a). These measures were then entered into polynomial regression models to check for linear and quadratic relationships to boundarylessness, employing a significance threshold of $P<.05$. We also performed a seed-based connectivity analysis using each of our a priori ROIs as seeds, with a peak-level threshold of $P<.001$ and a cluster-level threshold of $P<.05$, false discovery rate (FDR) corrected.

For the two tasks, SRP and checking-in, contrasts between the condition of interest and each of the two control conditions were calculated using SPM, first for each participant (first level) and then for all participants (second level). Six movement parameters and variables for scrubbing outlier volumes were added as covariates at the first level. Data were first analysed at the group level using contrasts between the condition of interest and the closest control condition for each task (Self vs. Valence for SRP and Arrow vs. Symbol for checking-in). To look for correlations between boundarylessness and brain activity during the condition of interest, as part of our preregistered plan, we extracted mean beta values for each participant from these contrasts in our a priori ROIs, as defined by the Neuromorphometrics atlas in SPM (Bakker et al. 2015; see Fig. S1b). The analysis was thresholded at $P<.001$ uncorrected at the peak level and $P<.05$ FDR corrected at the cluster level. Due to the exploratory nature of the checking-in task, we decided to also look for correlations to activity in all clusters that were significant at the group level, using the same threshold. This analysis was not part of the preregistered plan but was justified by the novelty of this task. Finally, an exploratory (preregistered) whole-brain analysis was performed looking for clusters where activity significantly correlated with boundarylessness in the condition of interest compared to the two control conditions, using a grey matter mask and a significance threshold of $P<.05$ FDR corrected at the cluster level and a cluster size threshold of $k>10$ (80 mm^3). In all cases we evaluated linear and quadratic relations.

Results

Participants

We recruited and interviewed 32 participants (Fig. 1 and Table S1). Four of these were not included in MR analyses: two cancelled beforehand due to illness, another cancelled at the beginning of the scanning due to ear pain while in the scanner, and one had to be excluded because of brain pathology. Two resting-state runs had to be discarded, one due to technical problems and one due to the participant keeping their eyes open. For two participants, neither of the task runs could be performed due to discomfort in the scanner. In addition, one checking-in run had to be discarded due to technical problems and another due to post-scanning interviews revealing that the participant had misunderstood the task. Thus, the final sample consisted of 26 scans for resting state and SRP, and 24 scans for checking-in, with some variation in the participant groups for each run. The distribution of self-rated boundarylessness of these three groups is displayed in Table S1. Boundarylessness correlated with meditation experience, measured both in years (Pearson's $r=0.46$, $P=.01$), hours per week ($r=0.46$, $P=.01$), estimated total hours ($r=0.58$, $P=.001$), and the number of days on retreat ($r=0.39$, $P=.04$), but not with age ($r=0.07$, $P=.71$).

Two of the participants were left-handed. As neither of the tasks were language-dependent and our ROIs are bilateral, we did not expect handedness to influence the results. The main analyses were run with and without these two participants, which confirmed that there were no alterations other than a slight loss of power.

Resting state

Polynomial regression analysis revealed a significant quadratic relation between boundarylessness and DMN connectivity such that lower and higher levels of boundarylessness were related to greater connectivity ($\beta=0.87$, $P<.001$; Fig. 2). A post-hoc analysis of within- and between connectivity of the FPN and SLN yielded no significant results, but a trend for a quadratic relation with SLN connectivity ($\beta=.50$, $P=.08$; Fig. S3). All model parameters for these analyses are presented in Table S2.

Looking at the connectivity between each pair of DMN hubs separately, the quadratic relation with boundarylessness held separately for the mPFC–right IPL ($\beta=0.93$, $P<.001$) and mPFC–PCC ($\beta=0.67$, $P=.016$), but not for the other four pairs (for details, see Table S2). However, whole-brain seed-based analysis at a stricter significance threshold revealed quadratic relations between the right IPL and a cluster in left angular gyrus/intraparietal sulcus and another cluster in the PCC/precuneus (Table 1 and Fig. 3).

There were no linear correlations between boundarylessness and functional connectivity between our a priori ROIs. The seed-based analysis revealed linear relations between boundarylessness and connectivity of both left and right IPL seeds to a cluster in the cuneus (Table 2 and Fig. 4).

Tasks

Because the field of view was narrow in the inferior to superior dimension for some of our participants, we could not analyse parts of superior parietal, temporal, and fronto-polar areas at the

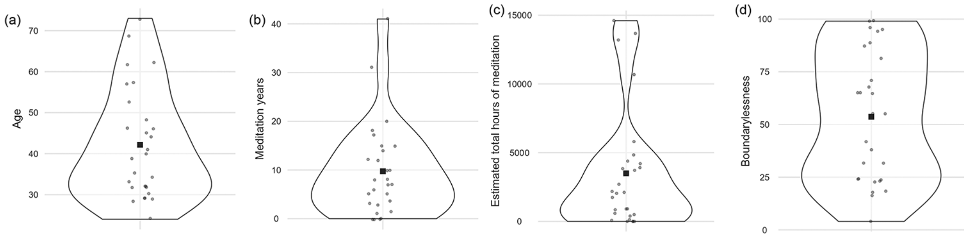


Figure 1 Distributions of (a) age, (b) meditation experience in years, (c) estimated total hours of meditation, and (d) self-rated boundarylessness for the total sample of 28 participants (further details in Table S1)

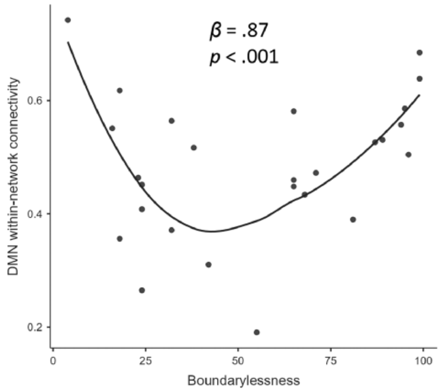


Figure 2 Quadratic relation between boundarylessness and DMN connectivity, with smoothed regression line (see also Table S2 and Fig. S3)

group level for either of the two task runs (see Fig. S2). This loss unfortunately included our a priori ROI the mPFC. To address this limitation, we redefined the mPFC ROI as a sphere with 20-mm radius around the peak coordinates (–6, 48, 0) for the mPFC/ACC cluster derived in the meta-analysis by Qin et al. (2020; see Fig. S1b).

SRP behavioural responses

We examined the correlations between boundarylessness and self-endorsement of the (partly overlapping) word categories positive, negative, fluid, and constant (Fig. S4). With the removal of one participant who did not answer any of the self-questions, there was a positive linear correlation between boundarylessness and endorsing fluidity words ($r = 56$, $P = .003$, Fig. 5a). This relation held for both the positively and negatively valenced words separately (positive: $r = 0.39$, $P = .048$; negative: $r = 0.56$, $P = .003$). In addition, there was an inverted U-shaped relation between boundarylessness and endorsing constancy words ($\beta = –0.60$, $P = .013$, Fig. 5b), which held for the positive but not the negatively valenced words (positive: $\beta = –0.55$, $P = .021$; negative: $\beta = –0.34$, $P = .172$). There were no significant correlations between boundarylessness and the total number of positive and negative words endorsed as self-descriptive or between boundarylessness and response times (all βs and rs < |.34|, all Ps > .09).

SRP fMRI group results

A whole-group analysis ($n = 26$) yielded three large clusters of increased BOLD responses for Self > Valence, in the PCC/precuneus, mPFC/superior frontal gyrus, and left angular gyrus. There were also three clusters of greater BOLD response for Valence > Self, across left and right intraparietal sulcus, lateral occipital cortex, and inferior temporal gyrus. All significant clusters are presented in Table 3 and Fig. 6.

SRP correlations with boundarylessness

There was a significant inverted U-shaped relation between activity in Self > Valence and boundarylessness in our mPFC ROI ($\beta = –0.67$, $P = .008$). This was also reflected in the explorative whole-brain analysis of this contrast, which revealed a cluster in the mPFC that was correlated quadratically with boundarylessness ($\beta = –0.93$, $P < .001$; Fig. 7). There was no significant whole-brain correlations with boundarylessness in the contrast Self > Case.

Checking-in behavioural responses

There was a positive linear correlation between boundarylessness and response times for the math questions ($r = 0.46$, $P = .017$). Correlations were not significant between boundarylessness and correct answers or the number of answers (both r < |.14|, P > .49).

Phenomenology of focusing on the centre of experience

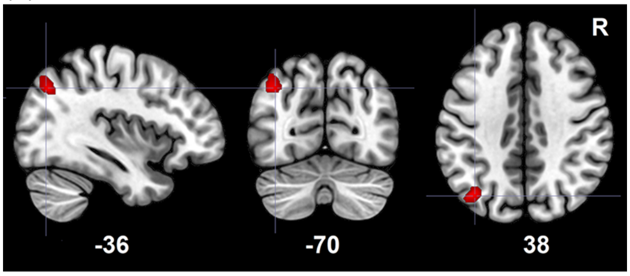
Post-scanning interviews revealed that most participants, 21 out of 24, experienced a clear difference between the checking-in prompting arrow and the neutral symbols, however in different ways: while some saw it as mentally taxing, others felt it to be relaxing; some felt it to be centring, others described it rather as expanding. When practising the task during the interviews, participants likewise reported very different responses to the instruction, but there was a pattern in that participants who rated low

Table 1. Results from quadratic seed-based analysis of resting-state data.

									Model parameters		
Seed	Peak T	Cluster P	x	y	z	mm^3	Location		β	R^2	P
R IPL	5.54	.003	–36	–70	38	1056	L	angular gyrus and IPS	1.06	0.62	<.0001
	5.85	.011	–4	–52	20	752	L	PCC and precuneus	1.01	0.52	<.0001

Clusters where functional connectivity with the right IPL seed correlated quadratically with boundarylessness. Thresholded at $P < .001$ at the peak level, uncorrected for multiple comparisons, $k > 10$ voxels (80 mm^3). Cluster P is FDR corrected. L = left; R = right. Clusters displayed in Fig. 3.

(a)



(b)

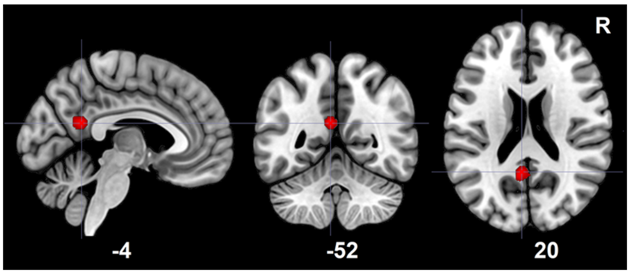


Figure 3 Results from seed-based analysis of resting-state data on the MNI template. Cluster in the (a) left angular gyrus/intraparietal sulcus and (b) PCC/precuneus where the strength of functional connectivity with the R IPL seed correlated quadratically with boundarylessness. Thresholded at $P < .001$ at the peak level, uncorrected for multiple comparisons, and $P < .05$ at cluster level, FDR corrected. Numbers denote slices at cluster peak values. Cluster details are in Table 1

Table 2. Results from linear seed-based analysis of resting-state data.

Seed	Peak T	Cluster P	x	y	Z	mm^3	Location		r
R IPL	6.7	.000	2	−76	26	2128	R	Cuneus	0.82
L IPL	5.5	.000	2	−74	24	1680	R	Cuneus	0.81

Clusters where functional connectivity with the right and left IPL seeds correlated linearly with boundarylessness. Thresholded at $P < .001$ at the peak level, uncorrected for multiple comparisons, $k > 10$ voxels (80 mm^3). *T* denotes peak level, *P* denotes cluster level (FDR corrected), and *r* denotes Pearson correlation between cluster mean beta values and boundarylessness. Clusters displayed in Fig. 4. L = left; R = right.

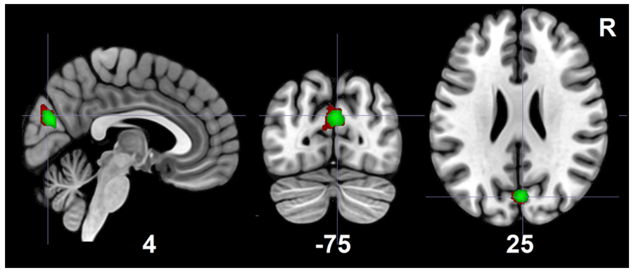


Figure 4 Results from seed-based analysis of resting-state data on the MNI template. Overlapping clusters where the strength of functional connectivity with seeds in the right IPL (red) and left IPL (green) correlated linearly with boundarylessness. Thresholded at $P < .001$ at peak level, uncorrected for multiple comparisons, and $P < 0.05$ at cluster level, FDR corrected. Cluster details are in Table 2

in both boundarylessness and perspectival ownership tended to respond in everyday terms, such as ‘focusing on the stomach’, while participants rated intermediate in boundarylessness and high in perspectival ownership described it as like stepping back into a restful peace, and participants rated high in boundarylessness and low in perspectival ownership described the task as hard, as looking for something which could not be found. See Table 4 for example quotes.

Checking-in fMRI group results

Whole-group analysis ($n = 24$) for Arrow vs. Symbol showed significantly increased BOLD signal responses in a large cluster stretching over the bilateral anterior precentral gyrus [Brodmann area 6 [BA6]), including the premotor cortex, SMA, pre-SMA, and frontal eye fields, and stretching into the bilateral dorsal anterior cingulate cortex. There was also increased activation in the left and right anterior insula and operculum, left supramarginal gyrus, left frontal pole, bilateral occipital cortex including a part of the left precuneus, and bilateral caudate nucleus/putamen including a part of left thalamus. There was significantly decreased activation in the bilateral PCC/precuneus and ACC/mPFC, right angular gyrus, right posterior insula, right middle temporal gyrus, and right frontal pole for Arrow vs. Symbol. All significant clusters are presented in Table 5 and Fig. 8.

Checking-in correlations with boundarylessness

Activity in our a priori ROIs did not correlate significantly with boundarylessness for this task. Looking at correlations with the group-level clusters, we found that deactivation in the PCC/precuneus cluster correlated negatively with boundarylessness ($r = -0.41$, $P = .04$; Fig. 9). Exploratory whole-brain correlations with boundarylessness on the contrasts Arrow vs. Symbol and Arrow vs. Math yielded no results at the chosen significance threshold.

Discussion

The quadratic relations to boundarylessness

Rather than a simple linear relation between boundarylessness and DMN connectivity, we found a U-shaped relation to DMN within-network connectivity, so that participants rating low and high on this scale showed higher DMN connectivity, while participants in the middle-range had lower within-DMN connectivity. In addition to being strongly connected to self-specificity at several levels (Northoff 2016), DMN activity has often been related to unhappiness stemming from rumination and mind-wandering and an inability to stay focused on a task or in the present moment (Andrews-Hanna et al. 2014). Thus, it might seem counterintuitive that increased DMN connectivity would relate to an increased sense of self-boundarylessness, as trait self-transcendence is strongly connected to well-being (Reed 2018, Haugan et al. 2022). However, mind-wandering or day-dreaming can also be a rich source of pleasure and creativity (Baird et al. 2012, Andrews-Hanna et al. 2014, Shofty et al. 2022), and a free-flowing mind can be a source of self-insight if we are present to and accepting of it (Josipovic 2013). Perhaps persons in the high end of boundarylessness can reap the benefits of DMN activity without its disadvantages. If, as our data suggest, the path to boundarylessness is curved, it might be that one has to leave a dysfunctional pattern of mind-wandering before returning to a more wholesome one. The idea of a curved path to enlightenment is reflected in some meditation traditions, such as in this quote attributed to Zen master Dōgen:

> Before one studies Zen, mountains are mountains and waters are waters; after a first glimpse into the truth of Zen, mountains are no longer mountains and waters are no longer waters; after enlightenment, mountains are once again mountains and waters once again waters.

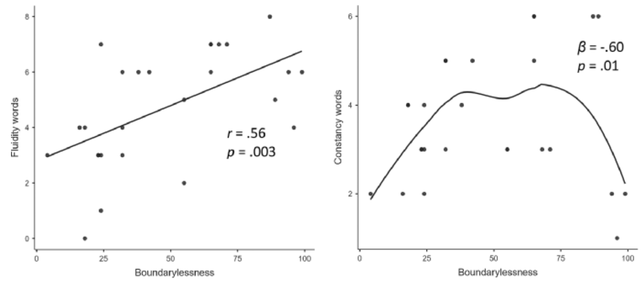


Figure 5 Correlations between self-rated boundarylessness and number of words relating to fluidity or constancy endorsed as descriptive of oneself. (a) Fluidity words, total = 8. (b) Constancy words, total = 8

Table 3. Group-level activations and deactivations for Self compared to Valence.

Contrast	Peak *T*	Cluster *P*	x	y	z	mm^3	Location	
Self > Valence	10.7	.000	−6	−50	32	14 616	L/R	PCC and precuneus
	8.91	.000	−16	26	38	40 232	L/R	mPFC and superior frontal gyrus
	6.48	.000	−44	−54	20	5080	L	Angular gyrus
Valence > Self	7.64	.000	38	−86	10	17 128	R	Intraparietal sulcus, lateral occipital cortex, and inferior temporal gyrus
	6.48	.003	−42	−60	−10	1832	L	Inferior temporal gyrus
	5.44	.000	−28	−52	50	6896	L	Intraparietal sulcus and lateral occipital cortex

Thresholded at $P < .001$ at the peak level, uncorrected, and k > 10 voxels (80 mm^3). *T* denotes peak level, and *P* denotes cluster level (FDR corrected). L = left; R = right. Also displayed in Fig. 6.

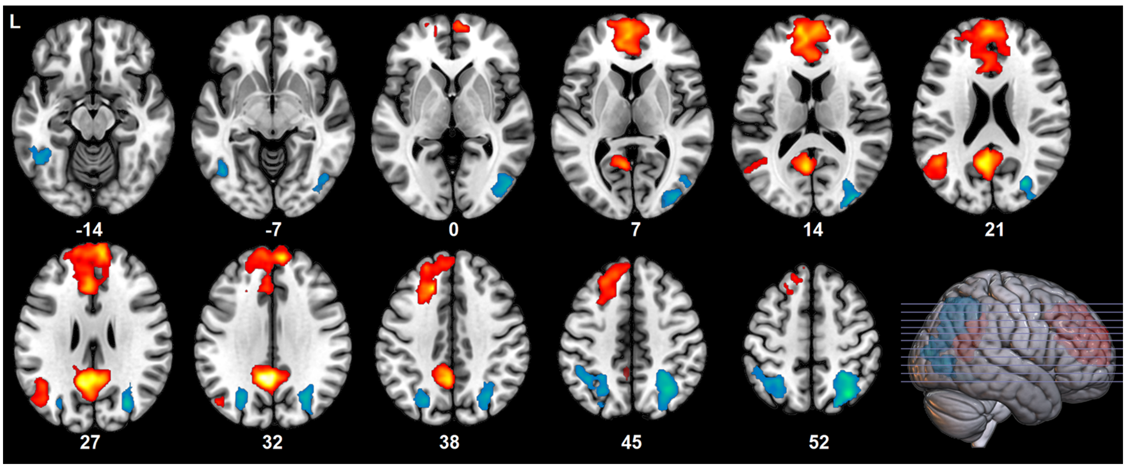


Figure 6 Group-level activations for Self > Valence (red) and Valence > Self (blue) in the SRP task on the MNI template. Thresholded at $P < .001$ at peak level, uncorrected, and $P < .05$ at cluster level, FDR corrected. Numbers denote axial slices. Cluster descriptions are in Table 3

In research on brain plasticity, nonlinear patterns of brain activation and grey matter volume changes as an effect of practice are well known (e.g. Kilgard 2012, Wenger et al. 2017). When we learn something new, the brain needs to engage more neurons and build new synapses, but such expansion cannot go on indefinitely. Thus, with time, synaptic pruning takes place and neuronal activation stabilizes in patterns that can afford the acquired skill in a more economic fashion. Something similar might be at play here, so that, e.g., the self-specifying aspect of the DMN gets 'pruned away' in people with high trait boundarylessness, so that strong DMN integrity no longer corresponds to a salient sense of self. Given our findings for the checking-in task of a negative linear correlation between boundarylessness and deactivation of the PCC/precuneus, it may be that the phenomenological difference between high and low scorers, who manifested the same level of DMN connectivity, was mediated by differences in the baseline activation of this DMN hub. The most likely interpretation of the lower PCC deactivation for highly boundaryless participants is that the baseline activity in the PCC was lower for them during the control condition (passively viewing symbols) and that the decrease in this region therefore was less pronounced for them when given a task. Decreased PCC activity is one of the most robust findings in studies on meditation, both as state and trait (Fox et al. 2016, Cooper et al. 2022). PCC activity has been hypothesized to relate to being 'caught up' in experience, as in feeling attachment to or identifying with various things, such as holding on to an opinion, identifying as being a certain kind of person, or experiencing craving (Brewer et al. 2013), all things which appear to dissolve along with the sense of self-boundaries. It could thus be that a DMN with lower PCC activity is freed from some of the negative aspects associated with this network, while retaining the positive ones.

A recent review of neural correlates of nondual awareness as a state and trait effects of meditation suggested a nonlinear path of changes in network connectivity (Cooper et al. 2022). Specifically, the authors suggested that DMN–FPN connectivity

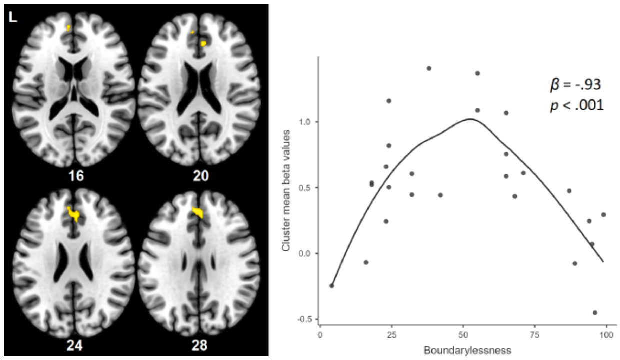


Figure 7 Clusters in the mPFC derived from whole-brain explorative correlation with boundarylessness for the group contrast Self > Valence in the SRP task: (a) imposed on MNI template and (b) mean beta values with smoothed regression line. $T = 5.37$, size 1512 mm^3, peak coordinates $x = -8$, $y = 58$, and $z = 12$; cluster level $P = .009$, FDR corrected. Numbers denote axial slices

Table 4. Reactions to the checking-in task instruction to focus on the centre of experience, the 'experiencer' or 'observer'.

Boundarylessness	Example quotes
Low	"Then I'm thinking about my brain." (Participant 29, boundarylessness rating 4).
	"I'm thinking it means to listen inwardly. To try to be attentive to what I am trying to tell myself. Not rationally, but what I feel, what my needs are" (Participant 34, boundarylessness rating 18).
Intermediate	"For me it feels like I'm just resting into … a very peaceful place. Like a piece of solid ground where I can rest my attention" (Participant 3, boundarylessness rating 42).
	"I feel different in my body, other sensations, kind of euphoric … It's like a different frequency, where the self is… . I feel that peace." (Participant 6, boundarylessness rating 55).
High	"There is supposed to be some experiencer here who experiences, and I'm supposed to find it. And so far I have been unable to." (Participant 8, boundarylessness rating 94).
	"What I do is, because I know people say they are in their heads, and I have a memory of being in my head, I try to focus on – or to be more precise, focus finds its way to – the head… . The only thing to be found there is some sensations, and focus, which is also kind of like a sensory impression." (Participant 9, boundarylessness rating 96).
	"What happens is that if there was any kind of centre before, even a flicker of a centre, it disappears completely when you say this to me. It just expands. (Participant 14, boundarylessness rating 95).

and SLN activity show a U-shaped relation to meditation proficiency (and to trait nondual awareness, which was assumed to follow from all meditation training). Similarly, Bauer et al. (2019) hypothesized that increased anticorrelation is an intermediate step towards a sustained, effortless state of connectivity between these two networks. Although we did not find such a pattern for DMN–FPN connectivity, there was a trend for SLN connectivity to follow this pattern (Table S2 and Fig. S3), and the SLN is known to mediate the shift between the other two networks (Sridharan et al. 2008).

The nonlinear relation between boundarylessness and DMN connectivity was mostly driven by connectivity between the right IPL and mPFC. Interestingly, Josipovic (2014) reports increased connectivity between the right angular gyrus and mPFC as a correlate of nondual awareness meditation. Seed-based analysis of our data further revealed that connectivity between the right IPL and smaller clusters within the two other hubs of the DMN, the left angular gyrus/IPS and PCC/precuneus, was related to boundarylessness in the same way. The right IPL is known for its role in spatial self-location and perspective-taking (Ionta et al. 2011, 2014, Kessler and Braithwaite 2016), and in a review, Park and Blanke (2019) suggest that sensed self-location is mediated by a TPJ–PCC–IPS network. Our findings thus suggest that the brain correlates of the sense of spatial self-location vary with boundarylessness in a U-shaped manner. Speculatively, it could be the case that a sense of boundedness—as in being only one's body—and a sense of boundarylessness—as in being everywhere or everything—share the neural underpinnings of 'embodiment', albeit of very different substrates. Indeed, results along these lines can be found in Braithwaite et al. (2017), who found that participants prone to have out-of-body experiences expressed a kind of hyper-embodiment, and in Fingelkurts et al. (2022), who found that while some experiences of body boundary dissolution or out-of-body experiences were accompanied by decreased synchrony between the right posterior DMN hubs, others showed increased such synchrony.

We additionally found an inverted U-shaped relation between boundarylessness and mPFC activation during the processing of self-referential words, so that participants in the intermediate range of boundarylessness displayed a higher BOLD signal from this area. This finding can be interpreted in light of the qualitative analysis of interview data (Lindström et al. in preparation), where we observed a quadratic relation between self-rated boundarylessness and the strength of perspectival ownership of experience. Participants who reported the highest levels of perspectival ownership identified as a kind of detached witness most of the time. This was described as a pleasant mode of being, attained after years of meditation. Participants assigned to this group self-rated in the intermediate range of boundarylessness. This is in stark contrast to descriptions by participants in the lowest and highest range of boundarylessness, who described a low or non-existent sense of perspectival ownership of experience. Most participants in the low end of boundarylessness did not at all relate to descriptions of witnessing experiences, whereas participants in the high end of boundarylessness described a nondual experience with no separation between experiencer and

Table 5. Group-level activations for Arrow compared to Symbol.

Contrast	Peak *T*	Cluster *P*	x	y	z	mm³	Location	
Arrow > Symbol	9.42	.000	52	0	50	27 336	R/L	BA6 (PMC, SMA, pre-SMA, and FEF) and ACC
	8.65	.000	62	8	14	7856	R	Anterior insula and operculum
	7.03	.004	−48	−42	32	1784	L	Supramarginal gyrus
	6.30	.004	−52	36	−4	1856	L	Frontal pole
	6.21	.000	−58	10	10	5888	L	Anterior insula and operculum
	5.43	.000	36	−76	14	2816	R	Lateral occipital cortex
	5.40	.000	−10	−72	56	7584	L	Lateral occipital cortex and precuneus
	4.95	.020	−16	−6	8	1128	L	Caudate nucleus, putamen, and thalamus
	4.69	.012	24	−6	10	1328	R	Caudate nucleus and putamen
Symbol > Arrow	9.73	.000	8	−46	38	20 584	R/L	PCC and precuneus
	8.07	.000	6	42	30	18 000	R	ACC and mPFC
	7.67	.000	54	−62	28	7640	R	Angular gyrus
	5.49	.016	36	−14	16	1312	R	Posterior insula
	5.00	.040	64	−38	−6	904	R	Middle temporal gyrus
	4.52	.024	26	56	10	1112	R	Frontal pole

Thresholded at $P < .001$ at the peak level, uncorrected, and $k > 10$ voxels (80 mm³). *T* denotes peak level, and *P* denotes cluster level (FDR corrected). PMC = premotor cortex; FEF = frontal eye fields; ACC = anterior cingulate cortex; L = left; R = right. Clusters displayed in Fig. 8.

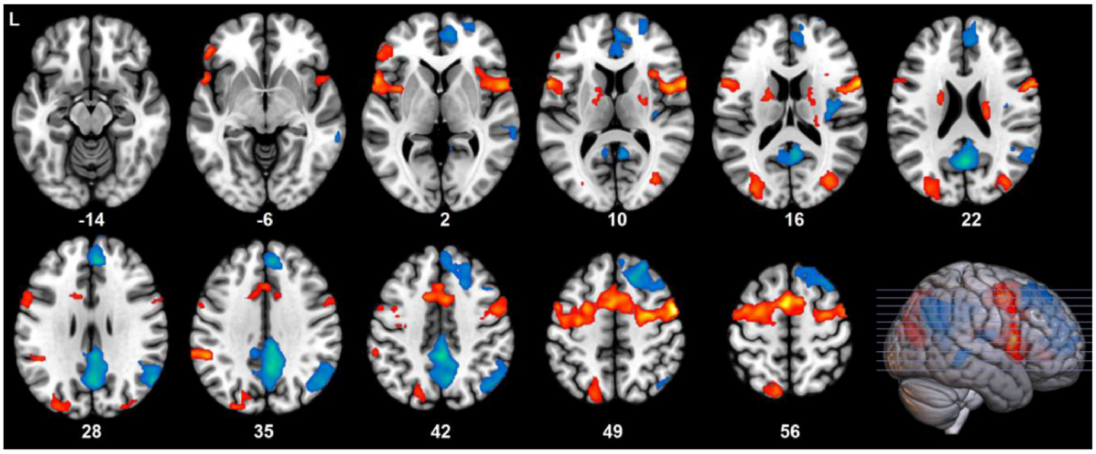


Figure 8 Group-level activations for Arrow > Symbol (red) and Symbol > Arrow (blue), thresholded at $P < .001$ at peak level, uncorrected, and $P < .05$ at cluster level, FDR corrected, on the MNI template. Numbers denote axial slices. Cluster descriptions are in Table 5

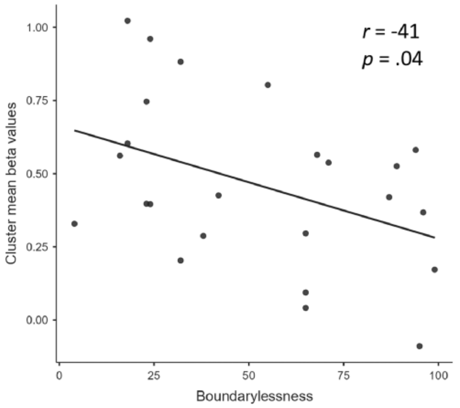


Figure 9 Correlation between boundarylessness and cluster mean beta values of the group-level cluster in the PCC/precuneus from the contrast Symbol > Arrow, displayed in Table 5 and Fig. 8

experience and thus no sense of being an experiencer of experiences. Based on this quadratic relation between boundarylessness and perspectival ownership in everyday self-experience, it is reasonable to assume that the quadratic relation of boundarylessness to mPFC activity, and possibly also that to DMN connectivity during rest, has something to do with this phenomenological construct. This interpretation is strengthened by the finding of an inverted U-shaped relation between boundarylessness and endorsing constancy words as descriptive of oneself during the SRP task, which pertained especially to positively valenced constancy words, such as 'evig' (eternal) and 'stabil' (stable). Endorsing such words seems to be well in line with the sense of a central self-core observing all experiences. As mentioned earlier, some previous findings indicate a role for the mPFC in minimal self (e.g. Dor-Ziderman et al. 2013, Fingelkurts et al. 2016b, Fingelkurts et al. 2020). Intriguingly, in a case study of eight instances of altered self-experience (Fingelkurts et al. 2022), the small reported changes in the phenomenological dimension 'Observing' in all cases varied in the same direction as mPFC synchrony strength, again indicative of a special role for the mPFC for the minimal sense of observing. Even though the SRP task was designed to elicit a narrative sense of self, it might be that participants with a strong sense of perspectival ownership adopted the stance of the observing witness towards the presented words, rather than narratively thinking about themselves as persons continuous through time. However, the suggestion that the mPFC is central to the sense of perspectival ownership of experience is contradicted by our finding of decreased activity at the group level in this area during the checking-in task, which aimed to enhance this sense. An alternative explanation might be that participants in the intermediate range of boundarylessness had lower baseline mPFC activity, which led to a larger increase in the self-referential task. This interpretation would, conversely, point towards a 'decrease' in mPFC activity as central to a strengthened sense of perspectival ownership of experience.

The review by Cooper et al. (2022) found that the results on mPFC activity was the most divergent of all network hubs investigated, which could be an indication that this area is especially prone to a nonlinear development with meditation practice. Indeed, the idea of a quadratic relation between brain activity and meditation proficiency can shed new light on the often contradictory findings on neural correlates of meditation (Cooper et al. 2022; see also Brefczynski-Lewis et al. 2007). Various studies define meditation and proficiency differently, so that, e.g., someone with 2000 hours of meditation experience is labelled 'beginner' in one study and 'expert' in another, depending on the rest of the sample. This complication can be largely remedied by instead using a phenomenological measure as the independent variable.

A final, alternative approach would be to claim that the 'return to the beginner's brain' evinced by very boundaryless participants is a step backwards and that participants in the intermediate range of boundarylessness, with their lower DMN integrity and higher mPFC activity in response to SRP, exhibit an optimal way of functioning. Indeed, several participants self-rating in the intermediate range did mention being 'done' with their practice, having achieved a desired transformation of their sense of self with regard to functionality in everyday life. This suggestion would be in line with the common finding that neural extremes in either direction are suboptimal compared to the intermediate (Northoff and Tumati 2019). We cannot confirm whether the sentiment of an optimal functionality is correct as we did not include any measures of well-being in this study.

Brain correlates of focusing on the centre of experience

It is clearly not warranted to conclude that we have been able to conclusively identify the neural correlates of the sense of perspectival ownership of experience via the checking-in task, as there is too much room for ambiguity regarding interpretation and execution of the instruction, and how this relates to the philosophical meaning of the concept. Indeed, if the Arrow condition had successfully captured the trait-level sense of perspectival ownership, we would have expected to see quadratic relations of brain data to boundarylessness, given the results of the interview analysis (Lindström et al. in preparation). Instead, the only correlation of brain activation in this task to boundarylessness was linear: a negative correlation to PCC deactivation that, as mentioned earlier, can be assumed to stem from a lower baseline PCC activity in the more boundaryless participants. It is likely that this very basal aspect of self corresponds to kinds of brain activity that were not probed in this investigation, e.g. long-range temporal correlations as suggested by Northoff and Smith (2022) or brain entropy as suggested by Carhart-Harris et al. (2014).

Nevertheless, the group results for the exploratory checking-in task offer important information. We found that when participants were prompted to 'focus on the centre of their experience', there was decreased activation in the main DMN hubs as compared to passively viewing symbols, an expected finding for any task. As predicted, we also found increased activation in the bilateral anterior insula and a small part of the left thalamus. The main increase was however in a large, bilateral frontal cluster spanning almost the entire BA6. These findings converge with previous reports on brain correlates of meditation. Specifically, a pattern very similar to ours, including increases in the BA6, putamen, insula, and supramarginal gyrus and decreases in the PCC, precuneus, and angular gyrus, correlated with meditation onset in a study by Bærentsen et al. (2010). It thus seems that this prompt led our group of participants, both non-meditators and advanced meditators, to a brain state very similar to that of beginning meditation. Despite quite a large disparity in the phenomenological descriptions (see Table 4), our robust group-level result indicates a powerful effect of this instruction for participants with varying meditation experience and sense of self-boundaries.

Although BA6 was not included as an a priori ROI for our investigation, this area has been implicated in many previous studies on sense of self. Dor-Ziderman et al. (2013) found beta activity in the right premotor cortex as one of the effects of cueing for minimal self, and Qin et al. (2020) found the right premotor cortex to be a correlate of both narrative self and self-related exteroceptive processing. In Dor-Ziderman et al.'s follow-up study (2016), activity in the right SMA diminished in the boundaryless condition. Lehmann et al. (2001) investigated the EEG activity in the gamma-band for a single experienced meditator who entered four distinct states, one of which was 'self-dissolution'. The gamma correlates of this state differed from the other states by increased activity in the right BA6. In the review by Fox et al. (2016), increases in BA6 were identified as correlates of three of the four types of meditation surveyed: open monitoring, focused attention, and mantra recitation, but not loving-kindness/compassion meditation. In their complementary review on structural effects of meditation, the BA6 was among the areas morphologically altered in meditators (Fox et al. 2014). The authors speculate that this large region is involved in general attention regulation, specifically attention to the present moment, which is central to many styles of meditation (Fox et al. 2014, 2016). The right premotor cortex is also known to be involved in the sense of body ownership (Ehrsson et al. 2004, Convento et al. 2018). Insular activation, as was also found at the group level, is likewise common to many kinds of meditation but most strongly related to meditation styles with a focus on bodily awareness (Fox et al. 2014, 2016). Explicit attention to the body during the checking-in condition was however only mentioned by 5 of our 24 participants in the post-scanning interviews.

Several of the regions showing increased activation during checking-in, namely posterior inferior frontal sulcus, anterior insula, frontal operculum, and pre-SMA, are 'multiple demand regions', involved in many kinds of cognitive challenges and highly sensitive to meditation training (Raffone and Srinivasan 2017, Raffone et al. 2019). The anterior insula, premotor cortex, and specifically SMA/pre-SMA are also involved in the sense of agency (David et al. 2008, Haggard 2017). Agency is a fundamental aspect of the minimal self, and the finding that agency regions are engaged during checking-in can be taken to indicate that the sense of being an observer relates to the sense of being an agent, something which has been suggested by, among others, Gallagher (2013).

Behavioural results

Contrary to what we expected, there was no significant correlation between boundarylessness and endorsing positive words or not endorsing negative words as descriptive of oneself. This can be attributed to a ceiling effect, as most participants self-endorsed most words in both of these categories (Fig. S4). However, as predicted, a correlation was found regarding the fluidity words, most strongly so for the negatively valenced ones, such as 'ombytlig' (capricious) and 'tom' (empty): a larger proportion of these adjectives were endorsed as self-descriptive by participants who self-rated as being more boundaryless. For the constancy words a quadratic relation was found, as discussed earlier.

Somewhat surprisingly, we found a correlation between boundarylessness and response times to simple math tasks. Previous studies indicate a correspondence between meditation experience and shorter response times to tasks (see Cahn and Polich 2006 and Chiesa et al. 2011 for reviews). For the SRP task there were no correlations with response times, in opposition to our expectation of shorter response times to the self task for more boundaryless participants.

Conclusions, limitations and recommendations

Of our a priori hypotheses, we found support for relations between boundarylessness and DMN connectivity in the resting state (U-shaped), with mPFC activity in the narrative self task (inverted U-shaped) and with PCC/precuneus activity in the minimal self task (negative). We also found that boundarylessness correlated with endorsing more fluidity words as self-descriptive, but rather than a negative relation with endorsing constancy words, there was again an inverted U-shaped relation to boundarylessness. A major caveat of the present study was the loss of brain data in ventral and dorsal brain areas for some participants in the task runs. Nevertheless, our analyses yielded interesting results for the included areas. We recommend future studies to investigate brain regions we could not investigate here, in particular the ventral mPFC. A larger sample size would have increased power, as would making group comparisons rather than correlation analysis. However, the sample did not easily lend itself to a group contrast; splitting the measure of interest, boundarylessness, by the mean was not warranted, and indeed our analyses showed that relevant information would have been lost by doing so. With a larger sample size and without the loss of data from superior and inferior brain areas in the task runs, it is likely that we would have found support for more of our hypotheses.

We did not differentiate between meditation techniques, which can be seen as a limitation. However, the focus was not on meditation per se but on variations in the trait-level sense of self-boundaries. Meditators were recruited simply because it is well known that meditation can induce alterations in trait self-experience, and participants did not meditate in the scanner. We recommend future studies to use a continuous rating tool, such as that developed by Dambrun (2016), to assess trait boundarylessness. Substantial meditation experience can lead to different kinds of descriptions of trait-level changes in self-experience—as involving a strengthened sense of self in the form of perspectival ownership of experience or, alternatively, as a nondual state that lacks this sense of self. Given our results, it seems that this differentiation is reflected in the brain.

Acknowledgements

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Supplementary data

Supplementary data are available at *NCONSC* online.

Conflict of interest:

None declared.

Data availability

Unthresholded statistical maps of the task group results are available at NeuroVault, https://identifiers.org/neurovault.collection:13102. Study materials and preregistration are available at Open Science Framework, https://osf.io/uvkqa.

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