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Intrinsic functional network contributions to the relationship between trait empathy and subjective happiness

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ABSTRACT

Subjective happiness (well-being) is a multi-dimensional construct indexing one's evaluations of everyday emotional experiences and life satisfaction, and has been associated with different aspects of trait empathy. Despite previous research identifying the neural substrates of subjective happiness and empathy, the mechanisms mediating the relationship between the two constructs remain largely unclear. Here, we performed a data-driven, multi-voxel pattern analysis of whole-brain intrinsic functional connectivity to reveal the neural mechanisms of subjective happiness and trait empathy in a sample of young females. Behaviorally, we found that subjective happiness was negatively associated with personal distress (i.e., self-referential experience of others' feelings). Consistent with this inverse relationship, subjective happiness was associated with the dorsolateral prefrontal cortex exhibiting decreased functional connectivity with regions important for the *representation* of unimodal sensorimotor information (e.g., primary sensory cortices) or multi-modal summaries of brain states (e.g., default mode network) and increased functional connectivity with regions important for the attentional *modulation* of these representations (e.g., frontoparietal, attention networks). Personal distress was associated with the medial prefrontal cortex exhibiting functional connectivity differences with similar networks—but in the opposite direction. Finally, intrinsic functional connectivity within and between these networks fully mediated the relationship between the two behavioral measures. These results identify an important contribution of the macroscale functional organization of the brain to human well-being, by demonstrating that lower levels of personal distress lead to higher subjective happiness through variation in intrinsic functional connectivity along a neural representation vs. modulation gradient.

1. Introduction

Subjective happiness, also commonly referred to as subjective well-being, is a multi-dimensional construct that indexes one's evaluation of everyday emotional experiences and life satisfaction, and is typically linked to high positive and low negative affect (Diener et al., 2016). Prior research demonstrated clear benefits associated with greater levels of happiness - happier individuals tend to have better physical health and greater longevity, improved social relationships, and higher job satisfaction and performance, among others (De Neve et al., 2013, Diener and Tay, 2012, Dolcos et al., 2018). Not surprisingly, subjective happiness is also related to various aspects of trait empathy (Choi et al., 2016, Grühn et al., 2008, Wei et al., 2011), which broadly indexes one's ability to understand others' feelings and mental states based on a clear psychological distinction between the self and others (Decety and Lamm, 2006). Trait empathy is related to various dimensions of happiness/well-being, including personal growth, purpose in life, and self-acceptance (Choi et al., 2016); some aspects of empathy are also associated with prosocial and altruistic behaviors (Batson, 2009), which in turn lead to greater happiness (Aknin et al., 2013, Aknin et al., 2012). Despite the wealth of behavioral evidence linking subjective happiness and trait empathy, the neural mechanisms mediating this relationship remain largely unexplored.

Previous functional neuroimaging studies examining different aspects of happiness and well-being have most consistently identified the role of the default mode network (DMN), a large-scale functional network in the brain that supports its ability to construct and maintain an internal model of the world (Barrett, 2017, Buckner, 2012,

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Buckner et al., 2008, Buckner and DiNicola, 2019, Hassabis and Maguire, 2009, Mesulam, 2002). Higher subjective happiness has been associated with decreased intrinsic functional connectivity within the DMN, involving the medial prefrontal cortex and posterior cingulate cortex (Luo et al., 2015, Luo et al., 2017). These regions are typically referred to as the "core" areas of the network, playing a pivotal role in the integration of salient information coming from the external world and the body's internal milieu (Andrews-Hanna et al., 2014). Other studies have found that some aspects of well-being (e.g., meaning in life) were positively correlated with intrinsic functional connectivity within the medial temporal lobe subsystem of the DMN, including the retrosplenial cortex and parahippocampal cortex (Waytz et al., 2015).

Subjective happiness has also been linked to differences in intrinsic functional connectivity between the DMN and other functional networks. For instance, subjective happiness was positively associated with intrinsic functional connectivity between the precuneus (part of the DMN) and right amygdala (Sato et al., 2019). Intriguingly, the authors found that subjective happiness was positively associated with effective (i.e., directed) connectivity from the amygdala to the precuneus but not the other way around, suggesting that only some but not all aspects of information flow between the two regions are related to subjective happiness. Furthermore, subjective happiness was negatively associated with functional connectivity between the DMN and salience network[1] (SN), as measured by the Pearson correlation of the associated independent components (Shi et al., 2018). The authors also showed through an analysis of dynamic functional connectivity that subjective happiness was negatively associated with the fraction of time spent on brain states characterized by weaker connectivity between the DMN, SN, and frontoparietal (FPN) networks, as well as stronger connectivity within the DMN and FPN. The SN and FPN, and their interaction with the DMN, are thought to be critical for coordinated processing of information from the external and internal environment (Barrett, 2017, Chen et al., 2013, Menon, 2011). Collectively, these findings suggest that efficient internetwork information transfer might be a characterization of greater happiness.

Turning to trait empathy, this construct has also been linked to intrinsic functional connectivity within and between various functional networks of the brain. For instance, trait empathy (measured by the mean of all items from the Interpersonal Reactivity Index; Davis, 1980) was positively associated with functional connectivity within the DMN, involving the medial prefrontal cortex (Kim et al., 2017). A similar pattern of functional connectivity results was identified in a more recent study (Esménio et al., 2019) in which the authors also found that trait empathy was associated with changes in effective connectivity within this network, characterized by negative associations in general but also positive associations with some connections (e.g., from the posterior cingulate cortex to bilateral inferior parietal lobule, from the right inferior parietal lobule to the medial prefrontal cortex).

Importantly, trait empathy is a multi-dimensional construct (Davis, 1980), and naturally, different facets of empathy seem to be associated with intrinsic functional connectivity of distinct networks/regions. In particular, empathic concern (the tendency to have feelings of warmth and compassion for others) and perspective taking (the ability to adopt the perspective of other people and to see things from their point of view) were associated with dissociable functional connectivity between regions including the medial prefrontal cortex, insula, and amygdala (Cox et al., 2012). Empathic concern was also positively correlated with intrinsic functional connectivity within the somatomotor network and between "bottom-up resonance" (including somatomotor network nodes, amygdala, and insula) and "top-down control" networks (including nodes of the FPN, SN, and DMN) (Christov-Moore et al., 2020). Personal distress (the tendency to have feelings of anxiety and discomfort in response to observing others' negative emotional experiences) was positively associated with functional connectivity between the dorsomedial prefrontal cortex and unimodal sensory regions, whereas it was negatively associated with functional connectivity between the dorsomedial prefrontal cortex and regions part of the FPN (Luo et al., 2018). In addition, an analysis of dynamic functional connectivity revealed that personal distress was positively associated with the fraction of time spent on brain states characterized by greater functional connectivity between the anterior insula (a core node of the SN) and other regions part of the same broader network including the anterior midcingulate cortex (Pasquini et al., 2020b). This is consistent with the role of the SN in processing of ascending viscerosensory signals (Barrett, 2017, Craig, 2009, Kleckner et al., 2017, Seeley et al., 2007), which is closely associated with aspects of empathy (Critchley and Harrison, 2013). Reduced structural integrity of the SN nodes is linked to lower empathy (Pasquini et al., 2020a, Rankin et al., 2006).

Collectively, these findings reviewed here suggest that both subjective happiness and trait empathy are associated with modulation of intrinsic functional connectivity within and between multiple functional networks including the DMN, SN, FPN, along with unimodal exteroceptive networks. However, it remains unclear which functional connectivity patterns support the relationship between the two constructs. Clarification of this issue requires measuring and relating subjective happiness and trait empathy within the same sample, then examining whether indices of intrinsic functional connectivity significantly mediate the observed relationship. Indeed, prior work on subjective happiness demonstrated that the relationship between basic personality traits (e.g., extraversion and neuroticism) and happiness was mediated by intrinsic functional connectivity (Kong et al., 2015). It is therefore possible that the brain's intrinsic connectivity patterns also subserve the link between empathy and happiness.

In the current study, we tested a sample of healthy young females to examine how subjective happiness and different facets of trait empathy are related to one another, and which indices of intrinsic functional connectivity, if any, would mediate the relationship between the two. We sought to identify and characterize differences in intrinsic brain connectivity as a function of subjective happiness and trait empathy using functional connectivity multi-voxel pattern analysis (MVPA) (Nieto-Castanon, 2020), an unbiased, data-driven approach to examine whole-brain intrinsic functional connectivity derived from functional magnetic resonance imaging (fMRI) data collected at rest. The efficacy of this method has been established in prior studies examining healthy and clinical populations (e.g., Arnold Anteraper et al., 2020, Arnold Anteraper et al., 2019, Beaty et al., 2015, Guell et al., 2020). This technique, along with *post hoc* seed-based correlation analysis, allowed us to reveal the most important features from the high-dimensional, whole-brain connectivity structure without *a priori* hypotheses about the topography and direction of functional connectivity differences. We then compared the topography of our results to that of established canonical functional networks (Yeo et al., 2011). This allowed us to characterize the pattern of significant functional connectivity differences in terms of a commonly used parcellation scheme to describe the functional organization of the brain.

2. Materials and methods

2.1. Participants

Seventy undergraduate and graduate students (M_{age} = 21.67, SD_{age} = 1.79; all females) were recruited from the Kyoto University

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[1] In the current study, we use this term to refer to a broader functional network that has been variably called the "ventral attention network" (Corbetta et al., 2008) and the "cingulo-opercular" network (Dosenbach et al., 2008, Power et al., 2011). It is important to note that the nodal composition of these networks and that of the "salience network" (Seeley et al., 2007, Uddin, 2015) are not exactly identical (Uddin et al., 2019). However, we elected to use the term "salience network" to keep a consistency with our prior work on intrinsic functional connectivity (Zhang et al., 2019) as well as the broader literature on the neural mechanisms of empathy (e.g., Pasquini et al., 2020a, Pasquini et al., 2020b).

community and were paid for their participation in this study. We exclusively recruited female participants in order to minimize the effect of sex-related differences on trait empathy and the associated neural mechanisms (Christov-Moore et al., 2014, Davis, 1980). All participants were healthy, right-handed, native Japanese speakers, with no history of psychiatric or neurological conditions. Data from two participants were excluded from the analyses due to extreme values on behavioral measures (based on a criterion of 3 standard deviations), leaving 68 participants for behavioral and fMRI data analyses. All participants provided written informed consent under a protocol approved by the Institutional Review Board of the Graduate School of Human and Environmental Studies, Kyoto University (27-H-2, 29-H-14).

2.2. *Measures*

2.2.1. *Subjective happiness*

Subjective happiness was assessed using the Japanese version of the Subjective Happiness Scale (Lyubomirsky and Lepper, 1999, Shimai et al., 2004), in which participants were asked to indicate the extent of agreement with each of the four statements on a 7-point scale. Example items of this scale include “In general, I consider myself:” (1 = *not a very happy person*, 7 = *a very happy person*) and “Some people are generally very happy. They enjoy life regardless of what is going on, getting the most out of everything. To what extent does this characterization describe you?” (1 = *not at all*, 7 = *a great deal*). Each participant’s overall subjective happiness was determined by the mean of the four individual ratings, after reverse-coding one of them. Higher scores indicated greater levels of subjective happiness. The reliability and validity of this scale has been previously verified in a sample of Japanese participants (Shimai et al., 2004). The Cronbach’s alpha in the present study was 0.74.

2.2.2. *Empathy*

Different aspects of trait empathy were assessed using the Japanese version of the Interpersonal Reactivity Index (IRI, Davis, 1980, Sakurai, 1988), consisting of four 7-item subscales: Empathic Concern, Personal Distress, Perspective Taking, and Fantasy. Empathic Concern contains items assessing one’s tendency to experience warmth, compassion, and concern for others undergoing negative experiences; Personal Distress contains items assessing one’s tendency to experience feelings of discomfort and anxiety when witnessing negative experiences of others; Perspective Taking contains items assessing one’s tendency or ability to adopt the perspective of other people and to see things from their point of view; Fantasy contains items assessing one’s tendency to identify strongly with fictitious characters in books, movies, or plays. Empathic Concern and Personal Distress together measure affective aspects of empathy, whereas Perspective Taking and Fantasy together target cognitive aspects. Participants were asked to indicate the extent of agreement with each of the 28 statements on a 5-point scale using letter grades (A = *describes me very well*, E = *does not describe me very well*). Participants’ raw responses were subsequently converted to numerical values ranging from 0 to 4 (i.e., A = 4, B = 3, ..., E = 0), after which some individual item scores were reverse-coded. All seven individual scores were then summed within each subscale (min. = 0, max. = 28); higher scores indicated greater empathic tendencies in a given domain. The Cronbach’s alpha values in the present sample were as follows: 0.86 (total), 0.65 (Empathic Concern), 0.84 (Personal Distress), 0.81 (Perspective Taking), and 0.77 (Fantasy). Empathy was also assessed in this sample using the Japanese version of the Empathy Quotient (Wakabayashi et al., 2006), although this measure will not be discussed further in the present report. We focused on the IRI as an index of trait empathy in the present study given that all of the previous studies examining the relationship between intrinsic functional connectivity and trait empathy referenced herein have used this measure or its variants (Christov-Moore et al., 2020, Cox et al., 2012, Esménio et al., 2019, Kim et al., 2017, Luo et al., 2018, Pasquini et al., 2020b).

2.3. *Behavioral data analysis*

We first conducted zero-order correlation analyses among subjective happiness and the four IRI subscales to examine how the former is associated with different facets of empathy. We then performed a multiple linear regression analysis using the four IRI subscales as the predictor variables and subjective happiness as the outcome variable. Collinearity among the predictor variables was assessed by the variance inflation factors (VIF). Statistical significance of each covariate in these analyses was assessed at $\alpha = .05$. Zero-order correlations and multiple regression results revealed that personal distress was consistently negatively associated with subjective happiness (see 3.1. Behavioral data analysis below). We therefore focused our brain-behavior analyses on these two measures to examine their associations with intrinsic functional connectivity.

2.4. *MRI data acquisition*

All MRI data were acquired on a 3.0-T Siemens MAGNETOM Verio scanner using a 32-channel head coil located in the Kokoro Research Center, Kyoto University. Following the sagittal localizer, a series of functional images were acquired axially using an echoplanar sequence (repetition time [TR] = 2000 ms, echo time [TE] = 40 ms, field of view [FOV] = 224 × 224 mm^2, matrix size = 64 × 64, number of slices = 39, slice thickness/gap = 3.5/0 mm, voxel size = 3.5 mm isotropic, flip angle = 75°, 154 volumes). During the functional scan, participants were instructed to relax and fixate on a cross presented at the center of the screen. For all participants, high-resolution 3D MPRAGE structural images were also collected and used as anatomical references (TR = 2250 ms, TE = 3.51 ms, FOV = 256 × 256 mm^2, matrix size = 240 × 240, number of slices = 208, slice thickness/gap = 1.0/0 mm, voxel size = 1.0 mm isotropic).

2.5. *MRI data preprocessing*

Preprocessing of fMRI data was performed in SPM12 (v7487; Wellcome Department of Cognitive Neurology, London, UK). The first four functional images were discarded to allow scanner equilibrium effects. Functional images were then spatially realigned and resliced relative to the first volume to correct for between-scan motion (using a six-parameter rigid body transformation) and were also slice-time corrected relative to the first slice. Finally, these images were resampled to 2 mm isotropic voxels during direct normalization to the MNI152 space, after which they were spatially smoothed using a 6 mm Gaussian kernel, full-width at half-maximum. To address the spurious correlations induced by head motion, outlier scans were identified using the Artifact Detection Tools (ART, www.nitrc.org/projects/artifact_detect/). Specifically, a scan was defined as an outlier/artifact scan if (1) the global signal intensity was > 3 *SD* above the mean signal or (2) composite head movement exceeded 0.5 mm from the previous scan. The composite head movement was computed by first converting six rotation/translation head motion parameters into another set of six parameters characterizing the trajectories of six points located on the center of each of the faces of a bounding box around the brain. The maximum scan-to-scan movement of any of these points was then computed as the single composite movement measure (Chai et al., 2016). The mean of scan-to-scan motion across participants was 0.10 mm (*SD* = 0.05). Each outlier scan was represented by a single regressor in the general linear model for each participant, with a 1 for each outlier scan and 0’s elsewhere.

In addition, physiological and other spurious sources of noise were estimated and regressed out using the anatomical CompCor method (Behzadi et al., 2007), as implemented in the CONN toolbox (Whitfield-Gabrieli and Nieto-Castanon, 2012). Global signal regression was not performed because of its potential impact on anti-correlations, which would render the results more difficult to interpret (Murphy and Fox, 2017). The normalized anatomical image for each participant was segmented into gray matter (GM), white matter (WM), and cerebrospinal fluid (CSF) masks in SPM12. In order to minimize partial voluming with GM, WM and CSF masks were eroded by one voxel, resulting in substantially smaller masks than the original segmentations (Chai et al., 2012). The eroded WM and CSF masks were then used as noise ROIs. Signals from the WM and CSF noise ROIs were extracted from the unsmoothed functional images to avoid additional risk of contaminating WM and CSF signals with GM signals. As part of the denoising procedure, the following nuisance variables were regressed out from the data: five principal components of the signals from WM and CSF noise ROIs, residual head motion parameters (three rotation and three translation parameters, along with their first-order temporal derivatives), each outlier/artifact scan, and linear trends. Finally, a temporal band-pass filter of 0.008-0.09 Hz was applied to the time series.

2.6. *Functional connectivity multi-voxel pattern analysis (MVPA)*

We identified brain regions whose functional connectivity was associated with subjective happiness and personal distress using a data-driven, whole-brain multi-voxel pattern analysis (MVPA) as implemented in the CONN toolbox. Features of interest were extracted at the first level using principal component analysis (PCA). In the first step, for each participant and for each voxel, 64 subject-specific PCA components were identified to characterize its entire pattern of correlations with all the other voxels in the brain. This step generated a lower-dimensional representation of whole-brain correlation structure similar to other established data-driven approaches (e.g., Calhoun et al., 2011). In the second step, jointly across all participants but separately for each voxel, the three strongest components were retained from a PC decomposition of the between-participants variability in voxel-to-voxel connectivity maps. This resulted in three values per participant/voxel that represented the entire connectivity pattern between a given voxel and the rest of the brain. We analyzed simultaneously these three component maps by an *F*-test in a single group-level analysis separately for subjective happiness and personal distress to identify voxels whose functional connectivity patterns varied as a function of the behavioral measures (for a detailed description of the methodology, see Arnold Anteraper et al., 2019, Nieto-Castanon, 2020). All MVPA results were thresholded using a voxel-wise intensity threshold of $p < .001$ with cluster-level correction for false discovery rate (FDR) at $p < .05$.

2.7. Post hoc *seed-based connectivity analysis*

Upon identification of the significant MVPA clusters, we conducted *post hoc* seed-based connectivity analysis to characterize functional connectivity differences as a function of subjective happiness and personal distress. For each participant, we calculated Pearson's correlation coefficients between the time course of the significant MVPA clusters and that of all other voxels in the brain, which were *z*-transformed prior to group-level analyses. Thresholding of results from this *post hoc* analysis is arbitrary given that it is formally not part of our confirmatory test; its purpose was rather to characterize the MVPA results in terms of the topography and direction of functional connectivity differences. Hence, for this analysis, we used a voxel-wise intensity threshold of $p < .05$ along with cluster-level correction for FDR at $p < .05$.

To facilitate the topographic characterization of functional connectivity differences, we compared all suprathreshold MVPA and seed-based correlation maps with the macroscale organization of intrinsic functional connectivity. Specifically, we calculated the extent of voxel-wise spatial overlap between these group-level statistical maps and large-scale functional networks as defined by a common parcellation scheme (Yeo et al., 2011). This procedure identified the relative proportion of significant voxels belonging to each of the seven canonical networks (i.e., visual, somatomotor, dorsal attention [DAN], SN, limbic, FPN, and DMN). Additionally, we used the finer-grained, 17-network solution of the same cortical parcellation scheme to clarify the contribution of different components within the DMN to our results (Andrews-Hanna et al., 2010, Uddin et al., 2009). Specifically, we calculated the degree of spatial overlap between the group-level statistical maps and voxel-wise binary maps representing the core, dorsal medial, and medial temporal subsystems of the DMN (Andrews-Hanna et al., 2014) (Supplementary Fig. S1).

2.8. *Mediation analysis*

Finally, to examine the role of intrinsic functional connectivity in the relationship between personal distress and subjective happiness, we performed a mediation analysis using PROCESS macro version 3.5 (Hayes, 2017) in IBM SPSS. Informed by the results of our behavioral multiple regression analysis, we modeled personal distress as the predictor variable (X) and subjective happiness as the outcome variable (Y). This approach is also consistent with prior behavioral (e.g., Choi et al., 2016) and neuroimaging (e.g., Kong et al., 2015) studies examining the relationship between personality traits and aspects of well-being, in which these measures were modeled as the predictor and outcome variables, respectively, in regression analyses. We defined the mediator variables based on the statistical maps resulting from the functional connectivity MVPA and *post hoc* seed-based connectivity analysis described above (see also 3.2. Functional connectivity correlates of subjective happiness and personal distress). Similar approaches to mediation analyses based on voxel-wise overlap in statistical maps have been described previously (Torrisi et al., 2013, Wager et al., 2009). In particular, our functional connectivity MVPA identified the left dorsolateral prefrontal cortex (dlPFC) and the right medial prefrontal cortex (mPFC), whose whole-brain functional connectivity patterns were associated with subjective happiness and personal distress, respectively. Visual inspection of results from the *post hoc* seed-based connectivity analysis revealed similar networks of regions, whose functional connectivity with the dlPFC/mPFC was associated with subjective happiness/personal distress, albeit in the opposite direction. This pattern is also consistent with the inverse relationship observed between the two measures (see 3.1. Behavioral data analysis). Therefore, to identify brain regions whose functional connectivity with the PFC seeds were significantly associated with both subjective happiness (via the left dlPFC) and personal distress (via the right mPFC), we first calculated the conjunction of two thresholded brain-behavior correlation maps with alternate signs. Namely, conjunction #1 = positive correlation clusters from the dlPFC-seeded map and negative correlation clusters from the mPFC-seeded map, and conjunction #2 = positive correlation clusters from the mPFC-seeded map and negative correlation clusters from the dlPFC-seeded map (Supplementary Fig. S2). It is possible to derive conjunction maps based on the same sign (i.e., positive correlation clusters from both the dlPFC-seeded and mPFC-seeded maps). However, these alternative conjunction maps yielded few overlapping voxels (38 for the positive-positive conjunction, 19 for the negative-negative conjunction) and hence were not analyzed further. We then computed one-sided mean functional connectivity of each seed within these conjunction masks, resulting in four connectivity values (Z-transformed Pearson's r values) per participant (i.e., dlPFC-conjunction #1, dlPFC-conjunction #2, mPFC-conjunction #1, mPFC-conjunction #2), which we considered in our mediation models.

We tested a serial multiple mediator model with two mediators from each seed, in which one mediator (M_1) is hypothesized to exert causal influence on another (M_2). In this model, path a_1 was calculated from regressing M_1 on X, path b_1 was calculated from regressing Y on M_1 while controlling for X and M_2, path a_2 was calculated from regressing M_2 on X while controlling for M_1, path b_2 was calculated from regressing Y on M_2 while controlling for X and M_1, and path d_{21} was calculated from regressing M_2 on M_1 while controlling for X (Hayes, 2017). Three indirect effects were estimated: The specific indirect effect of X on Y through only M_1 was $a_1 b_1$, the specific indirect effect through only M_2 was $a_2 b_2$, and the specific indirect effect through both M_1 and M_2 serially was

Table 1
Means, standard deviations, and zero-order correlations.

Variable	*M*	*SD*	1	2	3	4
1. Subjective happiness	5.22	0.77				
2. Empathic concern	17.75	4.38	.081			
3. Perspective taking	18.32	5.35	.154	.392**		
4. Personal distress	14.69	6.19	-.266*	.369**	-.004	
5. Fantasy	18.59	5.27	-.188	.460**	.353**	.301*

Note: N = 68. *M* = mean; *SD* = standard deviations; IRI = interpersonal reactivity index.

* $p < .05$

** $p < .01$.

$a_1 d_{21} b_1$. A schematic diagram illustrating this model structure is shown in Supplementary Fig. S3. A bias-corrected bootstrap 95% confidence interval was generated for each indirect effect based on 5,000 bootstrap samples, along with a completely standardized effect as the effect size measure (Hayes, 2017, Preacher and Kelley, 2011). An empirical 95% confidence interval not including zero indicated a significant indirect effect at $p < .05$.

2.9. Data/code availability statement

The behavioral data and unthresholded statistical maps analyzed in this study are available through the Open Science Framework (https://osf.io/ps6c8/). Due to a lack of consent of the participants, raw structural and functional MRI data cannot be shared publicly. Sharing of these data would be considered upon reasonable request and only under circumstances where data privacy can be assured. SPM is freely available software (https://www.fil.ion.ucl.ac.uk/spm/software/), distributed under the terms of the GNU General Public License as published by the Free Software Foundation. CONN is freely available (https://www.nitrc.org/projects/conn/) under the MIT license for non-commercial use. PROCESS macro version 3.5 is freely available software (http://processmacro.org/index.html).

3. Results

3.1. Behavioral data analysis

Table 1 summarizes the means and standard deviations of behavioral measures, along with zero-order correlations among them. Scatterplots illustrating the relationship between subjective happiness and the four IRI subscales are shown in Supplementary Fig. S4. Results of the multiple linear regression analysis indicated that the model explained 17% of the variance in subjective happiness: $R^2 = .168$, $F(4,63) = 3.18$, $p < .019$. Examination of each predictor variable revealed that personal distress (β = -.275, t = -2.14, $p < .036$) and fantasy (β = -.273, t = -2.02, $p < .048$) were negatively associated with subjective happiness. Neither empathic concern ($\beta = .247$, $t = 1.74$, $p < .087$) nor perspective taking ($\beta = .153$, $t = 1.17$, $p < .247$) was associated with subjective happiness at $p < .05$. All values of the VIF were less than 1.53, suggesting that the present regression model was not significantly influenced by collinearity among the predictor variables (Hair et al., 1998).

3.2. Functional connectivity correlates of subjective happiness and personal distress

Whole-brain functional connectivity MVPA revealed several clusters showing significant associations with subjective happiness. The largest cluster was located in the left dlPFC (peak MNI coordinates: x = -38, $y = 26$, $z = 44$, BA 8/9, 194 voxels; Fig. 1A), followed by smaller clusters in the ventrolateral PFC (BA 47), precuneus, and angular gyrus (Supplementary Fig. S5). The extent of spatial overlap between the dlPFC and canonical functional networks was as follows: 55% DMN (dorsomedial subsystem), 35% FPN, 0.5% SN, and 9.5% unknown (Yeo et al., 2011). Whole-brain (cortical) functional connectivity based on the left dlPFC seed is shown in Supplementary Fig. S6. To characterize functional connectivity differences as a function of subjective happiness, we performed a *post hoc* seed-based correlation analysis using as a seed the left dlPFC cluster identified by MVPA above as showing the maximal effect size. This analysis revealed widespread regions whose functional connectivity with the left dlPFC was positively or negatively associated with subjective happiness. Specifically, cortical regions whose functional connectivity with the left dlPFC was positively associated with subjective happiness included the bilateral middle/inferior frontal gyri, insula, inferior parietal lobule, pre-supplementary motor area, and precuneus. In contrast, regions whose functional connectivity with the left dlPFC was negatively associated with subjective happiness included the midline cortical areas (e.g., mPFC, pregenual and subgenual cingulate, posterior cingulate, retrosplenial cortex), superior frontal gyrus, angular gyrus, lateral temporal gyri/anterior temporal lobe, and lateral occipital cortex (Fig. 1B). These cortical areas predominantly belonged with the FPN, DAN, and SN (showing positive correlation) as well as the DMN (core and dorsal medial subsystems), visual, and somatomotor networks (showing negative correlation) (Fig. 1C). Interestingly, we also identified a small fraction of the DMN voxels whose functional connectivity with the dlPFC seed was positively associated with subjective happiness. These voxels were localized almost exclusively to the left inferior frontal gyrus, part of the dorsal medial subsystem (Supplementary Fig. S7).

In addition, the whole-brain MVPA also revealed two clusters showing significant associations with personal distress. These clusters were identified in the right mPFC ($x = 12$, $y = 50$, $z = 8$, BA 10, 34 voxels; Fig. 2A) and right lateral orbitofrontal cortex (Supplementary Fig. S8). The mPFC cluster completely overlapped in space with the DMN (core subsystem) (Yeo et al., 2011). Whole-brain (cortical) functional connectivity based on the right mPFC seed is shown in Supplementary Fig. S9. We performed a *post hoc* seed-based correlation analysis focusing on the right mPFC to characterize the MVPA results. This analysis showed that cortical regions whose functional connectivity with the right mPFC seed was positively associated with personal distress included the bilateral cortical midline regions, primary motor cortex, primary and secondary visual areas, and parahippocampal gyrus. In contrast, regions whose functional connectivity with the right mPFC was negatively associated with personal distress included the right inferior frontal gyrus, insula, and temporo-parietal junction (Fig. 2B). These cortical regions primarily belonged with the visual network and DMN (largely core and medial temporal subsystems) (showing positive correlation) as well as the FPN and SN (showing negative correlation) (Fig. 2C and Supplementary Fig. S10).

3.3. Brain-behavior mediation analysis

Finally, we performed a mediation analysis to assess indirect effects of personal distress on subjective happiness through intrinsic functional connectivity. We focused on testing serial multiple mediator models to examine the role of intrinsic functional connectivity of the dlPFC and mPFC seeds identified from whole-brain MVPA in mediating the link between personal distress and subjective happiness. Results of this analysis revealed a significant net negative indirect effect of personal distress on subjective happiness through two mediators representing intrinsic functional connectivity: One between the dlPFC and the networks implicated in the representation of unimodal sensorimotor signals or their multimodal summary representations (i.e., the DMN, visual, and somatomotor networks) and another between the dlPFC and the networks implicated in the attentional modulation of these representations (i.e., the FPN, SN, and DAN) (Fig. 3). This mediation model did not yield a specific indirect effect of both M_1 and M_2 when the order of the two mediators was reversed ($a_1 d_{21} b_2$ = -0.01, 95% confidence interval [-0.08, 0.04]), when the order of X and Y was reversed ($a_1 d_{21} b_2$ = -0.0008, 95% confidence interval [-0.09, 0.09]), or when the order of X, M_1, M_2, and

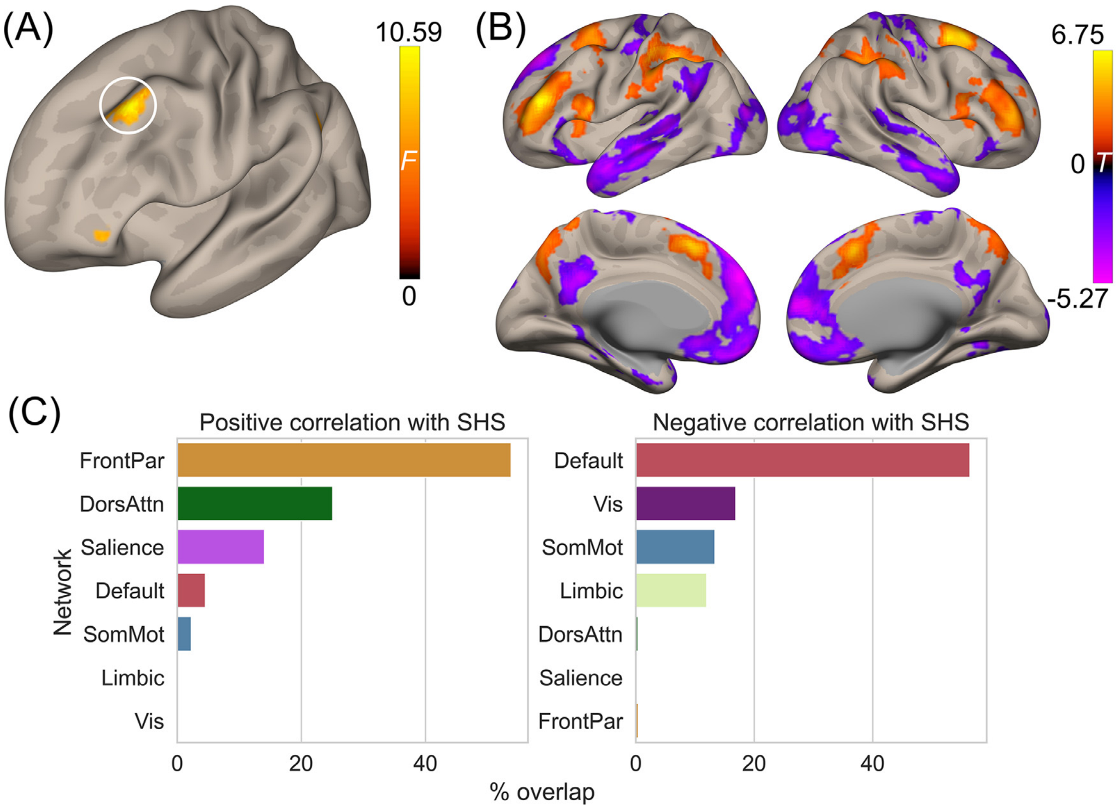

Fig. 1. Intrinsic functional connectivity correlates of subjective happiness. (A) The left dlPFC whose whole-brain functional connectivity patterns showed significant associations with subjective happiness. (B) Cortical regions whose functional connectivity with the dlPFC seed illustrated in (A) showed significant positive (warmer colors) or negative (colder colors) associations with subjective happiness. The *T*-contrast map was thresholded at a voxel-wise intensity threshold of $p < .001$ with cluster-level correction for false discovery rate (FDR) at $p < .05$ (two-sided). (C) The extent of spatial overlap between the correlation maps shown in (B) and seven canonical functional networks (Yeo et al., 2011). SHS = subjective happiness, FrontPar = frontoparietal network, DorsAttn = dorsal attention network, Salience = salience network, Default = default mode network, SomMot = somatomotor network, Limbic = limbic network, Vis = visual network.

Y was completely reversed ($a_1 d_{21} b_2$ = -0.09, 95% confidence interval [-0.23, 0.04]). These results are consistent with the idea that lower personal distress leads to greater subjective happiness through decreased intrinsic functional connectivity between the dlPFC and modulation-related networks, resulting in increased connectivity between the dlPFC and representation-related networks. The corresponding serial mediator model for the mPFC seed did not reveal significant indirect effects regardless of how the mediators were modeled.

4. Discussion

Three major findings emerged from the present study. First, when multiple aspects of trait empathy were considered, personal distress was the only aspect that was consistently and negatively associated with subjective happiness. Second, subjective happiness was associated with differences in intrinsic functional connectivity between the dlPFC and regions primarily part of the FPN, DAN, and SN (positive correlation) and the DMN, visual, and somatomotor networks (negative correlation). Personal distress showed the opposite pattern of brain-behavior correlations compared with subjective happiness, as the former was associated with differences in intrinsic functional connectivity between the mPFC and the visual network and DMN (positive correlation) and the FPN and SN (negative correlation). Finally, intrinsic functional connectivity between the dlPFC and large-scale functional networks significantly mediated the negative impact of personal distress on subjective happiness, through variation in functional connectivity with networks implicated in the unimodal or multimodal representation of sensorimotor information (*representation* networks) and those important for modulating such representations (*modulation* networks). These findings are discussed in turn below.

4.1. Relationship between personal distress and subjective happiness

Our finding that personal distress was negatively associated with subjective happiness is consistent with prior work identifying similar associations between this component of trait empathy and aspects of psychological well-being (e.g., Choi et al., 2016). Personal distress is characterized by the tendency to have feelings of anxiety and discomfort in response to observing others' negative emotional experiences, and has been linked to neuroticism (Bartholow et al., 2005) and symptoms of depression (Thoma et al., 2011). Therefore, self-centered processing of others' negative experiences might be particularly detrimental to the maintenance of subjective happiness. Interestingly, empathic concern was not associated with subjective happiness, although some prior work demonstrated significant associations between empathic concern and aspects of well-being (Choi et al., 2016, Grühn et al., 2008, Wei et al., 2011). Future work should examine more diverse samples including both sexes and/or in different cultures to examine the possibility that the relationship between empathy and subjective happiness is modulated by these factors.

4.2. Functional connectivity correlates of subjective happiness and personal distress

Our MVPA results identified a cluster in the left dlPFC whose intrinsic functional connectivity was significantly associated with subjective happiness. Characterization of its topography informed by a common corti-

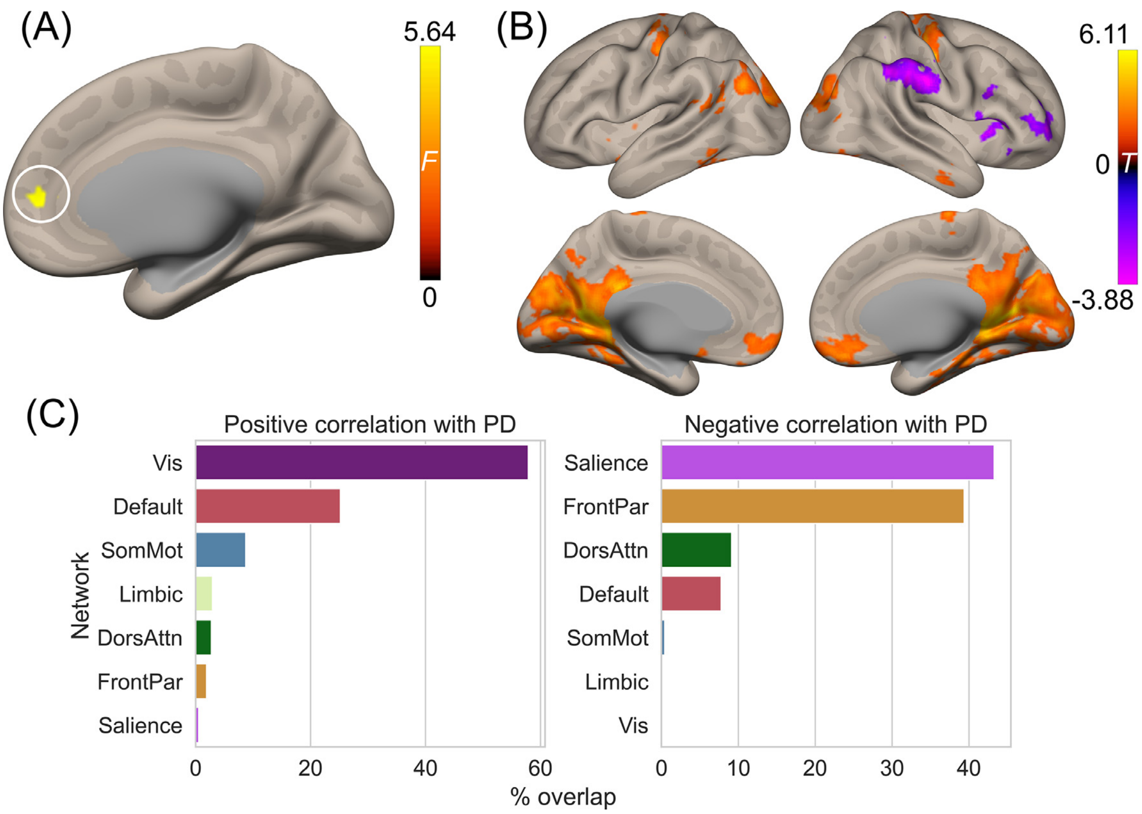

Fig. 2. Intrinsic functional connectivity correlates of personal distress. (A) The right mPFC whose whole-brain functional connectivity patterns showed significant associations with personal distress. (B) Cortical regions whose functional connectivity with the mPFC seed illustrated in (A) showed significant positive (warmer colors) or negative (colder colors) associations with subjective happiness. The *T*-contrast map was thresholded at a voxel-wise intensity threshold of $p < .001$ with cluster-level correction for false discovery rate (FDR) at $p < .05$ (two-sided). (C) The extent of spatial overlap between the correlation maps shown in (B) and seven canonical functional networks (Yeo et al., 2011). PD = personal distress, FrontPar = frontoparietal network, DorsAttn = dorsal attention network, Salience = salience network, Default = default mode network, SomMot = somatomotor network, Limbic = limbic network, Vis = visual network.

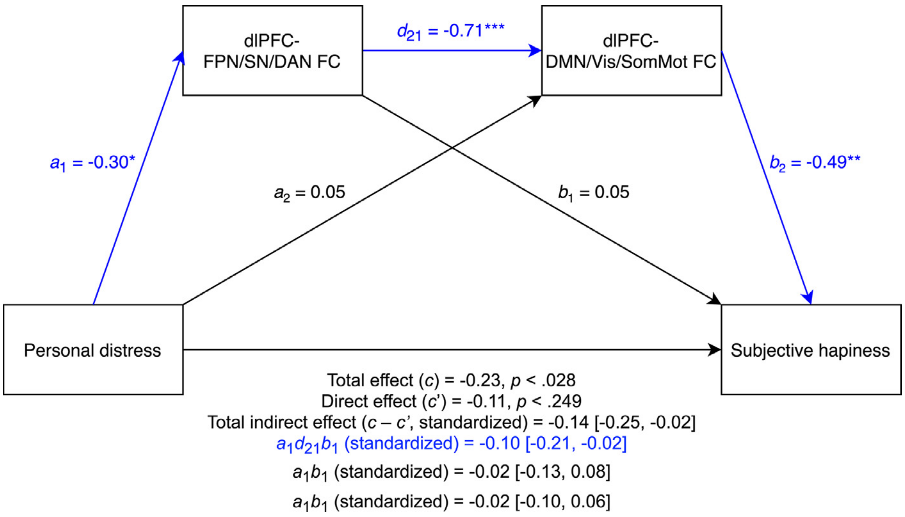

Fig. 3. Intrinsic functional connectivity between the dlPFC and large-scale functional networks mediates the relationship between personal distress and subjective happiness. Higher scores on personal distress lead to decreased functional connectivity between the dorsolateral prefrontal cortex (dlPFC) and cortical regions part of the frontoparietal (FPN), salience (SN), and dorsal attention (DAN) networks, which are implicated in the attentional modulation of mental content representations (unimodal sensorimotor signals or multimodal summary representations of these signals). This in turn results in greater functional connectivity between the dlPFC and regions part of the default mode (DMN), visual (Vis), and somatomotor (SomMot) networks involved in the representation of these signals, which ultimately results in reduced subjective happiness. $^*p < .05$, $^{**}p < .005$, $^{***}p < .001$. Significant effects are illustrated in blue font/arrows. FC = functional connectivity.

cal parcellation scheme revealed that this dlPFC cluster was functionally affiliated with the DMN and FPN. The dlPFC is typically considered part of the FPN (e.g., Dosenbach et al., 2008), but it is important to note that previous studies of cortical parcellations have consistently identified areas in the lateral PFC as also belonging to the DMN (Gordon et al., 2016, Gordon et al., 2017, Ji et al., 2019, Power et al., 2011, Yeo et al., 2011). The DMN and FPN are typically negatively correlated with each other (Fransson, 2005, Greicius et al., 2003, Uddin et al., 2009) and a greater degree of this anticorrelation predicts superior cognitive performance and fluid intelligence (Cole et al., 2012, Hampson et al., 2010, Keller et al., 2015). Therefore, it is possible that the dlPFC identified by our MVPA is one of the regions where the two networks functionally interface with one another. This interpretation is consistent with prior work examining the fractionation of the FPN. Specifically, a subsystem of the FPN that includes a node overlapping with/adjacent to the left dlPFC identified in the present study exhibited stronger (more positive) functional connectivity with the DMN than the other FPN subsystem at rest and across task conditions (Dixon et al., 2018). This suggests that part of the FPN is involved in executive aspects of internally-oriented processes subserved by the DMN. One possibility is that a subsystem of the FPN more strongly connected to the DMN improves the precision of the brain's internal model of the world based on statistical regularities (e.g., suppressing mental simulations whose priors are low; Barrett, 2017). This is in line with our finding that the left dlPFC cluster partially overlapped with the dorsal medial subsystem of the DMN. This particular DMN subsystem is implicated in the representation of semantic and conceptual knowledge (Andrews-Hanna et al., 2014), which is hypothesized to serve as simulations that guide processing of sensory inputs (Barrett, 2017).

A *post hoc* seed-based correlation analysis further revealed that subjective happiness is associated with intrinsic functional connectivity between the left dlPFC and widespread regions functionally affiliated with a variety of networks in the brain. Brain regions whose connectivity with the left dlPFC was positively associated with subjective happiness primarily belonged with the FPN, DAN, and SN, which are broadly implicated in the modulation of sensory and motor representations (e.g., attention regulation, goal maintenance, strategy selection, or performance monitoring) (Corbetta and Shulman, 2002, Dosenbach et al., 2008, Menon and Uddin, 2010, Miller and Cohen, 2001). In contrast, regions whose functional connectivity with the left dlPFC was negatively associated with subjective happiness largely belonged with the DMN and the visual/somatomotor networks, which are involved in representing low-dimensional, multi-modal summaries of brain states vs. more precise sensorimotor signals, respectively (Fernandino et al., 2015). We and others have previously demonstrated that this "modulation vs. representation" distinction is one of the principal gradients along which intrinsic functional connectivity is organized in the human brain (Margulies et al., 2016, Zhang et al., 2019). Our findings therefore suggest that the left dlPFC's functional affiliation has important implications for the maintenance of subjective happiness, such that its increased affiliation with the modulation networks (largely the FPN) and decreased affiliation with the representation networks (largely the DMN) is associated with greater subjective happiness.

The FPN, DAN, and SN collectively constitute a domain-general cortical system that implements flexible cognitive control (Duncan, 2010, Fedorenko et al., 2013), which is capable of modulating other networks by virtue of their major nodes exhibiting a high degree of global functional connectivity in the brain (Cole et al., 2010, Power et al., 2011). Not surprisingly, disruption of functional connectivity within these networks has been associated with a variety of psychiatric and neurological disorders (Cole et al., 2014, Menon, 2011). It is therefore possible that greater intrinsic functional connectivity between the dlPFC and modulation networks reflects the ability to exert adaptive cognitive control, which might be associated with higher subjective happiness. In contrast, stronger functional connectivity within the DMN has been linked to symptoms of psychopathology, including major depression (Kaiser et al., 2015, Menon, 2011, Whitfield-Gabrieli and Ford, 2012). Notably, greater intrinsic functional connectivity within the DMN was associated with both decreased subjective happiness and increased ruminative tendencies in healthy young adults (Luo et al., 2015). Therefore, it is possible that greater intrinsic functional connectivity between the dlPFC and the rest of the DMN at least in part reflects greater engagement of self-referential thoughts among those who perceive themselves as relatively less happy.

Intriguingly, we identified a small set of voxels belonging with the DMN whose functional connectivity with the left dlPFC seed was positively associated with subjective happiness. A follow-up analysis using a finer-grained parcellation scheme revealed that these voxels were almost exclusively localized to the left inferior frontal gyrus part of the dorsal medial subsystem of the DMN (Andrews-Hanna et al., 2014). Unlike the other regions part of this DMN subsystem (e.g., anterior temporal lobe, dorsal mPFC), the left inferior frontal gyrus has not been consistently identified as part of the DMN. For instance, at higher resolution, this region was labeled as a node of the language network (Ji et al., 2019). There also appears to be considerable variability in the network to which this and the surrounding cortical regions are assigned (Gordon et al., 2017). This finding therefore warrants replication in future studies based on more diverse samples and using different analytical approaches, which would help clarify its functional significance.

Overall, our results are consistent with other previous studies directly identifying the relationship between indices of subjective happiness and intrinsic functional connectivity involving the DMN, FPN, and SN (Luo et al., 2015, Luo et al., 2017, Sato et al., 2019, Shi et al., 2018). It is important to note, however, that these studies have largely focused on analyses using *a priori* seed regions or independent components representing each network in low-dimensional space, thus limiting the ability to reveal subtle effects that may involve interactions between (overlapping) subregions of these networks. Our data-driven analytical approach took advantage of both the sensitivity of voxel-wise analyses and whole-brain correlation structure; this allowed us to identify both relatively local and global features of the relationship between subjective happiness and intrinsic functional connectivity.

Turning to personal distress, MVPA also revealed a cluster in the right mPFC whose functional connectivity patterns were significantly associated with this aspect of trait empathy. This right mPFC cluster was located entirely within the DMN, and its intrinsic functional connectivity with the representation networks and modulation networks were positively and negatively associated with personal distress, respectively. A few studies published to date identified the relationship between personal distress and intrinsic functional connectivity (Luo et al., 2018, Pasquini et al., 2020b). One study found that personal distress was positively correlated with functional connectivity between the mPFC and visual/somatomotor areas, whereas it was negatively correlated with functional connectivity between the mPFC and the FPN, including the dlPFC and the mid cingulate cortex (Luo et al., 2018). Our findings are overall consistent with these results, providing support to the relationship between the mPFC (a DMN node) and the representation/modulation networks as an intrinsic functional connectivity signature of personal distress.

Specifically, greater functional connectivity between the mPFC and the posterior medial parietal cortex (intra-DMN connectivity) linked to higher levels of personal distress is consistent with evidence that DMN hyperconnectivity was associated with symptoms of depression (Kaiser et al., 2015, Thoma et al., 2011). The DMN and unimodal exteroceptive networks have been characterized as exhibiting most dissimilar connectivity patterns in the cerebral cortex, likely owing to their role in internal vs. external modes of processing, respectively (Margulies et al., 2016, Zhang et al., 2019). It is therefore possible that greater functional connectivity between the DMN and unimodal exteroceptive networks reflects reduced functional segregation, as has been observed in autism spectrum disorder characterized by deficits in social cognition (Hong et al., 2019). In addition to the FPN, the SN is also typically anticorrelated with the DMN at rest (Buckner et al., 2013). Thus, one possibility is that increased functional connectivity (e.g., reduced anticorrelation) between the DMN and the FPN/SN linked to higher levels of personal distress represents a functional imbalance between internally-oriented vs. externally-oriented attentional processing (Andrews-Hanna et al., 2014). Higher levels of personal distress were also associated with more time spent on brain states characterized by greater functional connectivity within the broader SN (Pasquini et al., 2020b), supporting the idea that hyperconnectivity of this network is linked to affective disturbances (Menon, 2011). Interestingly, brain regions whose functional connectivity with the prefrontal seeds were significantly associated with subjective happiness or personal distress were partially overlapped. This raises the intriguing possibility that prefrontal functional connectivity with these overlapping regions might subserve the link between personal distress and subjective happiness, which we tested through a mediation analysis.

4.3. *Intrinsic functional connectivity of the dlPFC mediates the relationship between personal distress and subjective happiness*

Our mediation analysis showed that intrinsic functional connectivity between the left dlPFC and the modulation networks and between the left dlPFC and the representation networks fully mediate the relationship between personal distress and subjective happiness. Higher levels of personal distress, due to a blurred psychological distinction between the self and others (Decety and Lamm, 2006), might lead to dedifferentiated neural representations of self- and other-relevant experiences. These representations are likely subserved by the DMN, particularly the mPFC and the posterior cingulate cortex, where not only self-relevance is tracked, but also the closeness in social space (e.g., self, family/friends, celebrities) might be encoded (Courtney and Meyer, 2020, Feng et al., 2018, Katsumi and Dolcos, 2018, Yamawaki et al., 2017). Higher degrees of personal distress are closely associated with symptoms of depression (Schreiter et al., 2013, Thoma et al., 2011) and might therefore lead to aberrant (e.g., decreased) connectivity within the FPN and the attention networks (Kaiser et al., 2015, Menon, 2011). It is possible that path a_1 of our model represents this link between personal distress and intrinsic functional connectivity between the left dlPFC and the modulation networks.

The dlPFC, as a possible site of convergence between the FPN and the DMN (or between the modulation and the representation networks more generally), may change its functional connectivity profile as a result of a reduction in its affiliation with the modulation networks. Indeed, hypoconnectivity within/between the FPN and the attention networks coupled with hyperconnectivity within the DMN (and between the DMN and the FPN) are a characteristic of clinical and subclinical depression (Broyd et al., 2009, Greicius et al., 2007, Kaiser et al., 2015, Schultz et al., 2018, Whitfield-Gabrieli and Ford, 2012). It is therefore possible that path d_{21} of our model represents this shift in the left dlPFC's functional affiliation with intrinsic connectivity networks. In extreme cases, decreased anticorrelation between the FPN and the DMN may be associated with cognitive impairment (e.g., executive dysfunction), whereas greater intra-DMN connectivity could reflect engagement of maladaptive behavior such as excessive rumination (Hamilton et al., 2011). In the context of personal distress, these connectivity changes may be associated with increased cognitive load and affective burdens due to vicarious experiences of others' emotional distress, which could collectively lead to lower subjective happiness. Path b_2 of our model possibly represents this. Overall, the current mediation results suggest an important role of the dlPFC in coordinating the dynamics of whole-brain functional networks anchored in the FPN and the DMN. It is possible that optimal interactions of these networks occur as a result of distinct mental representations of the self and others, which might ultimately lead to increased happiness.

4.4. *Limitations*

The following three limitations of the present study should be acknowledged. First, our sample consisted only of college-aged Japanese females, and therefore it remains unclear to what extent the current results are generalizable to samples with different demographic characteristics. There is evidence suggesting that subjective happiness is closely associated with social relations and group harmony in primarily collectivistic (e.g., Japanese) cultures, whereas it is associated more with personal achievement and self-esteem in primarily individualistic (e.g., North American) cultures (Hitokoto and Uchida, 2015, Uchida and Kitayama, 2009). These findings have important implications for possible cultural differences in the relationship between trait empathy and subjective happiness, and the mechanism that mediates this. Second, subjective happiness in this study was defined by a few items that index global characteristics of happiness (Lyubomirsky and Lepper, 1999, Shimai et al., 2004), which did not allow us to examine different aspects of happiness and well-being (e.g., Luo et al., 2017). Future work should capitalize on a comprehensive assessment of neuropsychological functioning and personality characteristics to reveal the neurobehavioral mechanisms of subjective happiness with increased specificity. Finally, it is important to acknowledge that, although we used a well-established cortical parcellation scheme (Yeo et al., 2011) in our interpretation of the results, variability also exists across different parcellation schemes in the number of networks as well as their spatial topography (Uddin et al., 2019). Future work should therefore make sure that consistent findings emerge regardless of which parcellations are used for *post hoc* characterization of the results. Alternatively, voxel- or vertex-wise analyses of intrinsic functional connectivity in a low-dimensional gradient space may prove fruitful in describing how subjective happiness or empathy relate to the macroscale functional organization of the brain (Margulies et al., 2016).

5. Conclusions

In sum, our findings identify an important contribution of intrinsic functional connectivity to the relationship between personal distress and subjective happiness, linked to the interaction of large-scale networks involved in the unimodal or multimodal representation of sensorimotor signals and those involved in the attentional modulation of such representations. These findings advance our understanding of the neural substrates of subjective happiness and trait empathy and provide insights into possible ways to enhance well-being through interventions aimed at modulating the intrinsic functional organization of the brain.

Declaration of Competing Interest

None.

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Data/code availability statement

The behavioral data and unthresholded statistical maps analyzed in this study are available through the Open Science Framework (https://osf.io/ps6c8/). Due to a lack of consent of the participants, raw structural and functional MRI data cannot be shared publicly. Sharing of these data would be considered upon reasonable request and only under circumstances where data privacy can be assured. SPM is freely available software (https://www.fil.ion.ucl.ac.uk/spm/software/), distributed under the terms of the GNU General Public License as published by the Free Software Foundation. CONN is freely available (https://www.nitrc.org/projects/conn/) under the MIT license for non-commercial use. PROCESS macro version 3.5 is freely available software (http://processmacro.org/index.html).

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2020.117650.

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