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Archival Report

Modulation of Posterior Default Mode Network Activity During Interoceptive Attention and Relation to Mindfulness

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ABSTRACT

BACKGROUND: Interoceptive attention to internal sensory signals, such as the breath, is fundamental to mindfulness. However, interoceptive attention can be difficult to study, with many studies relying on subjective and retrospective measures. Response consistency is an established method for evaluating variability of attention on exteroceptive attention tasks, but it has rarely been applied to interoceptive attention tasks.

METHODS: In this study, we measured consistency of response times on a breath-monitoring task with simultaneous electroencephalography in individuals across the life span (15–91 years of age, $N = 324$).

RESULTS: We found that consistency on the breath-monitoring task was positively correlated with attentive performance on an exteroceptive inhibitory control task. Electroencephalography source reconstruction showed that on-task alpha band (8–12 Hz) activity was greater than that measured at rest. Low-consistency/longer breath responses were associated with elevated brain activity compared with high-consistency responses, particularly in posterior default mode network (pDMN) brain regions. pDMN activity was inversely linked with functional connectivity to the frontoparietal network and the cingulo-opercular network on task but not at rest, suggesting a role for these frontal networks in on-task regulation of pDMN activity. pDMN activity within the precuneus region was greater in participants who reported low subjective mindfulness and was adaptively modulated by task difficulty in an independent experiment.

CONCLUSIONS: Elevated pDMN alpha activity serves as an objective neural marker for low-consistency responding during interoceptive breath attention, scales with task difficulty, and is associated with low subjective mindfulness.

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Attention is the fundamental basis of cognitive control, enabling selective processing and action on goal-relevant stimuli while suppressing irrelevant distractions (1–3). Attention can be directed to external stimuli or internally generated sensations. Exteroceptive attention has been well studied and is known to be associated with the activity of several top-down cognitive control networks. These include the cingulo-opercular network (CON), which involves the anterior cingulate cortex and insula and is associated with attentional monitoring, and the central executive or frontoparietal network (FPN), which involves the dorsolateral prefrontal cortex, frontal eye fields, and superior parietal lobules, which are dynamically deployed for moment-to-moment attentional control and distractor suppression (4–7). An important role of these brain networks is to regulate activity within the default mode network (DMN) during exteroceptive tasks because elevated DMN activity has been associated with worse exteroceptive task performance, possibly due to its role in subjective mind wandering (8–10).

Interoceptive attention involves attention to internal sensations generated from the body while learning to monitor and disengage from irrelevant distractions (11,12). Interoceptive attention is a core skill that can be developed through mindfulness training. Many mindfulness traditions use attention to breath as a base practice to develop interoceptive attention (12–16). Previous attempts to capture neural correlates of attention during meditation have either contrasted meditation with other tasks or used random probes or self-report to retrospectively ask participants to identify distracted versus attentive states during meditation (17–22). These studies have suggested that attentive breath meditation involves regulation of default mode brain areas and engagement of the CON/FPN cognitive control circuits similar to those observed for exteroceptive tasks (18,23–25).

Recently, breath-monitoring tasks (such as breath counting or respiratory cycle tracking) have been developed to specifically assess interoception to breath while minimizing other aspects of meditation that may complicate interpretation (26–29). Due to the requirement for regular responses to track aspects of breath, such tasks offer an opportunity to understand aspects of respiratory interoception in a more experimentally tractable manner. In one recent study that used an active breath interoception task, accuracy of breath counting

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was positively linked to trait mindfulness and negatively linked to mind wandering and negative affect (26,27).

Several studies have been performed to investigate the neural processes involved in breath monitoring. In one early study (29), passive interoceptive attention was compared to an active exteroceptive attention task. Passive interoceptive attention was associated with greater activity/connectivity with the insula, as well as greater activity within posterior/midline DMN regions. Less activity was observed during interoception in lateral prefrontal brain regions associated with cognitive control compared with activity during exteroceptive attention tasks. Follow-up studies by the same group (28,30) in which active reporting was included (i.e., active interoception) demonstrated that greater activity in prefrontal regions was helpful in classifying exteroceptive attentional states, whereas greater activity in posterior cingulate/posterior DMN (pDMN) brain regions was helpful for classification of interoceptive attentional states (30). On balance, these data suggest that interoception is associated with activity of frontal brain networks, although to a lesser extent than during matched exteroception tasks, and may also be linked to greater activity in pDMN regions than standard exteroceptive tasks.

In this study, individuals ages 15 to 91 years engaged in an interoceptive breath-monitoring task. The task involved consistent eyes-closed monitoring of breathing, with a motor response (finger tap) after every 2 complete cycles of inhalation and exhalation. We used variability in breath-monitoring responses as a direct, objective marker of variability in task performance. Thus, we were able to contrast neural activity on this task in relation to rest and further characterize neural activity on this task during the more variable versus the more consistent breath cycles. The underlying premise of this analysis is that when participants are in a higher interoceptive attention state, they will show greater consistency in either respiratory cycle time and/or response patterns (i.e., responding more consistently after each 2 breath cycle). Thus, by comparing brain activity on consistent trials versus less consistent trials within each participant, we can examine brain regions and networks that underlie variability during performance of this interoceptive attention task while controlling for interindividual differences in baseline characteristics of respiration.

Overall, we had 3 goals in this study. First, we aimed to measure whether consistency of responding on this interoceptive attention task was related to performance on exteroceptive cognitive tasks. This question is important because it informs whether consistency on responses is related to any other general cognitive abilities (27,31). Second, we aimed to investigate the neural basis of consistent performance within individuals by comparing high-consistency versus low-consistency trials. We also compared activity on-task with activity measured at rest. Third, we wanted to understand whether brain activity on this task was related to validated subjective measures of mindfulness. Given previous data suggesting that pDMN activity occurs during interoception to breathing (29,30) and is linked to mind wandering (32), we hypothesized 1) that the pDMN would play a key role in task consistency; 2) that activity in the pDMN measured on-task would be linked to subjective mindfulness; and 3) that activity in the FPN/CON cognitive control networks may be involved in regulating the DMN during interoceptive attention to breathing.

METHODS AND MATERIALS

Participants

A total of 324 human subjects, 15 to 91 years of age (175 female, 136 male) participated in the main experiment. Participants were recruited by convenience sampling from the local university and the broader San Diego community using flyers and the online Research Match registry, as well as 2 local high schools in the case of adolescents. The participant sample size met criteria for investigating greater than small effect size outcomes across participants ($r > 0.15$) at a beta power of 0.8 and an alpha of 0.05, as calculated using G*Power software (33).

A total of 52 human subjects, 20 to 44 years of age (25 female, 27 male), who were also recruited by convenience sampling, participated in a second adaptive version of the main experiment. This sample size was powered for analyzing within-subjects effects of moderate effect size (Cohen's $d > 0.4$) at a beta power of 0.8 and an alpha of 0.05 (33).

A total of 16 human subjects, 18 to 44 years of age (12 female, 4 male), participated in a third experiment in which respiration was monitored simultaneously with the main experiment using the Vernier respiration monitoring chest belt.

All participants provided written informed consent for the study protocol (#180140) approved by the University of California San Diego Institutional Review Board; written informed parent permission was also obtained for youth under age 18. Specific informed consent was also obtained from participant(s) to use their identifying image in publications.

Experimental Design

Demographics and Mental Health. All participants provided demographic information via self-report. This included age, gender, race and ethnicity, and socioeconomic status shown in Table 1 for the main experiment. Race was reported as 1 of 7 categories (American Indian/Alaska Native, Asian, Black/African American, Caucasian, Native Hawaiian/Other Pacific Islander, more than 1 race, and unknown or not reported). Socioeconomic status composite scores were assessed using the Family Affluence Scale (34), which measures individual wealth based on ownership of objects of value (i.e., car/computer) and produces a composite score ranging from 0 (low affluence) to 9 (high affluence). All participants were healthy, and no participant reported any current or past history of clinical diagnoses or medications. Additionally, all participants provided subjective self-reports of trait mindfulness on the 14-item Mindful Attention Awareness Scale (35,36) and depression on the 9-item Patient Health Questionnaire (37).

Neurocognitive Assessments. All assessments were delivered on the *BrainE* Unity-coded platform developed and deployed by NEATLabs (38,39). In the main experiment, these included the interoceptive attention assessment that is the focus of this study, along with exteroceptive task assessments performed during the same session to evaluate inhibitory control, interference processing, working memory, and emotion bias [see Supplemental Methods for descriptions of exteroceptive tasks, which have also been described in recent publications (39–48)], and resting-state data. The Lab Streaming Layer (49) protocol was used to time stamp each

Table 1. Demographic and Mental Health Factors Self-Reported by Study Participants (*N* = 324)

	Median ± Median Absolute Deviation or *n* (%)
Demographics	
Age, Years	25.00 ± 15.16
Gender	
Female	175 (54.01%)
Male	136 (41.98%)
Other	3 (0.93%)
Ethnicity	
Asian	65 (20.06%)
Black/African American	4 (1.23%)
Caucasian	167 (51.54%)
More than one race	49 (15.12%)
Native American	3 (0.93%)
Native Hawaiian/Other Pacific Islander	1 (0.31%)
SES	5.00 ± 1.49
Mental Health	
Mindfulness (MAAS)	4.07 ± 0.82
Depression (PHQ-9)	4.00 ± 4.02

MAAS, Mindful Attention Awareness Scale; PHQ-9, Patient Health Questionnaire; SES, socioeconomic status.

stimulus/response event in each cognitive task. All study participants engaged with the neurocognitive assessments on a Windows 10 (Microsoft Corporation) laptop while sitting at a comfortable viewing distance. All assessments were completed within a 40-minute session.

Interoceptive Attention to Breathing. Participants accessed a task named Two Tap. They were instructed to close their eyes, breathe naturally, and respond every 2 breaths using the laptop spacebar. The computer screen appeared dark gray for the duration of the 5-minute task, which was implemented in two 2.5-minute blocks.

Adaptive Interoceptive Attention Assessment. In the second experiment, we implemented an adaptive version of the interoceptive attention task to better understand modulation of brain activity with changes in task difficulty. In this task, individuals were instructed in the first level to breathe normally and tap after every breath cycle. If they completed this level consistently, participants advanced to the second level, where they tapped every 2 breaths, and if they completed this level, they would advance to a final level, monitoring every 3 breaths. The total task time was 10 minutes.

Electroencephalography. In the main experiment and the second adaptive assessment experiment, electroencephalography (EEG) data were collected simultaneously with the interoceptive attention assessment using a 24-channel Smarting wireless EEG amplifier with saline-soaked electrodes in 10–20 standard layout. In the third experiment with simultaneous respiration monitoring, EEG data were collected using the 64-channel ANT Neuro EEGO system with gel electrodes in 10–20 standard layout. Additional details are provided in Supplemental Methods.

Behavioral Analyses. For the interoceptive attention task, behavioral data were analyzed for consistency of responses because participants made a response every 2 breaths. We calculated performance consistency = 1 − MAD RT / median RT, where MAD is the median absolute deviation of RT, and RT is response time. Consistency is usually defined as 1 − the coefficient of variation, where the coefficient of variation is the ratio of the standard deviation to the mean; in this case, because RTs within participants were not normally distributed, median and MAD metrics replaced standard deviation and mean metrics.

Behavioral performance on the exteroceptive cognitive tasks of inhibitory control, interference processing, working memory, and emotion bias were calculated as the efficiency on each task, calculated as the product of task accuracy × speed [additional details are provided in Supplemental Methods (50,51)]. For all behavioral performance data, >3 MAD outlier data were removed prior to statistical analyses, with outlier data exclusion being specified in advance based on our previous research (39,44,45,47).

Neural Analyses. We applied a uniform processing pipeline to EEG data acquired on the interoceptive attention task as well as resting-state data, as reported for several of our studies (39,43–48,52–54). This included 1) data preprocessing, 2) computing the EEG power spectrum, and 3) cortical source localization of the EEG data to estimate source-level neural activity and internetwork connectivity (INC). All details are provided in Supplemental Methods.

Statistical Analyses. Analyses for this study were not preregistered. We used robust linear regression to model breath attention performance consistency based on demographic (age, gender, race, socioeconomic status) and mental health (depression, mindfulness) predictors, as well as to correlate consistency with efficiency on exteroceptive cognitive tasks. Robust regression was used because it is less sensitive to outliers than the nonrobust version (55).

On-task neural activity as well as resting-state activity were analyzed in the alpha frequency band, with repeated-measures analyses of variance (rm-ANOVAs) used to compare task conditions and false discovery rate (FDR) corrections applied to significant testing across all regions of interest (ROIs). Correlations between task-related activity and INC were examined to find associations between these metrics. Associations of neural activity with mindfulness were compared in median splits of high- and low-mindfulness participants.

RESULTS

Performance Consistency of Interoceptive Attention

Participants (*N* = 324) engaged in the interoceptive, eyes-closed attention to breathing task, monitoring 2 breaths at a time, i.e., 2 complete inhalations and exhalations, and reported completions using finger-tap responses (task instructions are

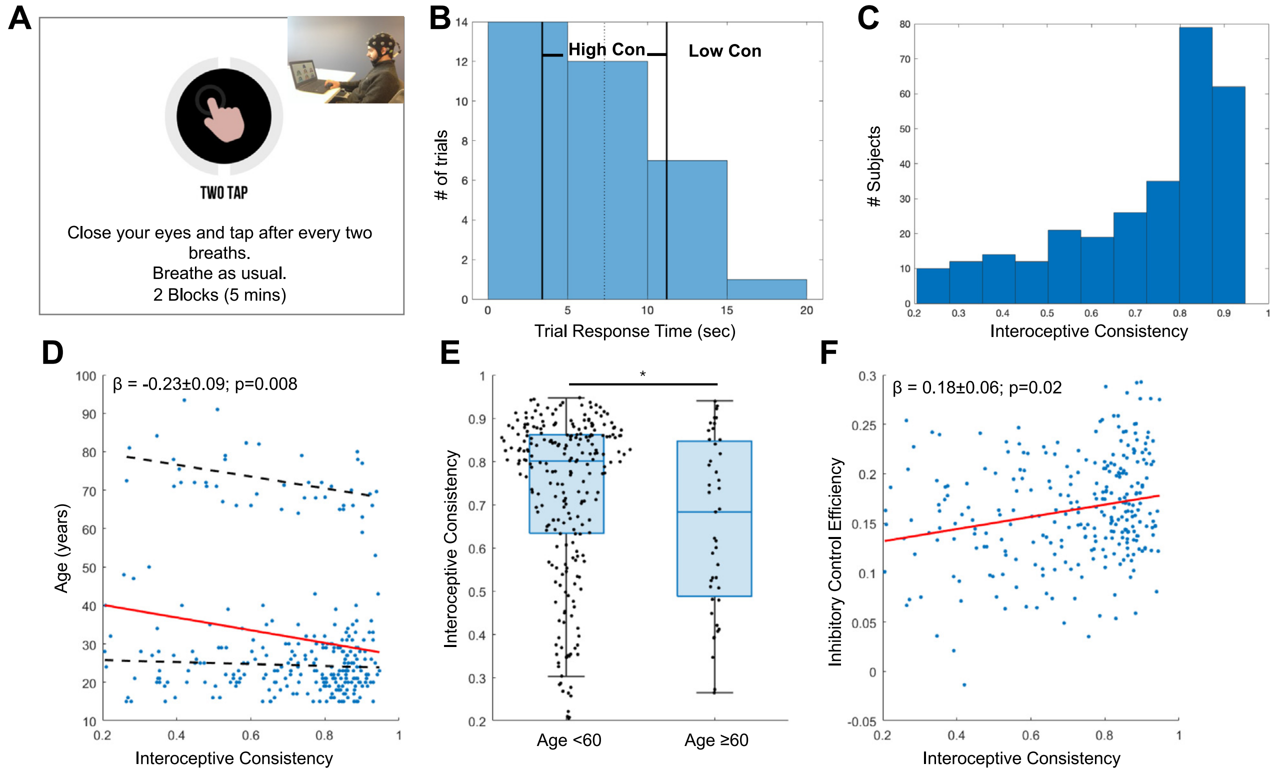

Figure 1. Interoceptive attention task characteristics. **(A)** The TwoTap interoceptive attention to breathing task was designed to assess consistent attention to breathing. Each participant was required to respond every 2 breaths, while electroencephalography was simultaneously recorded. **(B)** Histogram of breath response times (RTs) from an example participant, showing high-consistency trials (within 1 median absolute deviation [MAD] of the median RT) and low-consistency trials (within > median + 1 MAD RT). Thick vertical black lines denote the median ± MAD response boundary, and the dotted vertical line represents the median RT. **(C)** Overall interoceptive consistency, i.e., consistency of breath monitoring, is shown across all 324 study participants, calculated as 1 − MAD/median RT. **(D)** Interoceptive attention consistency was negatively related to age overall (red fitted line, $\beta = -0.23 \pm 0.09$; $p = .008$); however, there was no age effect in participants <60 years of age (lower dashed black line, $p = .17$) and only a trend for a negative age effect in participants ≥60 years of age (upper dashed black line, $p = .07$). **(E)** Interoceptive consistency was significantly lower in participants ≥60 years of age than in individuals <60 years of age ($p = .02$). Box plots show median with interquartile range and scatter and range of individual data. **(F)** Interoceptive attention consistency positively predicted cognitive performance efficiency (log sec^{-1} units) on the attended stimuli in the inhibitory control task; regression controlled for age. Con, consistency.

shown in Figure 1A, and the distribution of RTs for an example participant is shown in Figure 1B). RTs were 8.39 ± 2.20 seconds (median ± MAD) across all participants, and the task performance consistency distribution is shown in Figure 1C.

A robust regression model for consistency of interoceptive attention based on all demographic and mental health factors only showed a significant inverse relationship with age (standardized $\beta = -0.23 \pm 0.09$, $t_{180} = -2.7$, $p = .008$) (Figure 1D); no other factors were significant predictors of consistency ($p >$ .2). Given that older adults are known to have different cognitive abilities, we repeated the regression model with individuals <60 years of age ($\beta = -0.31 \pm 0.23$, $t_{148} = -1.37$, $p =$ .17) versus ≥ 60 years of age ($\beta = -1.2 \pm 0.65$, $t_{25} = -1.88$, $p = .07$); these results showed a near-significant trend for decline of interoceptive consistency only in older adults. Mean consistency in adults <60 years of age versus adults ≥ 60 years of age was significantly different (<60 years, mean ± SD = 0.73 ± 0.19; ≥60 years, mean ± SD = 0.65 ± 0.20; $t_{285} = 2.27$, $p = .02$) (Figure 1E). Given these effects, age was included as a covariate in subsequent analyses. Next, we investigated whether consistency of interoceptive attention could predict performance on exteroceptive cognitive tasks that participants performed during the same session. Robust regression models accounting for age showed that consistency of interoceptive attention significantly predicted efficiency on the inhibitory control task ($\beta = 0.18 \pm 0.06$, $t_{154} =$ 2.9, $p = .02$) (Figure 1F), where efficiency represents accurate and rapid responding to the attended stimuli on the exteroceptive task. Interoceptive consistency did not relate to performance on the working memory, emotion bias, or interference-processing tasks ($p > .2$).

Interoceptive Task-Related Neural Activity Shows Posterior Alpha Dominance and Is Distinct From Resting-State Activity

Here, we studied the neural differences between high-consistency (trials within 1 MAD of median RT) and low-consistency (trials >1 MAD of median RT) task performance in comparison with data recorded during eyes-closed rest.

First, we identified the dominant frequency band of neural activity associated with this task, observing a clear peak in the

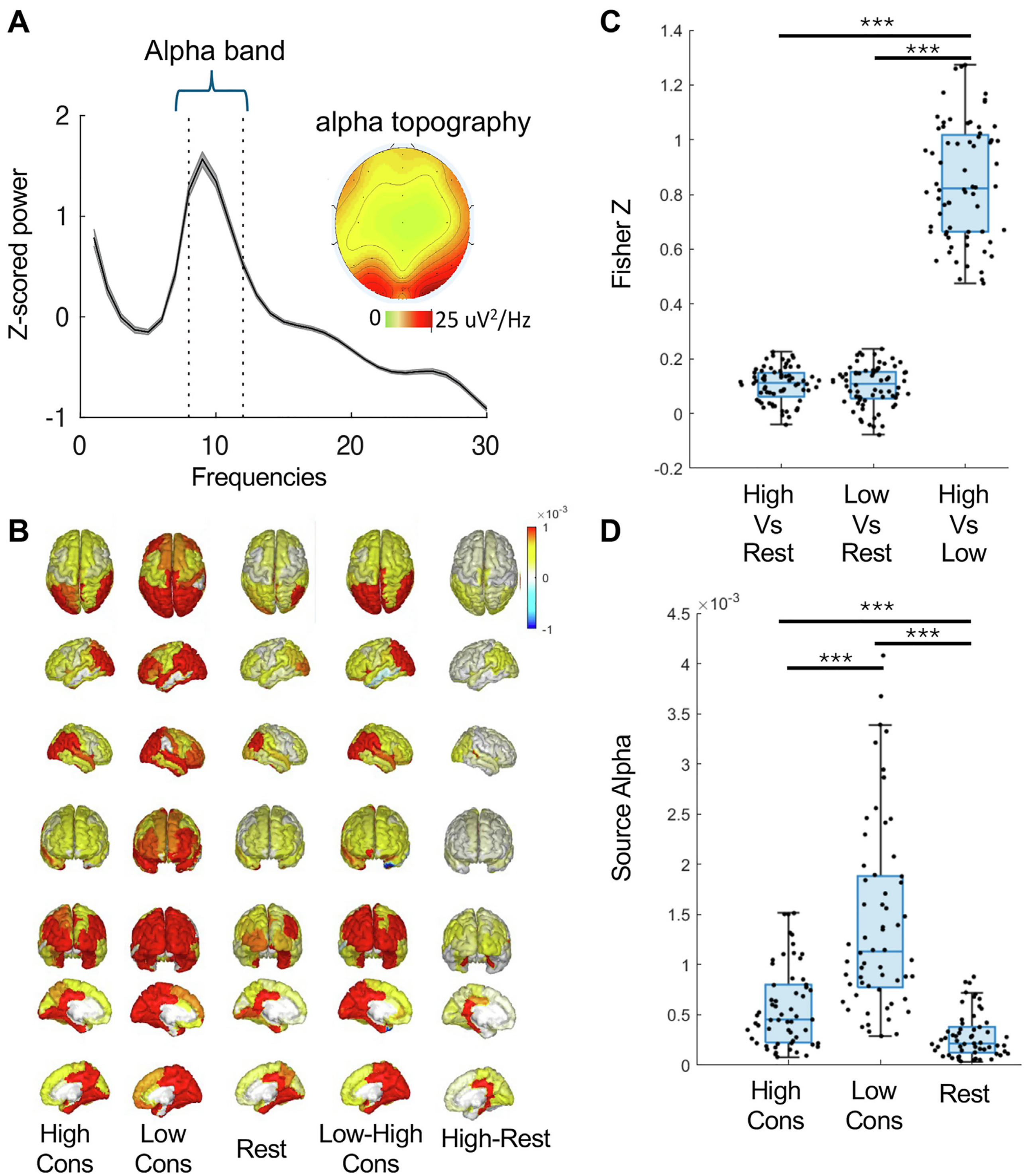

Figure 2. Interoceptive task-related electroencephalography brain activity and comparisons with resting state. **(A)** The power spectrogram of scalp electroencephalography in the eyes-closed task showed alpha band (8–12 Hz) dominance plotted across all participants and electrodes, with alpha scalp topography shown alongside. **(B)** Grand-average source-localized alpha band activity on high- and low-consistency trials, together with source maps of resting-state data recorded the same day from each participant. Differences in low- vs. high-consistency task activity and in high-consistency task vs. rest activity are also shown. Each map shows $p < .05$ activity false discovery rate corrected for comparisons across all brain regions. **(C)** Interparticipant correlation coefficients (Fisher's z-transformed Spearman's correlations) between alpha activity on task conditions and resting state are shown with scatters representing distribution across all 68 source-localized brain regions; task conditions were highly correlated with each other but not with rest. **(D)** Cortical source alpha activity averaged across all brain regions showed the highest activity for low-consistency trials followed by high-consistency trials and then rest, with significant differences in activity across all conditions. ***$p < .001$. Cons, consistency.

alpha-frequency band (8–12 Hz) (Figure 2A). Because this was an eyes-closed task, and posterior alpha predominates in eyes-closed EEG, next we wanted to verify to what degree alpha source–localized activity, i.e., alpha spectral amplitude, was related to breath monitoring or was just a consequence of closing the eyes such as at rest. Figure 2B shows task and rest alpha source–localized activity in all 68 ROIs with $p < .05$ threshold applied for significant positive alpha activity relative to 0 (single-sample t test) and FDR corrections applied for comparisons across all cortical regions. While the overall distribution of alpha activity appeared similar between these 3 conditions, quantitative differences emerged as described below.

Figure 2C shows interparticipant (Fisher's z-transformed) Spearman's correlations between task conditions and rest. rm-ANOVA showed an effect of condition ($F_{2,134} = 1239.28$, $p < .001$) with a mean correlation of 0.1 between activity during task trials versus rest and 0.84 between high- and low-consistency trials within the task. Post hoc tests showed a significant difference between within-task trial correlations and task versus rest correlations ($p < .001$). Relatedly, overall cortical source-localized alpha activity also differed between high- and low-consistency trials and rest ($F_{2,134} = 44.96$, $p < .001$), with the largest activity amplitude being observed on low-consistency trials followed by high-consistency trials and then rest ($p < .001$ for the difference between conditions) (Figure 2D). These differences between the high- and low-consistency and the high-consistency and rest conditions are also visualized in Figure 2B (right 2 panels, FDR-corrected condition differences across 68 ROIs). Condition correlations and source activity differences were not affected when age was controlled for in the analyses.

Interoceptive Attention Task-Related Network Activity

To better understand how alpha activity on the task conditions and rest are organized relative to canonical cognitive control and default mode networks, we averaged their source-localized activity into 5 networks: the FPN, CON, anterior DMN, pDMN, and medial temporal DMN (Figure 3A). An rm-ANOVA model with within-subjects factors of 5 networks and 3 conditions showed a main effect of network ($F_{4,1224} = 20.53$, $p < .001$), condition ($F_{2,612} = 53.76$, $p < .001$), and a condition × network interaction ($F_{8,2448} = 10.72$, $p < .001$). Post hoc tests showed that in all networks, there was significantly greater activity on low-consistency than high-consistency trials and significantly greater activity for high-consistency trials than rest (Figure 3B). The differential low- versus high-consistency trial activity was greatest in pDMN compared with all other networks ($p < .0001$) (Figure 3C). The rm-ANOVA model results did not differ when age was added as a covariate, and there were no significant age interactions with either network or trial type.

Association of pDMN Activity With Frontal Network During Task

Previous functional magnetic resonance imaging research has suggested that DMN activity may be regulated by interactions with the FPN and CON (56). Here, we investigated whether EEG source–localized pDMN activity, which showed the largest differential high- versus low-consistency activity, is related to connectivity to the FPN/CON. For this, we calculated INC as temporal correlations between the pDMN and FPN/CON networks. Then, we correlated pDMN-FPN and pDMN-CON INC to pDMN activity both during the task and at rest. Spearman's correlations were used to protect against outliers.

On both high- and low-consistency trials, pDMN activity showed a significant negative correlation with both pDMN-FPN (high: $\rho_{306} = -0.24$, $p = 1.2 \times 10^{-5}$; low: $\rho_{306} = -0.19$, $p = .0006$) and pDMN-CON (high: $\rho_{306} = -0.18$; $p = .001$, low: $\rho_{306} = -0.14$, $p = .01$) connectivity, while these correlations were not significant at rest ($p > .4$) (Figure 4). Thus, for both high- and low-consistency trials, greater pDMN connectivity with FPN/CON was associated with lesser pDMN activity, suggesting top-down regulation of pDMN activity by frontal networks during the task. There was no difference in these activity-connectivity associations between task trial types.

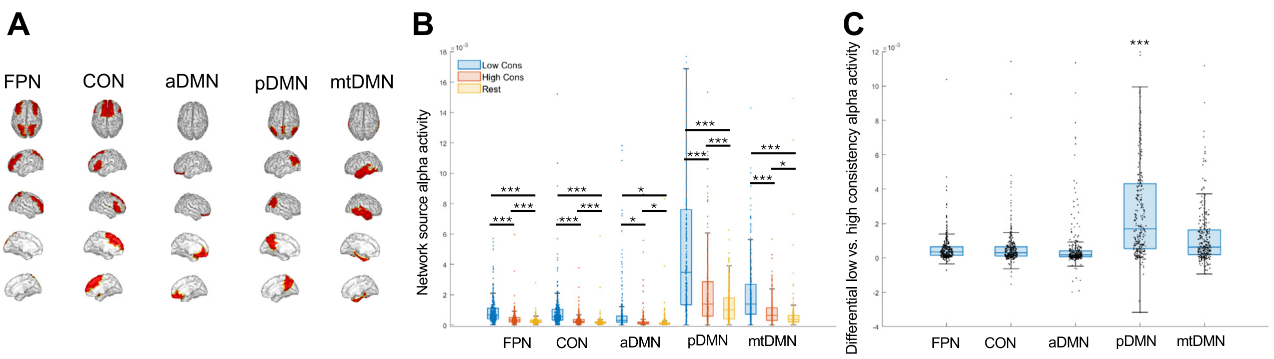

Figure 3. Network activity during the interoceptive task and at rest. **(A)** To better understand patterns of neural activity on the interoceptive task and at rest, source-localized activity was averaged within canonical brain networks, specifically the 2 frontal cognitive control networks, the frontoparietal network (FPN) and cingulo-opercular network (CON), and the 3 components of the default mode network (DMN), the anterior (aDMN), posterior (pDMN), and mediotemporal DMN (mtDMN). Brain regions included within each network are colored in red and shown in top view as well as lateral/medial left/right views. **(B)** Box plots show alpha activity in each network on low-consistency and high-consistency trials compared with rest. In all cases, low-consistency trial activity was greater than high-consistency trial activity, which was greater than rest. **(C)** Differential low- minus high-consistency alpha activity in source units showed the largest activity differential in the pDMN compared with all other networks. *$p < .05$, ***$p < .001$. Cons, consistency.

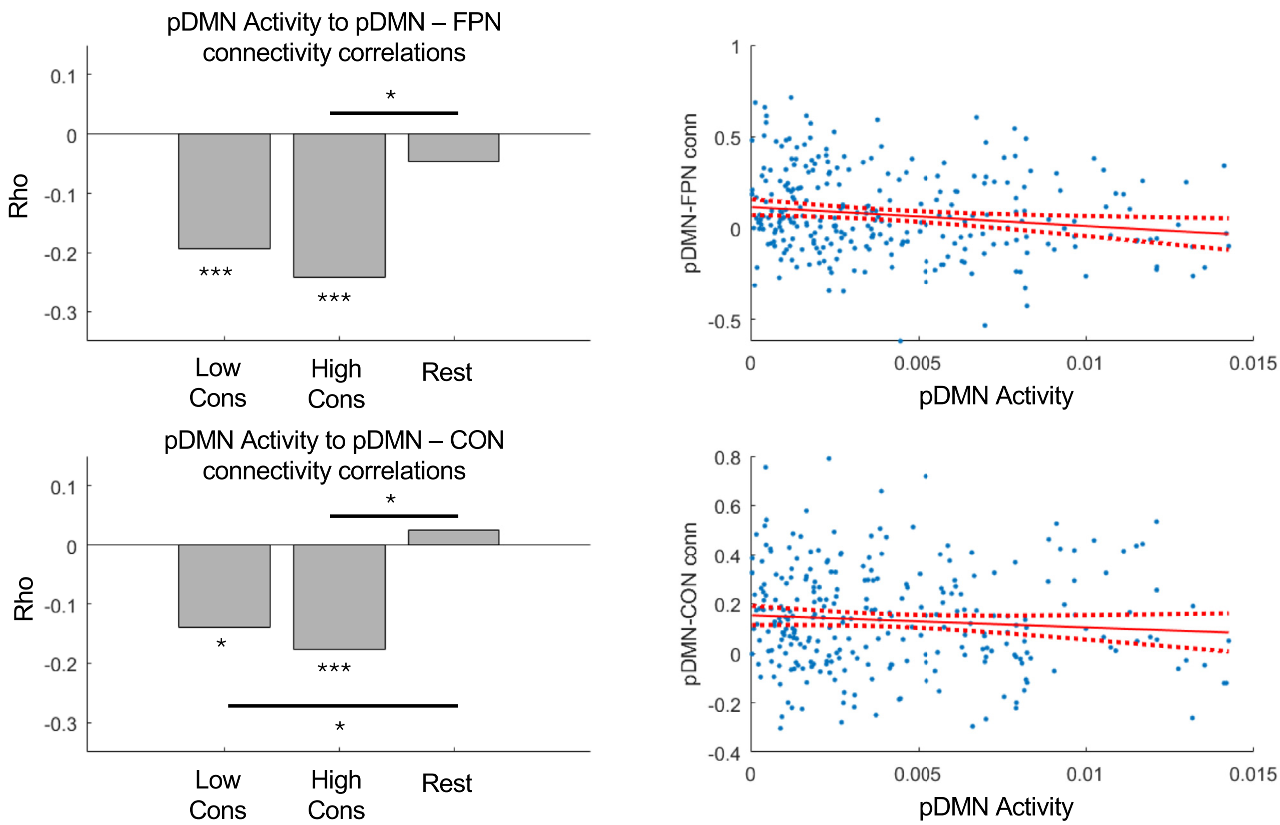

Figure 4. Relationship between posterior default mode network (pDMN) activity and internetwork connectivity. Spearman's rho correlations between pDMN activity and its connectivity with the frontoparietal network (FPN) (top left) and cingulo-opercular network (CON) (bottom left) are shown for low- and high-consistency trials and at rest. pDMN activity showed significant inverse Spearman's correlations with internetwork connectivity for low- and high-consistency trials but not at rest. These activity-connectivity correlations differed significantly from rest for high-consistency trials for both FPN and CON associations and also for low-consistency trials for FPN associations. Scatter plots at right show pDMN activity vs. internetwork connectivity relationships on low-consistency trials with the FPN (top right, $\rho = -0.19$, $p = .0006$) and CON (bottom right, $\rho = -0.14$, $p = .01$). *$p < .05$, ***$p < .001$. Cons, consistency.

These associations differed significantly from rest for high-consistency trials for both the FPN and CON and for low-consistency trials for CON, tested using the Dunn Clark test ($p < .05$, FDR corrected) (Figure 4). Adding partial correlations with age as a covariate did not change these overall results. Notably, neither pDMN-CON nor pDMN-FPN INC values differed between task conditions or at rest ($p > .2$, data not shown), suggesting that INC itself was not affected by the task.

Neurobehavioral Relationships

Previous work has linked increased activity within the DMN to increased levels of mind wandering and rumination (32,57,58). Because we observed the largest low- versus high-consistency differences in the pDMN, we hypothesized that this regional activity might be negatively related to real-world subjective mindfulness (Mindful Attention Awareness Scale measure). Within the pDMN, we found greater activity in the left precuneus region in participants with low mindfulness than in those with high mindfulness on the low- minus high-consistency trial differential ($F_{1,277} = 8.08$, $p = .005$), as well as separately on low-consistency ($F_{1,277} = 10.86$, $p = .001$) and high-consistency ($F_{1,290} = 8.06$, $p = .005$) trials (Figure 5). Low- and high-mindfulness participants were separated by median split. ANOVA effects were FDR corrected for multiple comparisons within the pDMN network. These relationships were not affected by including age in the model. ROIs in other networks did not show any such significant effects. Mindfulness was not significantly related to the interoceptive task performance consistency measure or to efficiency on the inhibitory control task ($p > .6$). Depression symptoms did not show any significant FDR-corrected relationships with neural activity.

Additional independent experiments showing that task-related pDMN activity was adaptively modulated by task difficulty, as well as results of simultaneous assessment of respiratory dynamics and validation of cortical source-localization with high-density channels, are shown in Supplemental Results.

DISCUSSION

Interoceptive attention is an important ability that allows us to focus on internal sensations as goal-relevant information and suppress irrelevant internally generated distractions (11,12). Previous work has shown that breath-monitoring tasks can be

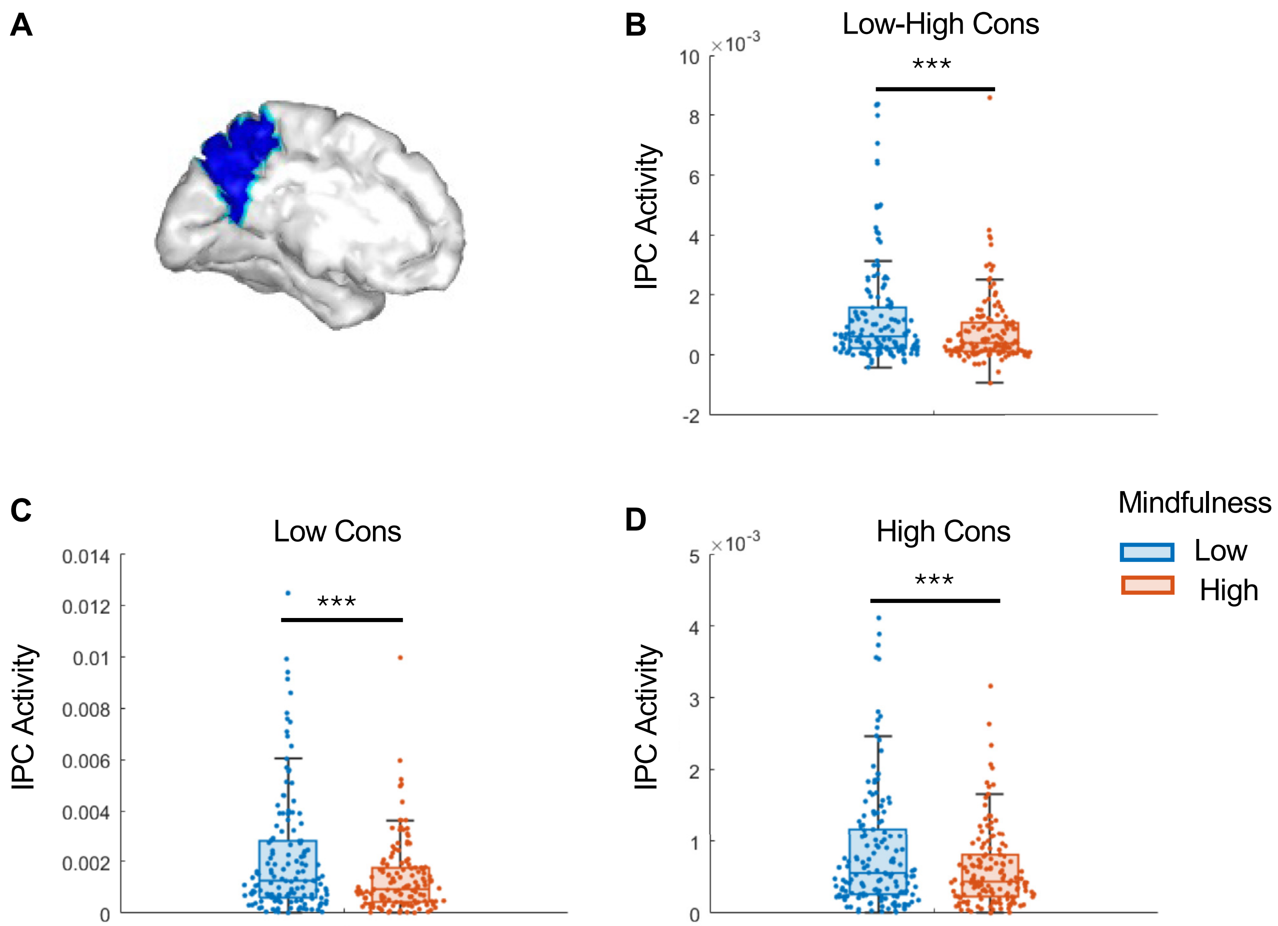

Figure 5. Neurobehavioral relationship with mindfulness. **(A)** Only alpha source activity in the left precuneus brain region (lPC) of the posterior default mode network showed associations with subjective mindfulness measured by the Mindful Attention Awareness Scale. Results in **(B–D)** compare activity for participants scoring low mindfulness in blue vs. high mindfulness in red per median split and are false discovery rate corrected for within-network region of interest (ROI) comparisons. Comparisons of lPC activity are shown in **(B)** for the low- minus high-consistency trial differential, **(C)** for low-consistency trials, and **(D)** for high-consistency trials. ***$p \leq .005$. Cons, consistency.

used to objectively identify processes relevant to interoceptive attention (26,27), with a focus on comparing response accuracy with objective monitoring of respiratory rate or respiratory cycle (28,30,59). In this study, we used consistency of responding on a breath-monitoring task as a distinct and relatively unstudied performance metric during interoceptive attention. Response consistency has been used as a performance metric on exteroceptive continuous performance tasks and is different from accuracy (60–62). Here, we made several important findings related to understanding the neurophysiological processes that occur during interoceptive attention, response consistency, and the relationship between these measures and subjective mindfulness.

First, we found that consistency of responses on this interoceptive attention task can be sensitive to age, with significantly greater consistency being found in individuals <60 years of age versus older adults. Related research has also shown that interoceptive awareness for heartbeat signals declines with age (63). This finding is consistent with much research on exteroceptive attention, particularly research that has shown superior performance efficiency and processing speed in younger adults (45,64,65). We also found that interoceptive attention consistency positively predicted performance efficiency on the inhibitory control task—a type of exteroceptive Go/NoGo continuous performance task (40,41). Previous work has shown that interoceptive mindfulness training enhances neural processes associated with behavioral inhibition on similar Go/NoGo tasks (66). Our findings suggest that there may be common attentional control functions invoked in both the interoceptive and exteroceptive tasks, especially because they were both continuous performance tasks (27,31).

Second, we found that source-localized alpha-frequency activity on the task is larger and distinct from activity that occurs during rest. This increase in overall brain activity is consistent with a functional magnetic resonance imaging study showing widespread activation during interoceptive attention relative to a comparable simple exteroception task (67). In addition we found even greater activity on low- versus high-consistency task trials. These trial-type differences were greatest in the pDMN network but were also observed in other DMN and cognitive/prefrontal brain regions. There are at least 3 interpretations related to these brain findings. First, response variability on this task (lower consistency) may be associated with increased mind wandering, reflected in increased activity across DMN and frontal brain regions. Prior studies back this interpretation in that mind-wandering is associated with increased behavioral variability (68,69) and greater activity in both DMN and lateral executive control regions (32,70). A second interpretation of this data is that on more variable trials, increased brain activity was observed as a compensatory mechanism to bring participants back on task. Consistent with this theory, prior work has suggested that increased DMN activity in certain contexts may be associated with lower behavioral variability (69) and an increase in interoceptive attention (29). This is also consistent with the general idea that on more difficult attentive tasks, there is more widespread brain activity, i.e., activity scales with difficulty (67). A final interpretation that we cannot rule out is that the trial-related differences in brain activity are driven by physiological differences related to breathing. Respiration has been linked to connectivity of the DMN (71–73,74) and shown to modulate posterior alpha power (75)—an effect that is related to modulation of aperiodic brain activity (75,76). To address this, in supplementary experiments, we found that variability on the task is associated with longer inhales/exhales. This finding mirrors what has been described by others—that increased respiratory variability is associated with sighing, i.e., an increase in deep breathing (77,78). Interestingly, sighing is also linked with diminished attentional stability (77). Moreover, prior work comparing the neurophysiological correlates of deep breathing to regular breathing did not find differences in alpha-scalp power/activity (79,80). As attentional variability, respiratory variability, and deeper breathing are all inter-related, our study was not suitable to adequately disambiguate these 3 aspects that may drive neural changes.

With regard to neurobehavioral associations, we found that greater activity in the precuneus region of the pDMN was significantly related to lower subjective mindfulness. This finding is consistent with a large body of literature primarily from functional magnetic resonance imaging studies, as nicely summarized in a systematic review (81) that showed that both short- and long-term meditation training was associated with reduction in subjective markers of mind wandering that are in turn linked with reduced activity in DMN brain regions. Thus, here we showed an electrophysiological correlate of this neurobehavioral relationship that can be captured using a brief interoceptive attention assessment in a large sample across the life span that provides confidence that results will be generalizable beyond our study (82,83). However, it is important to note that while mindfulness was physiologically related to pDMN activity, it was not related to the interoceptive performance consistency measure, i.e., individuals with greater subjective mindfulness did not have more consistent task performance. This evidence is consistent with studies that have compared meditators (who regularly practice attention to internal body sensations) with nonmeditators and found no difference in interoceptive monitoring of heartbeat signals (84,85).

Limitations of our study include low-density EEG-derived source reconstructions in the large sample experiment, although it is important to note that we validated these results in the supplementary independent experiment with dense electrodes. We also do not have formal documentation of the extent of meditation experience in our participants, although no participant explicitly noted having long-term experience. Relatedly, long-term meditation experience has been shown to slow down overall respiration rates (86). Therefore, not knowing the respiration rates in our large sample is a limitation, although in the supplementary experiment, we found no relationship between overall respiration rates and response consistency. Our findings are also associative, and future studies may causally verify our results using specific circuit perturbation/neuromodulation strategies like electrical/magnetic brain stimulation or neurofeedback (87–89). Overall, our results demonstrate the neural correlates of inconsistent versus consistent interoceptive breath attention, revealed as pronounced activity in the pDMN that is inversely related to connectivity with the FPN and CON. This pDMN activity also distinguishes individuals with low versus high mindfulness and thus may serve as a functional marker in future studies that aim to train interoceptive abilities and mindfulness (90).

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The *BrainE* software is copyrighted for commercial use (Regents of the University of California Copyright No. SD2018-816) and free for research and educational purposes. The datasets that were generated and analyzed during the current study are available from the datadryad.org repository: https://doi.org/10.5061/dryad.80gb5mkwk.

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