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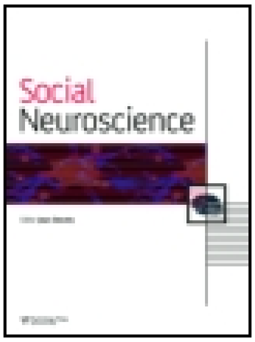

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Abstract

Mindfulness can be viewed as an important dispositional characteristic that reflects the tendency to be mindful in daily life, which is beneficial for improving individuals' both hedonic and eudaimonic well-being. However, no study to date has examined the brain regions involved in individual differences in dispositional mindfulness during the resting state and its relation with hedonic and eudaimonic well-being. To investigate this issue, the present study employed resting-state functional magnetic resonance imaging (rs-fMRI) to evaluate the regional homogeneity (ReHo) that measures the local synchronization of spontaneous brain activity in a large sample. We found that dispositional mindfulness was positively associated with the ReHo in the left orbitofrontal cortex (OFC), left parahippocampal gyrus (PHG) and right insula implicated in emotion processing, body awareness and self-referential processing, and negatively associated with the ReHo in right inferior frontal gyrus (IFG) implicated in response inhibition and attentional control. Furthermore, we found different neural associations with hedonic (i.e., positive and negative affect) and eudaimonic well-being (i.e., the meaningful and purposeful life). Specifically, the ReHo in the IFG predicted eudaimonic well-being whereas the OFC predicted positive affect, both of which were mediated by dispositional mindfulness. Taken together, our study provides the first evidence for linking individual differences in dispositional mindfulness to spontaneous brain activity and demonstrates that dispositional mindfulness engages multiple brain mechanisms that differentially influence hedonic and eudaimonic well-being.

Keywords: Spontaneous brain activity; Eudaimonic well-being; Hedonic well-being; Dispositional mindfulness

Introduction

Mindfulness has been defined as an attention to and awareness of one's ongoing sensory, cognitive and emotional experiences in the context of an accepting, non-judgmental stance toward those experiences (Brown & Ryan, 2003; Brown, Ryan, & Creswell, 2007). A roughly opposed concept is mind-wandering, which reflects intermittent shifts of attention away from the task at hand toward internal information (Mrazek, Smallwood, & Schooler, 2012; Smallwood & Schooler, 2006), in contrast to sustained attentiveness in mindfulness. Although mindfulness can be cultivated through various forms of mindfulness meditation training (e.g., Carmody & Baer, 2008; Falkenström, 2010; Keng, Smoski, & Robins, 2011), mindfulness has also been conceptualized as a trait-like or dispositional characteristic, in which mindfulness levels vary naturally in the general population, even without mindfulness training (Brown & Ryan, 2003). A large body of evidence has shown that the self-reported tendency to be mindful in daily life is positively correlated with psychological health and well-being and negatively correlated with psychological symptoms and distress (Bao, Xue, & Kong, 2015; Brown & Ryan, 2003; Brown et al., 2007; Grossman, Niemann, Schmidt, & Walach, 2004; Keng et al., 2011; Kong, Wang, & Zhao, 2014a; Schutte & Malouff, 2011). In this study, we investigated the brain regions involved in individual differences in dispositional mindfulness during the resting state and its relation with well-being.

The available neuroimaging literature on meditation has indicated an association with altered structures or activities in brain regions involved in attention (e.g., anterior cingulate cortex [ACC] and inferior frontal gyrus [IFG]), emotion processing (e.g., orbitofrontal cortex [OFC] and ventromedial prefrontal cortex [PFC]), self-processing (e.g., parahippocampal gyrus [PHG] and PFC), and interoception and body awareness (e.g., insula) (Farb et al., 2007; Goldin & Gross, 2010; Grant, Courtemanche, Duerden, Duncan, & Rainville, 2010; Hölzel et al., 2008, 2011; Lazar et al., 2000, 2005; Luders, Toga, Lepore, & Gaser, 2009; Lutz, Brefczynski-Lewis, Johnstone, & Davidson, 2008; Manna et al., 2010; Ott, Hölzel, & Vaitl, 2011; Tang, Tang, & Posner, 2013; Klimecki, Leiberg, Lamm, & Singer, 2013; Zeidan, Martucci, Kraft, Gordon, McHaffie, & Coghill,, 2011). Individual differences in dispositional mindfulness may be reliably detected through self-report questionnaires, as mindfulness traits may also be present in meditation-naive individuals (Baer, Smith, & Allen, 2004). To our knowledge, only several studies have explored the association between brain activity and individual differences in dispositional mindfulness. For instance, several functional magnetic resonance imaging (fMRI) studies have shown that higher levels of dispositional mindfulness is mostly associated with reduced amygdala activation and increased PFC activation during several emotion-processing tasks (Creswell, Way, Eisenberger, & Lieberman,, 2007; Lutz et al., 2013; Modinos, Ormel, & Aleman, 2010). However, it remains unknown whether and how the local synchronization of spontaneous brain activity could predict dispositional mindfulness. Therefore, here we explored the neural correlates of individual differences in dispositional mindfulness using resting-state fMRI (rs-fMRI), a promising tool for exploring the intrinsic functional architecture of the brain based on measurements of spontaneous low-frequency fluctuations (LFFs, 0.01–0.10 Hz) in the blood oxygenation level dependent signal (Biswal, 2012; Fox & Raichle, 2007; Raichle, 2010). It has been used to explore the neural basis of individual differences in behavioral performance such as intelligence, conflict adaptation and personality traits (Tian et al., 2012; Wang et al., 2014; Wang, Song, Jiang, Zhang, & Yu, 2011; Wei et al., 2011). Because it is a data-driven method that requires no a priori hypotheses about regions of interest, it can identify non-anticipated or transient task-related components (Zang, Jiang, Lu, He, & Tian, 2004).

The extant literature suggests that mindfulness is beneficial for improving well-being. Generally, well-being is composed of hedonic well-being and eudaimonic well-being, which have been long distinguished by philosophers (Aristotle, 1925). A hedonic approach of well-being equates well-being with pleasure and happiness and defines well-being in terms of pleasure attainment and pain avoidance (Ryan & Deci, 2001). Alternatively, a eudaimonic approach of well-being conceptualizes well-being in terms of the realization of one’s true potential (Ryff & Keyes, 1995) and the experience of purpose or meaning in life (Ryff, 1989). Contemporary psychological research has continued to distinguish these two types of well-being (e.g., Ryan & Deci, 2001), with empirical studies demonstrating that they are related but independent constructs using confirmatory factor analysis techniques (Gallagher, Lopez, & Preacher, 2009; Linley, Maltby, Wood, Osborne, & Hurling, 2009). Correlational studies have shown that measures of dispositional mindfulness are associated with higher levels of positive affect and eudaimonic well-being and lower levels of negative affect (e.g., Brown & Ryan, 2003; Keng et al., 2011; Kong et al., 2014a; Schutte & Malouff, 2011; Wang & Kong, 2014). Furthermore, numerous studies suggest that with an increase in mindfulness through interventions (e.g., meditation), individuals’ well-being also tends to increase (e.g., Falkenström, 2010; Fredrickson, Cohn, Coffey, Pek, & Finkel, 2008; Geschwind, Peeters, Drukker, van Os, & Wichers, 2011; Keng et al., 2011; Zeidan, Johnson, Gordon, & Goolkasian, 2010). Although previous studies have shown the associations between mindfulness and well-being, specific neurobiological mechanisms through which mindfulness exerts beneficial effects on well-being have not been understood. Given that hedonic and eudaimonic well-being are conceptually and empirically distinct constructs (Gallagher et al., 2009; Linley et al., 2009), spontaneous brain activity related to dispositional mindfulness might differentially predict both forms of well-being. Previous studies have shown that hedonic well-being is mostly associated with limbic regions such as the OFC (Berridge & Kringelbach, 2013; Kringelbach, 2005), whereas eudaimonic well-being is mostly associated with attention-related regions including the ACC and lateral PFC (Heller et al., 2013; Kong, Hu, Xue, Song, & Liu, 2015; van Reekum et al., 2007). Furthermore, a recent fMRI study found that compassion meditation training elicited activity in the OFC and increased positive affect, even in response to witnessing others in distress (Klimecki et al., 2013). Thus, we speculated that the OFC might predict hedonic well-being through dispositional mindfulness, whereas attention-related areas including the ACC and lateral PFC might predict eudaimonic well-being through dispositional mindfulness.

To investigate these issues, this study used well-validated behavioral measures of dispositional mindfulness and well-being, and rs-fMRI methodology. Here, we employed regional homogeneity (ReHo) to measure the local synchronization of spontaneous brain activity during rest, and then investigated the relationship between ReHo and dispositional mindfulness as measured by the Mindful Attention Awareness Scale (MAAS, Brown & Ryan, 2003). On the basis of previous neuroscience findings on mindfulness, we hypothesized that individual differences in dispositional mindfulness would be correlated with the ReHo in multiple brain regions associated with executive attention, emotion processing, body awareness and self-related processing. Furthermore, we examined the extent to which individual differences in dispositional mindfulness are able to mediate the relationship between mindfulness-related neural substrates and two types of well-being.

Methods

Participants

Two hundred and ninety healthy university students (157 females; mean age = 21.56 years, standard deviation (SD) = 1.01) from Beijing Normal University were recruited as paid participants. All participants reported no history of neurological or psychiatric disorders. Most of the participants were right-handed (n=272) based on a single-item handedness questionnaire (“Are you (a) right-handed, (b) left-handed, (c) mixed-handed?”). Previous neuroimaging studies have found that a limited number of left-handed participants has little influence on the research results when the sample is large (e.g., Kong et al., 2014b; Li et al., 2014); therefore we did not remove data from left-handed participants. Both behavioral and MRI protocols were approved by the Institutional Review Board of Beijing Normal University. Written informed consent was obtained from all participants prior to the study.

Psychological measures

To assess dispositional mindfulness we administered the Mindful Attention Awareness Scale (MAAS; Brown & Ryan, 2003), which consists of 15 brief statements. Items describe mindlessness in everyday situations (e.g., “I tend to walk quickly to get where I’m going without paying attention to what I experience along the way.” and ‘‘I tend not to notice feelings of physical tension or discomfort until they really grab my attention.’’). Respondents were asked to rate their agreement on a 6-point Likert-type scale (1 = almost always, 6 = almost never). Item scoring was reversed so that a higher score reflects a higher level of mindfulness. The scale has high internal consistency and validity (Bao et al., 2015; Brown & Ryan, 2003; Kong et al., 2014a; Lu et al., 2014). In this study, the scale exhibited adequate reliability (α = 0.85).

Emotional well-being (sometimes called hedonic well-being) refers to the emotional quality of an individual's everyday experience (Ryan & Deci, 2000; Kahneman & Deaton, 2010). It was assessed by the Positive and Negative Affect Schedule (PANAS; Watson, Clark, & Tellegen, 1988). The PANAS consists of a word list describing two different affect states (10 positive and 10 negative), for example, "excited" and "upset." Participants were instructed to indicate the extent to which they generally feel each affect using a 5-point Likert scale. Positive and negative affect scores were calculated separately, with higher scores indicating that participants feel more of that affect. The scale has high internal consistency and validity (Crawford & Henry, 2004; Sun & Kong, 2013; Watson et al., 1988). In this study, the positive affect scale (α = 0.81) and negative affect scale (α = 0.79) exhibited adequate reliability. One participant was excluded because of missing data.

Eudaimonic well-being was assessed with the 42-item Scales of Psychological Well-being (SPWB, Ryff et al., 2007). It is composed of the six dimensions (autonomy, environmental mastery, self-acceptance, positive relations with others, purpose in life, and personal growth). The SPWB is a highly reliable measure to assess eudaimonic well-being (Gallagher et al., 2009; Ryff, 1989, 2007). It includes items such as, ''Some people wander aimlessly through life, but I am not one of them" and ''I think it is important to have new experiences that challenge how you think about yourself and the world." Each dimension was measured with seven items and participants responded to each item using a 6-point Likert scale with response options ranging from strongly disagree to strongly agree. To compute an overall score of eudaimonic well-being, scores across the six subscales were calculated. Higher scores indicate higher levels of eudaimonic well-being. In the present study, the SPWB exhibited adequate internal reliability ($\alpha = 0.92$). Six participants were excluded because of missing data.

rs-fMRI data acquisition

The rs-fMRI scan was performed on a 3T scanner (Siemens Magnetom Trio, A Tim System) with a 12-channel phased-array head coil at Beijing Normal University Imaging Center for Brain Research, Beijing, China. During rs-fMRI scanning, participants were instructed to close their eyes, keep still, and not think about anything systematically or fall asleep. The resting state scanning consisted of 240 contiguous EPI volumes (TR = 2000ms; TE = 30ms; flip angle = 90°; number of slices = 33; matrix = 64 × 64; FOV = 200 × 200 mm^2; acquisition voxel size = 3.1 × 3.1 × 3.6 mm^3). Moreover, High-resolution T1-weighted images were acquired with magnetization prepared gradient echo sequence (MPRAGE: TR/TE/TI = 2530/3.39/1100 ms; flip angle = 7 degrees; matrix = 256 × 256) for spatial registration. One hundred and twenty-eight contiguous sagittal slices were obtained with 1 × 1 mm^2 in-plane resolution and 1.33 mm slice thickness.

Data preprocessing

We used FSL (www.fmrib.ox.ac.uk/fsl/) to preprocess the resting-state functional images.

The first four volumes of the rs-fMRI data were discarded for signal equilibrium. Preprocessing steps of rs-fMRI data included motion correction (by aligning each volume to the middle volume of the image with MCFLIRT), intensity normalization, removing linear trends and temporally band-pass filtering (0.01< f < 0.1 Hz). One participant whose head motion was greater than 3.0 mm displacement in any of the x, y, or z directions or 3.0° of any angular motion throughout the rs-fMRI scan was excluded from further analyses. Registration of each participant's functional images to the high-resolution anatomical images was carried out with FLIRT to produce a six-degrees-of-freedom affine transformation matrix. Registration of each participant's high-resolution anatomical image to a common stereotaxic space (the Montreal Neurological Institute 152-brain template with a resolution of 2 × 2 × 2 mm^3, MNI152) was accomplished using a two-step process (Andersson, Jenkinson, & Smith, 2007).

ReHo analysis

ReHo was performed on a voxel-by-voxel basis by calculating Kendall's coefficient of concordance (KCC) of time series of each of the 26 neighbors surrounding the center voxel (see Zang et al., 2004 for details). A KCC value was then attributed to the central voxel representing the ReHo, and individual ReHo maps were obtained. A larger ReHo value for a given voxel indicates a higher local synchronization of rs-fMRI signals among neighboring voxels. Then, individual ReHo maps were registered to MNI152 standard space by applying the previously calculated transformation matrix for further groupwise analyses. For standardization purposes, the individual data was transformed to Z score (i.e., minus the global mean value and then divided by the standard deviation) other than simply being divided by the global mean.

ReHo-behavior correlation analysis

To detect the brain regions whose ReHo values predict individual differences in dispositional mindfulness, we conducted a whole-brain correlation analysis with age and gender as the confounding covariates, and the score of dispositional mindfulness as the covariates of interest. Multiple comparison correction was performed using the 3dClustSim program in AFNI (http://afni.nimh.nih.gov/pub/dist/doc/program_help/3dClustSim.html). A corrected cluster threshold of $p < 0.01$ (single voxel p < 0.01, cluster size ≥ 91.4 voxels; 731.2 mm^3) was set. All significant correlations were presented in MNI coordinates.

Prediction analysis

To examine the robustness of the relation between ReHo and behavioral performance, a machine-learning approach with balanced fourfold cross-validation combined with linear regression conducted was used (Cohen et al., 2010; Qin, Young, Duan, Chen, Supekar, & Menon, 2014; Supekar et al., 2013). Mindfulness as a dependent variable and ReHo of the regions as an independent variable were treated as input to a linear regression algorithm. The $r_{\text{(predicted, observed)}}$ was used to measure how well the independent variable predicts the dependent variable. The correlation was estimated using a balanced fourfold cross-validation procedure in following steps. First, data were divided into four folds such that the distributions of these variables were balanced across folds. Second, a linear regression model was built using three folds, leaving out one fold, and this model was then used to predict the data in the left-out fold (i.e. predicted values). This procedure was repeated four times to compute a final $r_{\text{(predicted, observed)}}$ representing the correlation between the values predicted by the regression model and the observed values. Nonparametric testing approach was used to assess the statistical significance of the model. The empirical null distribution of $r_{\text{(predicted, observed)}}$ was estimated by generating 1,000 surrogate datasets under the null hypothesis that there was no association between ReHo and behavioral performance. We generated each surrogate dataset Di of size equal to the observed dataset by permuting the labels on the observed data points (i.e. the score of mindfulness). The $r_{\text{(predicted, observed)i}}$ (i.e., $r_{\text{(predicted, observed)}}$ of Di) was computed using the observed labels of Di and predicted labels using the fourfold-balanced cross-validation procedure described above. This procedure produced a null distribution of $r_{\text{(predicted, observed)}}$ for the regression model. The statistical significance (P value) of the model was then determined by counting the number of $r_{\text{(predicted, observed)i}}$ greater than $r_{\text{(predicted, observed)}}$ and then dividing that count by the number of Di datasets (i.e., 1,000).

Results

The neural correlates of dispositional mindfulness

Table 1 shows means, SDs, skewness, and kurtosis for all questionnaires. The kurtosis and skewness of all the scores ranged from -1 and +1, which indicated the normality of the data (Marcoulides & Hershberger, 1997). Correlation analysis revealed that dispositional mindfulness was positively correlated with the ReHo in three clusters including the right insula (MNI coordinate: 36, 14, -10; $r = 0.22$; $z = 3.64$; Cluster size = 920 mm^3; $p < 0.01$), left PHG (MNI coordinate: -20, -32, -14; $r = 0.23$; z =3.41; Cluster size = 880 mm^3; $p < 0.01$), and left OFC (MNI coordinate: -24, 14, -26; $r = 0.21$; $z = 3.86$; Cluster size = 768 mm^3; $p < 0.01$). Dispositional mindfulness was also negatively correlated with the ReHo in a cluster including the right IFG (MNI coordinate: 60, 10, 28; $r = -0.26$; $z = -4.10$; Cluster size = 1024

mm^3; $p < 0.01$) (Fig. 1 and 2, Table 2). No other significant relations were observed. To examine the robustness of the relation between ReHo and mindfulness, we applied a cross-validation method with a machine-learning algorithm (see Methods). We found that the ReHo values of the IFG ($r_{(predicted, observed)} = .22$; $p < .001$), PHG ($r_{(predicted, observed)} = .20$; $p < .001$), OFC ($r_{(predicted, observed)} = .19$; $p < .001$) and insula ($r_{(predicted, observed)} = .21$; $p < .001$) reliably predicted individual differences in dispositional mindfulness.

----Insert Table 1 here ----

----Insert Table 2 here ----

In order to assess the joint effects of the ReHo in the IFG, PHG, OFC and insula on dispositional mindfulness, we performed a multiple linear regression analysis. The dependent variable was participants' dispositional mindfulness scores, and the independent variables were the average ReHo values of the clusters including the PCG, PHG, OFC and insula. When all independent variables were simultaneously entered into the regression, the regression model explained 14% of the variance in dispositional mindfulness ($R^2 = 0.14$; $F_{[4, 285]} = 12.32$; $p < 0.001$) and all regression coefficients for these clusters were significant ($\beta = .14, -.21$, *ps* < 0.05). After sex and age were regressed out, all regression coefficients remained significant ($\beta = .12, -.20$, *ps* < 0.05). These findings suggest that resting-state activity in the IFG, PHG, OFC, and insula may independently predict individual differences in dispositional mindfulness.

----Insert Figure 1 here ----

----Insert Figure 2 here ----

Dispositional mindfulness mediated the association between spontaneous brain activity and

well-being

To test the relationship between dispositional mindfulness, well-being and spontaneous brain activity, we first performed a correlation analysis between dispositional mindfulness and well-being. We found that dispositional mindfulness was positively correlated with positive affect (r = 0.29, p < 0.001, FDR corrected) and eudaimonic well-being (r = 0.52, p < 0.001, FDR corrected), and negatively correlated with negative affect (r = –0.35, p < 0.001, FDR corrected). These results support the notion that dispositional mindfulness contributes to both hedonic and eudaimonic well-being.

Next, we carried out a correlation analysis to examine whether the brain regions involved in dispositional mindfulness are differentially associated with various forms of well-being. We found that eudaimonic well-being was significantly correlated with the ReHo in the IFG (r = –0.15, p = 0.030, FDR corrected). Positive affect was significantly correlated with the ReHo in the OFC (r = 0.17, p = 0.011, FDR corrected). No significant correlation between negative affect and these clusters was obtained. Furthermore, all these significant correlations remained after controlling for the effects of age and sex. In addition, we also applied a cross-validation method with a machine-learning algorithm to examine the robustness of the relation between ReHo and well-being. We found that the ReHo of the IFG reliably predicted individual differences in eudaimonic well-being ($r_{(predicted, observed)}$ = 0.12; p = .003), while the ReHo in the OFC reliably predicted individual differences in positive affect ($r_{(predicted, observed)}$ = 0.15; p = .001). The results indicated that the neurobiological systems subserving dispositional mindfulness differentially predicted hedonic and eudaimonic well-being.

The aforementioned results indicated that well-being, dispositional mindfulness and brain regions were closely linked to one another. However, the role of dispositional mindfulness in the relationships between intrinsic brain activity and well-being remains unknown. Thus, we further examined the association between the ReHo in these regions and well-being when controlling for the mindfulness factor. The associations observed in the previous analysis were no longer significant (*ps* > 0.05), suggesting a possible mediating role of dispositional mindfulness in the associations between the ReHo in these regions and well-being.

To examine this intuition, an INDIRECT macro implemented in SPSS (Preacher & Hayes, 2008) was used. With sex and age as covariates in the model, the mediation analysis showed that dispositional mindfulness significantly mediated the effect of the OFC on positive affect (95% confidence interval = [0.02, 0.11], $p < 0.05$), based on the criterion that an empirical 95% confidence interval of the significant indirect effect does not include zero with a bootstrap simulation (n = 5,000) (Fig. 3). Besides, dispositional mindfulness also significantly mediated the effect of the IFG on eudaimonic well-being (95% confidence interval = [-0.21, -0.08], $p < 0.05$) (Fig. 4).

----Insert Figure 3 here ----

In addition, we also used the same mediation analysis procedure to examine the mediational model where relevant brain regions mediated the relationship between dispositional mindfulness and well-being. The results showed that the empirical 95% CI of all the indirect effects included zero, indicating that these brain regions did not mediate the relationship between dispositional mindfulness and either form of well-being. Therefore, it is dispositional mindfulness that mediated the association between spontaneous brain activity and well-being.

Discussion

The present study employed the ReHo approach to investigate the neural correlates of individual differences in dispositional mindfulness and its associations with hedonic and eudaimonic well-being in a large sample. Behavioral results showed that dispositional mindfulness was related to hedonic (i.e., positive and negative affect) and eudaimonic well-being, which is in line with previous studies reporting the beneficial effects of mindfulness on well-being (Brown & Ryan, 2003; Brown et al., 2007; Grossman et al., 2004; Keng et al., 2011; Kong et al, 2014; Schutte & Malouff, 2011). ReHo results showed that dispositional mindfulness was positively associated with the ReHo of rs-fMRI signals in the left OFC, left PHG, right insula, and negatively associated with the ReHo in the right IFG. Interestingly, we found that the ReHo in the IFG predicted eudaimonic well-being, whereas the OFC predicted positive affect, both of which were mediated by dispositional mindfulness. To our knowledge, our findings provides initial evidence for linking individual differences in dispositional mindfulness to spontaneous brain activity and demonstrate possible neurobiological mechanisms that influence individual's well-being through dispositional mindfulness.

The finding that dispositional mindfulness is positively associated with the ReHo in the left OFC, left PHG, right insula, and negatively associated with the ReHo in the right IFG is consistent with previous studies in which state and dispositional mindfulness are related to structural changes or altered activities of the insula (Hölzel et al., 2008; Lazar et al., 2005; Lutz et al., 2013; Murakami et al., 2012; Zeidan et al., 2011), OFC (Klimecki et al., 2012; Luders et al., 2009; Zeidan et al., 2011), PHG (Leung, Chan, Yin, Lee, So, & Lee, 2013;

Murakami et al., 2012; Lazar et al., 2000) and IFG (Ding et al., 2015; Hasenkamp et al., 2012; Lee et al., 2012; Manna et al., 2010; Mascaro, Rilling, Negi, & Raison, 2013; Tang et al., 2013). Thus, these findings suggest that state and dispositional mindfulness might share **common** neural mechanisms. In addition, low ReHo in the OFC, PHG and insula among individuals with low mindfulness scores might reflect reduced cognitive processing in the affected regions, thus leading to low spontaneous brain activity among these individuals. High ReHo in the IFG among individuals with low mindfulness scores might imply a reorganization mechanism for neuroplasticity and cortical remapping or disruption of inhibitory mechanisms. Future studies are needed to investigate the physiological significance of ReHo before we can more accurately interpret the direction of the results.

Importantly, we found that the ReHo in the IFG, PHG, OFC and insula accounted for the unique variation in dispositional mindfulness, suggesting that these regions likely contribute to levels of mindfulness through different cognitive processes. First, the OFC has been implicated in regulating affective responses by reframing the contextual evaluation of sensory events (Rolls & Grabenhorst, 2008; Zeidan et al., 2011) and encoding reward value of pain or pleasure (Kringelbach et al., 2005; Leknes & Tracey, 2008; O'Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001; Peters & Büchel, 2010). Therefore, the mindfulness-related OFC involvement may reflect **altered processing of** reward and hedonic experience (e.g., positive affect) (O’Doherty et al., 2001; Peters & Büchel, 2010). Second, overwhelming evidence suggests that the functions of response inhibition and attentional control are localized to the right IFG (Aron, Fletcher, Bullmore, Sahakian, & Robbins, 2003; Aron, Robbins, & Poldrack, 2004; Hampshire, Chamberlain, Monti, Duncan, Owen, 2010). Behaviourally, mindfulness has been shown to relate to response inhibition and attentional control (Chambers, Lo, & Allen, 2008; Heeren, Van Broeck, & Philippot, 2009; Lee & Chao, 2012). Thus, response inhibition and attentional control might be an important mechanism for achieving mindfulness. Third, as a key node of the “default mode network” (DMN; Buckner, Andrews-Hanna, & Schacter, 2008; Fair et al., 2008), the PHG has been involved in self-processing such as self-evaluation and autobiographical memory retrieval (e.g., Levine, Turner, Tisserand, Hevenor, Graham, & McIntosh, 2004; Masaoka, Sugiyama, Katayama, Kashiwagi, & Homma, 2012; Northoff, Heinzel, de Greck, Bermpohl, Dobrowolny, & Panksepp, 2006; Pauly, Finkelmeyer, Schneider, & Habel, 2012). Behavioral studies have documented changes in self-concept such as more positive self-representation and higher self-acceptance following meditation practice (Hölzel et al., 2011). Therefore, the PHG involvement may reflect the beneficial changes in perspective on the self. Finally, the insula has been shown to be implicated in interoception and body awareness as well as emotional awareness (Craig, 2009; Singer, Critchley, & Preuschoff, 2009). Behaviorally, meditation practitioners report improved capability for body awareness (Hölzel et al., 2011). Such roles are consistent with the aspect of mindfulness that involves the focus of internal experience including sensory experiences of breathing and those related to emotions or other body sensations. These functions of all the brain regions seem to support Hölzel et al.’s (2011) theoretical view that mindfulness exerts its beneficial effects through an array of cognitive mechanisms, namely, executive attention, body awareness, emotion processing, and change in perspective on the self.

Interestingly, we found that dispositional mindfulness influenced individuals’ well-being through different brain mechanisms. On one hand, our finding fits nicely with our hypothesis that the OFC is associated with hedonic well-being through dispositional mindfulness. This is consistent with the recent finding that compassion training elicits OFC activity and increases positive affective experiences, in response to others' suffering (Klimecki et al., 2013). Previous imaging studies have demonstrated the role of the OFC in positive affect. For example, Welborn, Papademetris, Reis, Rajeevan, Bloise and Gray (2009) reported that larger OFC volume is associated with expressivity of positive emotions (but not of negative). Furthermore, trait positive affect corresponding to the personality dimension of extraversion was reported to be associated with structural changes or altered activation in the OFC (Cremers et al., 2011; Mobbs, Hagan, Azim, Menon, & Reiss, 2005; Omura, Constable, & Canli, 2005; Rauch, Milad, Orr, Quinn, Fischl, & Pitman, 2005). Overwhelming evidence suggests that the OFC represents the reward value, expected reward value and subjective pleasantness of foods and other reinforcers, all of which are essential for hedonic experience (Gottfried, O'Doherty, & Dolan, 2003; Kringelbach et al., 2005; O'Doherty et al., 2001; Peters & Büchel, 2010). Thus, the mindfulness-related OFC involvement may reflect increased capacities for processing hedonic experience, which leads to higher levels of positive affect.

On the other hand, the ReHo in the IFG significantly predicted eudaimonic well-being, which was entirely mediated by dispositional mindfulness. On one hand, this result indicates the important roles of the IFG in eudaimonic well-being. This is consistent with the previous studies exploring the neural basis of eudaimonic well-being. For example, eudaimonic well-being is found to be associated with activities of the PFC in response to affective stimuli

(Heller et al., 2013; van Reekum et al., 2007). On the other hand, our results substantiate that dispositional mindfulness may serve as a potential mechanism that explains the impact of the IFG on eudaimonic well-being. Previous studies have demonstrated the functions of the mindfulness-related region in response inhibition and attentional control (Aron et al., 2003, 2004; Hampshire et al., 2010). All these IFG-related processes are of great value for providing purpose and self-relevant goals as well as building social connections, which may lead to high levels of eudaimonic well-being.

Several limitations of the present study should be mentioned. First, because of the cross-sectional nature of this study, we cannot determine the direction of causation between dispositional mindfulness, well-being and the ReHo of brain regions. Longitudinal studies will be particularly useful to disentangle complex relationships between dispositional mindfulness, well-being and relevant brain regions. Second, this study used a sample of college students. Although college students are commonly chose as participants (e.g., Kong et al., 2014b; Murakami et al., 2012), the narrow age range might limit the generalizability of the results. Further investigation should use wider age ranges to explore the influence of age on these results. Third, the present findings are based on a single dimensional measure of mindfulness. Although the MAAS has been a widely used index of dispositional mindfulness in various studies of mindfulness (Brown & Ryan, 2003; Kong et al., 2014a; Wang & Kong, 2013), we believe that it would be important for the field to continue to explore other measures of mindfulness, to characterize and represent this multi-faceted construct more accurately. **Finally, the scales used in the study are not direct measures of either hedonic or eudaimonic well-being; therefore, further studies are needed to examine the relation**

between mindfulness and hedonic and eudaimonic well-being with direct measures.

To conclude, we employed the ReHo approach to investigate the potential neurobiological mechanisms subserving the contribution of dispositional mindfulness to hedonic and eudaimonic well-being of healthy individuals. We found that the ReHo values of the left OFC, left PHG, right insula, and right IFG could predict individual differences in dispositional mindfulness, revealing a potential resting-state neural mechanism for dispositional mindfulness. Moreover, although dispositional mindfulness contributed to both forms of well-being, there were apparently different neurobiological mechanisms through which dispositional mindfulness influenced various forms of well-being. Specifically, dispositional mindfulness mediated the effects of the IFG on eudaimonic well-being and that of the OFC on positive affect (i.e., hedonic well-being). Our findings might have important implications for how to implement mindfulness-related interventions aimed at enhancing various forms of well-being. Hölzel et al. (2011) have mentioned that various types of mindfulness practice may emphasize the different components of mindfulness. For example, breath awareness practice might mainly involve attention control and body awareness whereas loving-kindness and compassion meditation might involve emotion processing and the change in perspective on the self. Thus, further studies may develop appropriate types of mindfulness practice for different forms of well-being individuals would like to cultivate.

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Figure Legends

Fig. 1. Brain regions that correlated with individual differences in dispositional mindfulness. Dispositional mindfulness was negatively correlated with the ReHo in right inferior frontal gyrus (A) and positively correlated with the ReHo in the left parahippocampal gyrus (B), right insula (C) and left orbitofrontal cortex (D). The coordinate is shown in the MNI stereotactic space.

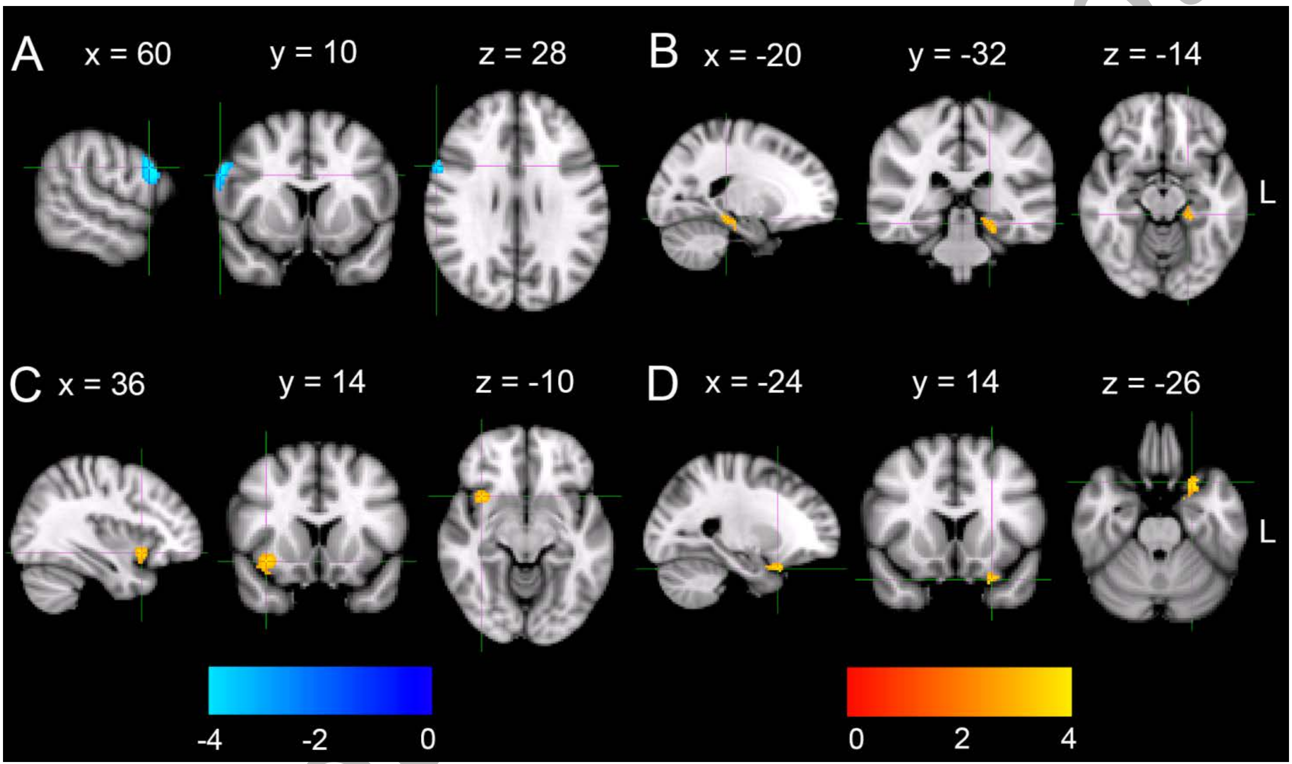

Fig. 2. Scatter plots depicting correlations between ReHo and individual differences in dispositional mindfulness. Scatter plots depicting correlations between dispositional mindfulness and ReHo in the right inferior frontal gyrus (A, r = -0.26, p < 0.001), left parahippocampal gyrus (B, r = 0.23, p < 0.001) right insula (C, r = 0.22, p < 0.001) and left orbitofrontal cortex (D, r = 0.21, p < 0.001) after adjusting for age and sex.

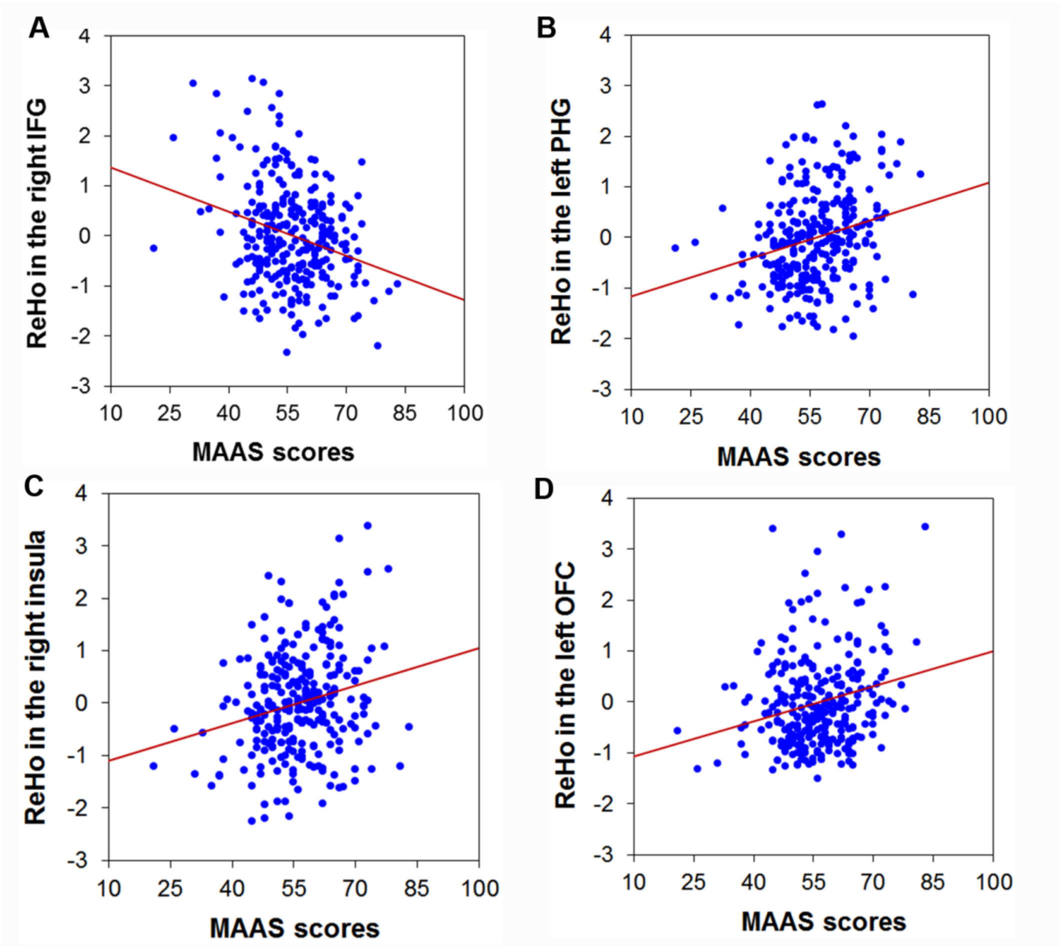

Fig. 3. Dispositional mindfulness mediates the association between spontaneous brain activity and hedonic well-being. Depicted is the path diagram (including standard regression coefficients) of mediation analysis demonstrating that spontaneous brain activity affects individuals' positive affect through dispositional mindfulness. *: $p < 0.05$. **: $p < 0.01$. ***: $p < 0.001$.

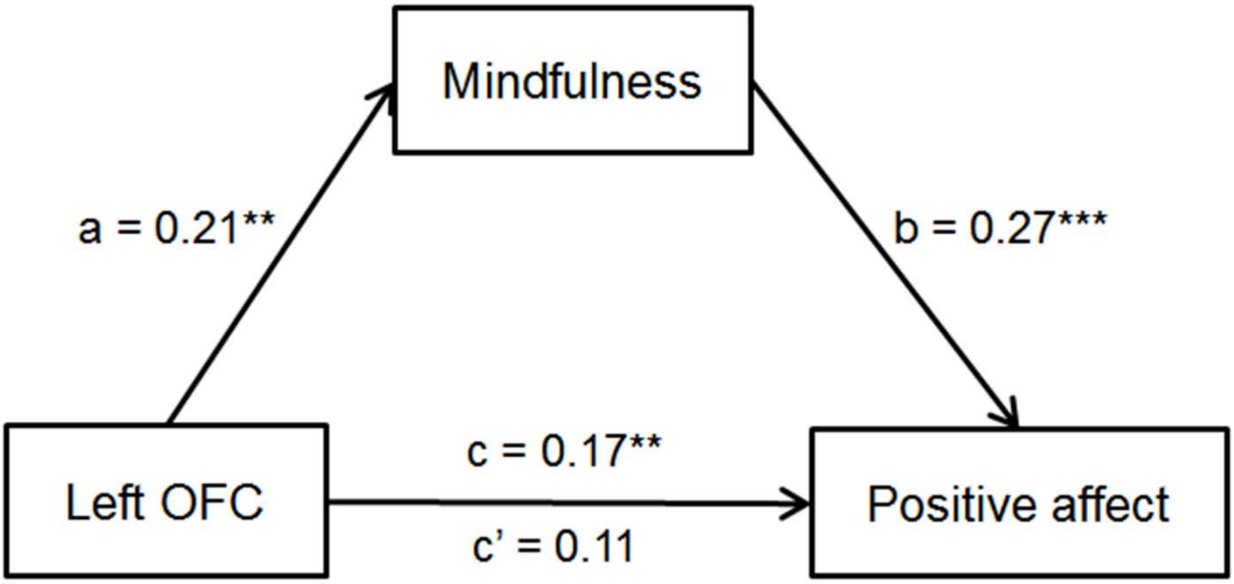

Fig. 4. Dispositional mindfulness mediates the association between spontaneous brain activity and eudaimonic well-being. Depicted is the path diagram (including standard regression coefficients) of mediation analysis demonstrating that spontaneous brain activity affects individuals' eudaimonic well-being through dispositional mindfulness. *: $p < 0.05$. **: $p < 0.01$. ***: $p < 0.001$.

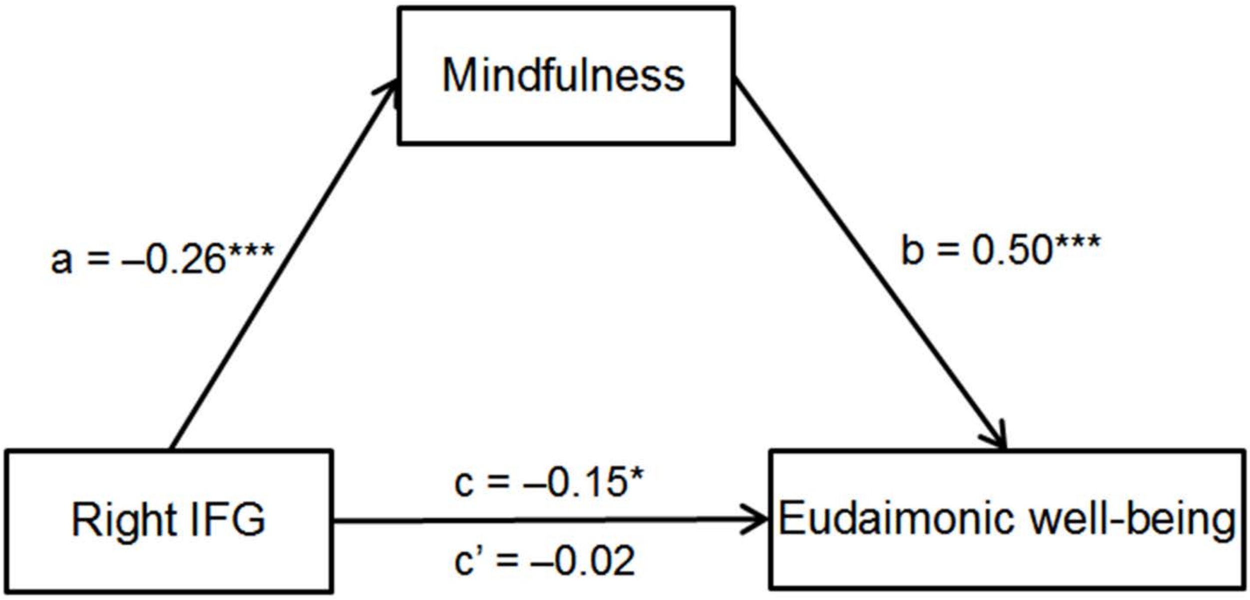

Table 1

Descriptive statistics for mindfulness, hedonic and eudaimonic well-being

	Minimum	Maximum	Mean	SD	Skewness	Kurtosis
Mindfulness	21	83	56.33	9.14	-0.17	0.80
Positive affect	20	48	34.14	4.80	-0.07	-0.14
Negative affect	12	40	24.40	4.72	0.41	0.36
Eudaimonic well-being	129	240	175.13	19.45	0.05	-0.21

Table 2

Brain regions that correlated with individual differences in dispositional mindfulness

Region	Side	MNI coordinate			Z	Cluster size
		x	*y*	*z*		(mm^3)
Positive correlation						
Insula	R	36	14	–10	3.64	920*
PHG	L	–20	–32	–14	3.41	880*
OFC	L	–24	14	–26	3.86	768*
Negative correlation						
IFG	R	60	10	28	-4.10	1024*

Note: MNI = Montreal Neurological Institute; L = left; R = right. OFC = Orbitofrontal cortex; PHG = Parahippocampal gyrus; IFG = Inferior frontal gyrus. * $p < 0.01$ (corrected).