Interoceptive Awareness and Affective Empathy Share Intrinsic Spatial Connectivity and Temporal Variability

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ABSTRACT

Awareness of internal bodily sensations (interoception, IA) and its connection to complex socio-emotional phenomena like empathy have been postulated, yet its neural basis remains poorly understood. The goal of the present fMRI study employs a data-driven approach to investigate whether Cognitive or Affective empathy and IA share spatial resting state connectivity (rsFC) and/or temporal variability. Healthy participants viewed an abstract movie demonstrated to evoke strong connectivity in intrinsic brain networks (*InScapes*), and resultant resting-state fMRI spatial connectivity and temporal variability data was correlated with their self-reported empathy and interoception scores (IRI and MAIA, respectively). We demonstrate a complex bidirectional behavioral and neurological relationship between empathy and IA, depending on the type of empathy interrogated: Affective empathy and IA are distributed across similar spatial and temporal neural systems, while Cognitive empathy and IA are only related temporally. Specifically, increased spatial rsFC within the R IFO was associated with a decreased awareness of inner body sensations, but increased vicarious emotional experience. Furthermore, enhanced information integration between an interoceptive experience network was related to both increased sensitivity of internal sensation, but in addition, to a dampening of discomfort arising from witnessing another's pain. Finally, improved processing between brain regions part of a mentalizing network related to not only a better sense of mind-body interconnectedness but also an improved ability to take someone's perspective. Our findings could have implications for understanding differences in empathic and interoceptive functioning without needing to probe participants with specialized tasks or questionnaires.

Keywords: Empathy, Interoceptive Awareness, fMRI, ICA, temporal variability

1. INTRODUCTION

Internal body signals relative to emotion processing has been a topic of long-standing interest (Gurney, 1884; Strack et al., 1988), with more recent evidence highlighting an intriguing bidirectional relationship between sensations that arise internally and emotional phenomena (Cameron, 2001; Craig, 2009; Damasio, 2005; Lane, 2008). A proposed biological basis that may clarify this interplay is interoception, namely – the afferent processing of internal bodily signals that arise from visceral organs (Cacioppo et al., 2000; Cameron, 2001; Craig, 2009; Johnson, 2001; Wiens, 2005). Indeed, neuroimaging findings corroborate a substantial overlap between the neural substrates of emotion and interoception (Adolfi et al., 2017; Critchley & Garfinkel, 2017), supporting the idea that central monitoring and representation of internal bodily signals plays a fundamental role in emotion. However, the relationship between the emotions of *another* individual and one's own body remains relatively unexplored.

Consider the ubiquitous scenario of listening to a close friend share a difficult moment. In order to accurately grasp the story from their perspective, you must map their internal sensations onto your emotional landscape, thereby creating a bridge towards proper understanding. This process hinges on two crucial socioemotional constructs: interoceptive awareness (IA) and empathy. IA represents the ability to accurately and consciously perceive changes in your internal bodily signals (Khalsa et al., 2018), while empathy refers to both vicariously experiencing and understanding the mental state of your friend (Davis, 1980). Thus, empathy can be further fractioned into two interrelated facets: Affective and Cognitive empathy. Affective empathy is conceptualized as the automatic process of vicariously experiencing the emotional state of another (Baron-Cohen & Wheelwright, 2004; Davis, 1980), while Cognitive empathy describes the individual's ability to accurately imagine another person's perspective (Davis, 1980; Decety & Jackson, 2004; Lawrence et al., 2006). Hence, in the context of the anecdote above, genuine understanding arises when the listener is aware of their own internal bodily sensations while taking into account the speaker's feelings and mental state. However, despite their importance in harmonious socioemotional exchange, it is currently unknown which specific facets of empathy dovetail with IA.

Neuroimaging research demonstrates that the neural substrates of empathy consistently overlap with the cortical regions involved in self-experience (Iacoboni, 2005; Jackson et al., 2005; Keysers et al., 2004; Wicker et al., 2003). For instance, during the experience of various aversive taste stimuli, activation of the anterior insula (AI) and inferior frontal operculum (IFO) were

observed in both the observer and experiencer (Jabbi et al., 2007). Similarly, observing others' pain has been found to robustly activate the AI and anterior cingulate cortex (ACC) (Jackson et al., 2005; Lieberman & Eisenberger, 2009; Singer et al., 2004), regions associated with one's own pain. One popular interpretation of such 'shared representation' between self and other's experience (Decety & Sommerville, 2003) posits that the brain represents others' experiences in terms of the experiences of the self. To wit, one's own internal state serves as a blueprint for understanding the experiences of others (Iacoboni, 2009; Rizzolatti et al., 2006; Singer & Lamm, 2009). Although this view has been broadly (and often implicitly) accepted, the neurobiological details of this putative self-referential process for understanding others remain largely unclear.

This lacuna may exist due to the interacting, but only partially overlapping neural bases of empathy's two facets (Fan et al., 2011). Affective empathy primarily elicits activations from regions implicated in rapid and prioritized processing of emotion signals, including: the amygdala, hypothalamus, orbitofrontal cortex (OFC) and AI (Decety et al., 2013). By comparison, Cognitive empathy, which shares similar neural networks with perspective-taking and mentalizing (Pardini & Nichelli, 2009) additionally involves the superior temporal sulcus (STS), temporoparietal junction (TPJ), fusiform gyrus (FG), and medial prefrontal cortex (mPFC; (Saxe & Powell, 2006)). To date, only one recent meta-analysis investigated convergent areas of activation between interoception, emotion and social processing (Adolfi et al., 2017). The results for the three domains converged in the AI, amygdala, right inferior frontal gyrus (IFG), basal ganglia and medial anterior temporal lobe (mATL), ascribing particular importance to the fronto-temporo-insular nodes (Adolfi et al., 2017). The authors conclude co-activation of these regions may result in an evaluative association of the internal milieu, and in combination with external cues, leads to complex social behavior (Adolfi et al., 2017).

Although this activation-based analysis revealed a number of regions known to play a role within a distributed socioemotional network, scant functional connectivity data exists directly addressing how these regions communicate. Indeed, only one study investigating empathy deficits in a patient with depersonalization disorder (body self-awareness disruption) employed graph-theory analyses and demonstrated both impaired IA and Affective empathy network measurements in the AI, ACC and somatosensory cortex (Sedeño et al., 2014). Although germane, the study only supports an association between these domains during active, task-relevant network configurations. Thus far, no evidence exists regarding this interrelation during resting state

(rsfMRI), despite studies showing individual differences in complex social processing (i.e. empathy) are reflected in intrinsic functional connectivity patterns (Bilevicius et al., 2018; Christov-Moore et al., 2020; Cox et al., 2012; Smith et al., 2009; Tavor et al., 2016).

Therefore, the present study employs a data-driven approach to investigate the similarities between Cognitive and Affective empathy and IA during the viewing of naturalistic stimuli in a resting state scan in healthy adults. Specifically, we aim to understand whether Cognitive and/or Affective empathy as measured by self-report questionnaires shares spatial resting state functional connectivity (rsFC) and/or temporal variability with IA. We hypothesize based on previous literature that 1) Affective empathy will share spatial rsFC with IA within amygdala, AI and IFG, given their involvement in the processing of emotion experienced in oneself and vicariously for others (Singer et al., 2004), while 2) Cognitive empathy will share temporal variability with IA within the right TPJ and precuneus, as these regions are posited to underlie explicit mentalizing (Bardi et al., 2017; Hyde et al., 2015; Kovács et al., 2014; Naughtin et al., 2017).

2. METHODS

2.1 Participants and Procedure

26 healthy young adults (m=21.85 y.o./16 female) without a reported history of neurological or psychiatric disorders were recruited for this study (Table 1). All participants were right-handed and had normal or corrected-to-normal vision and hearing. Participants were recruited through on-campus flyers. All participants were paid $20 for their participation. Experimental protocols were approved by University of Louisville's Institutional Review Board prior to data collection, and written informed consent was obtained from each participant prior to experimental sessions. The study took part on two separate days. On the first day, participants visited the lab to be briefed on the MRI protocol, fill out consent forms and behavioral assessments. On the second day, participants completed the rsfMRI scan at the University of Louisville, School of Medicine.

Table 1

Sociodemographic Characteristics of Participants

	Frequency	Min	Max	%
Gender	10	Male		38.5
	16	Female		61.5
	Total: 26			
Ethnicity	1	Hispanic/Latino		3.8
	24	Not Hispanic/Latino		92.3
	1	Unknown		3.8
Race	22	White		84
	1	African American		4
	2	Asian		8
	1	More than 1 Race		4
				Mean
Age		18	31	21.8
Education (Years)		12	21	14.2

2.2 Resting State Scan: Naturalistic Paradigm

The participants watched a 7 min abstract, nonsocial movie titled Inscapes previously demonstrated to evoke strong connectivity in intrinsic connectivity networks that are more similar to rest than those during conventional movies (Vanderwal et al., 2015). The movie features a series of technological-looking abstract shapes (**Figure 1**). Participants were told to keep their eyes open and relax while watching and listening to the movie. The stimulus was displayed using E-prime on an Invivo Esys LCD TV monitor at the back of the scanner bore, which was viewed by participants through a mirror on the head-coil. The video is freely available for download from HeadSpace Studios.

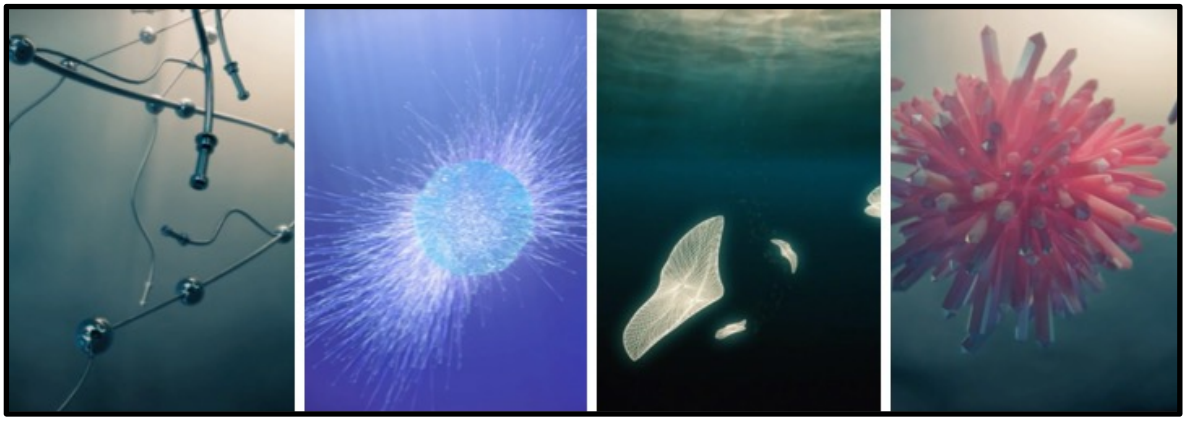


Figure 1: Still-shots from the InScapes Movie

2.3 Behavioral Assessments

2.3.1 Empathy Questionnaire – Interpersonal Reactivity Index (IRI)

Affective and Cognitive empathy was assessed using the Interpersonal Reactivity Index (IRI) (Davis, 1983). The IRI consists of 28 items rated on a 5-point scale with the anchors does not describe me well to describes me very well. The items are arranged into four subscales with seven items. Each subscale measures a distinct component of empathy: empathic concern (EC) (feelings of compassion and concern for others); personal distress (PD) (feelings of anxiety and discomfort that result from observing another person's negative experience); perspective taking (PT) (the ability to adopt the perspectives of other people and see things from their point of view); and fantasy subscale (FS) (the tendency to identify with characters in movies, books, or other fictional situations) (Davis, 1983). Affective empathy, the ability to infer an agent's feelings or emotions, was derived from summing the EC and PD subscales. Cognitive empathy, the ability to infer an agent's beliefs or thoughts, was derived from summing the FS and PT subscales. Total empathy was derived from aggregating Affective and Cognitive empathy scores. All scores were standardized by applying a z-score transformation, and later compared with the MAIA assessment and its subscales (see below) in subsequent analyses. The IRI internal consistency reported range from Cronbach's alpha .70 to .78 and test-retest reliability from .61 to .79 for males and .62 to .81 for females (Davis, 1983).

2.3.2 Multidimensional Assessment of Interoceptive Awareness (MAIA)

The Multidimensional Assessment of Interoceptive Awareness (MAIA) is a 32-item multidimensional instrument assessing Interoceptive Awareness (IA), the conscious perception of sensations from inside the body that create the sense of the physiological condition of the body, such as heart beat, respiration, satiety, and the autonomic nervous system sensations related to emotions (Mehling et al., 2012). Each statement is rated from 0 (never) to 5 (always) in terms of how often it applies to the participant generally in daily life. The statements are then separated into 8 subscales: Noticing, Non-Distracting, Not-Worrying, Attention-Regulation, Emotional Awareness, Self-Regulation, Body Listening and Trusting, which are further aggregated into 5 overall scales used in the present study: Awareness of Body Sensations (Noticing); Emotional Reaction and Attentional Response to Sensations (Not-Distracting, Not-Worrying); Capacity to Regulate Attention (Attention Regulation), Awareness of Mind-Body Integration (Emotional Awareness, Self-Regulation, Body Listening) and Trusting Body Sensations (Trusting). A total

Interoceptive Score (MAIA Total) was derived by summing all the aggregate scales. All scores were standardized by applying a z-score transformation, and later compared with the IRI and its subscales (see above) in subsequent analyses. The MAIA internal consistency reported range from Cronbach's alpha .66 to .82 (Mehling et al., 2012). Correlations between behavioral measurements were conducted with the Statistical Package for Social Sciences (Version 25.0.0; SPSS, INC.), and corrected for age, gender and multiple comparisons using false discovery rate $p<0.05$ (FDR) (Benjamini & Hochberg, 1995) with average matrix correlation.

2.4 MRI Data Acquisition and Preprocessing

All structural MRI images were acquired using a Siemens 3-T Skyra MR scanner. A 20-channel head coil was used for radiofrequency reception. Participants were given earplugs to reduce scanner noise and were additionally given headphones to receive instructions. Foam padding was added to limit motion if additional room remained within the head coil, and a piece of folded tape was placed over the participant's forehead as a reminder to remain still throughout the scan. Structural images were obtained via a T1-weighted magnetization-prepared rapid gradient-echo sequence (MPRAGE) in 208 sagittal slices. Imaging parameters were as follows: echo time (TE) = 2.26 ms, repetition time (TR) = 1700 ms, flip angle = 9.0°, field of view (FoV) = 204 mm, and voxel size = 0.8 x 0.8 x 0.8 mm. Scan parameters were consistent for all imaging sessions associated with this study. Functional blood oxygenation level-dependent (BOLD) images were collected using multi-band acceleration factor of 3. Imaging parameters were as follows: TE = 29 ms; TR = 2000 ms; flip angle = 62°; FoV = 250 mm; isotropic voxel size = 2.0 mm^3; 78 interleaved slices, GRAPPA on, Partial Fourier 7/8. Slices were oriented obliquely along the AC–PC line.

All analyses were conducted using the CONN toolbox 19.c (Whitfield-Gabrieli & Nieto-Castanon, 2012) based on SPM12 (Penny et al., 2007) in the 2017 version of MATLAB. Spatial preprocessing in the CONN toolbox included realignment, normalization and smoothing (6 mm FWHM Gaussian filter) using SPM12 default parameter settings. Anatomical volumes were segmented into gray matter, white matter and cerebrospinal fluid (CSF) areas, and the resulting masks were eroded to minimize partial volume effects. Physiological and other sources of noise were estimated and regressed out using CompCor (Behzadi et al., 2007), a method that performs principal component analysis to estimate the physiological noise from white matter and cerebrospinal fluid for each participant. Motion from the ART toolbox was also included as a

confound regressor. Next, a 0.01–0.10 Hz temporal band-pass filter standard for resting-state connectivity analyses was applied to the time series (Nieto-Castanon, 2015). In sum, detrending, outlier censoring, motion regression, and CompCor correction were performed simultaneously in a single first-level regression model, followed by band-pass filtering. These corrections yielded a residual BOLD time course at each voxel that was used for subsequent analyses.

2.5 Neuroimaging Analysis

2.5.1 Spatial Connectivity

Group-level independent component analysis (ICA) using the CONN toolbox was conducted to identify networks of spatially functionally connected brain regions during resting state (rsFC) that may be associated with IRI and MAIA scores. This involved the application of the fastICA algorithm to dynamic volumes concatenated across subject and resting state condition in order to identify independent spatial components and back-projection of these components to individual subjects, resulting in maps of regression coefficients representing rsFC between the network and every voxel in the brain (see Calhoun et al., 2001 for details). The optimum dimensionality of each fMRI data (i.e., the optimal number of components for each task condition) were estimated using the Minimum Description Length (MDL) criteria in GIFT software package. Forty independent components (ICs) were identified using spatial overlap of suprathreshold areas (Dice coefficient (Rombouts et al., 1998)), based on CONN's default network atlas with ROIs characterizing an extended set of classical brain networks: Default Mode Network (4 ROIs), SensoriMotor (2 ROIs), Visual (4 ROIs), Salience / Cingulo-Opercular (7 ROIs), DorsalAttention (4 ROIs), FrontoParietal / Central Executive (4 ROIs), Language (4 ROIs), Cerebellar (2 ROIs) (all ROIs defined from CONN's ICA analyses of HCP dataset / 497 subjects) (Nieto-Castanon, 2014). Noise components were further identified through visual inspection by two independent authors (TS and BD) (e.g., components largely overlapping CSF), resulting in the exclusion of 4 out of 40 ICs from further consideration. Each of the remaining 36 ICs was subsequently entered in multiple regressions with IRI and MAIA subscales, aggregate and Total scores. For each network, the resulting statistical maps were cluster thresholded at $p \leq 0.05$, voxel thresholded at $p < 0.001$ (FDR-corrected) using Gaussian Random Field Theory (Worsley et al., 1996), and corrected for age and gender. All coordinates reported below refer to peak activations in anatomical MNI space.

2.5.2 Temporal Variability

In order to assess efficient network communication and its relationship to either empathy or IA, we regressed temporal variability of each IC with IRI and MAIA questionnaires. Although rarely utilized as an individual difference measure (Samanez-Larkin et al., 2010), we were interested in whether empathy or IA shared temporal variability in BOLD signal (measured in CONN as SD_{BOLD}). Temporal variability is defined as a fluctuation of neural activity over time, and has been described as beneficial for the neural system's adaptability, efficiency and cognitive performance (Dai et al., 2016; Garrett et al., 2010, 2013; McIntosh et al., 2008; Vakorin, Lippé, et al., 2011; Vakorin, Mišić, et al., 2011). Posited to be influenced by dopamine levels (Li et al., 2001), increased BOLD temporal variability is thought to reflect greater network complexity important for information integration (Faisal et al., 2008; Garrett et al., 2010, 2013; Hudetz et al., 2015; Mišíc et al., 2011; Shew et al., 2009; Vakorin, Mišić, et al., 2011).

3. RESULTS

3.1 Behavioral Results

In order to establish the relationship between empathy and IA, all IRI and MAIA subscales, aggregate and Total scores were correlated (**Table 2**).

Table 2

Intercorrelations between IRI and MAIA Questionnaires and Descriptive Statistics

	1	2	3	4	5	6	7	8	9	10	11	12	Mean	STD
IRI Total (1)	--												75.79	11.12
IRI Affective Empathy (2)	0.60	--											31.84	6.3
IRI Personal Distress (3)	0.11	0.79	--										10.24	5.61
IRI Empathic Concern (4)	0.80	0.48	-0.17	--									21.6	3.85
IRI Cognitive Empathy (5)	0.83	0.05	-0.41	0.67	--								44	8.52
IRI Perspective Taking (6)	0.58	-0.15	-0.52	0.50	0.83	--							21.64	4.97
IRI Fantasy (7)	0.80	0.22	-0.18	0.61	0.84	0.39	--						22.36	5.25
MAIA Total (8)	-0.23	-0.64*	-0.66*	-0.08	0.16	0.31	-0.04	--					23.28	4.36
MAIA Awareness of Body Sensations (9)	-0.30	-0.36	-0.19	-0.29	-0.12	-0.17	-0.03	0.54	--				2.98	0.81
MAIA Emotional Reaction (10)	-0.33	-0.23	-0.21	-0.08	-0.25	-0.11	-0.31	0.37	-0.03	--			5.65	1.26
MAIA Capacity to Regulate Attention (11)	-0.33	-0.83*	-0.74*	-0.27	0.17	0.32	-0.03	0.79	0.48	0.24	--		3.05	0.94
MAIA Awareness of Mind Body Integration (12)	0.09	-0.34	-0.49*	0.16	0.35	0.41*	0.18	0.82	0.37	-0.05	0.50	--	8.12	2.46
MAIA Trusting Body Sensations (13)	-0.25	-0.55*	-0.53*	-0.12	0.08	0.31	-0.18	0.71	0.21	0.32	0.53	0.40	3.48	1.08

Table 2: Intercorrelations between IRI and MAIA Subscales and Descriptive Statistics (same subscale correlations not flagged for significance). * represents correlations statistically significant after multiple comparison correction. Uncorrected Mean and STD reported.

3.1.2 Relationship between Affective Empathy and Interoceptive Awareness

Excluding same-subscale correlations, negative relationships were observed between Affective empathy and the following MAIA subscales: Capacity to Regulate Attention ($r(26) = -0.83$, $p<0.01$), Trusting Body Sensations ($r(26) = -0.55$, $p<0.01$) and MAIA Total ($r(26) = -0.64$,

$p<0.01$). Similarly, we observed a negative relationship between the Personal Distress (PD) subscale and Capacity to Regulate Attention (r(26) = -0.74, $p<0.01$), Awareness of Mind Body Integration (r(26) = -0.49, $p<0.01$), Trusting Body Sensations (r(26) = -0.53, $p<0.01$) and MAIA Total (r(26) = -0.66, $p<0.01$). Within our sample therefore, we report a negative relationship between Affective empathy and IA (influenced by the PD scale, since EC exhibited no significant relationship).

3.1.3 Relationship between Cognitive Empathy and Interoceptive Awareness

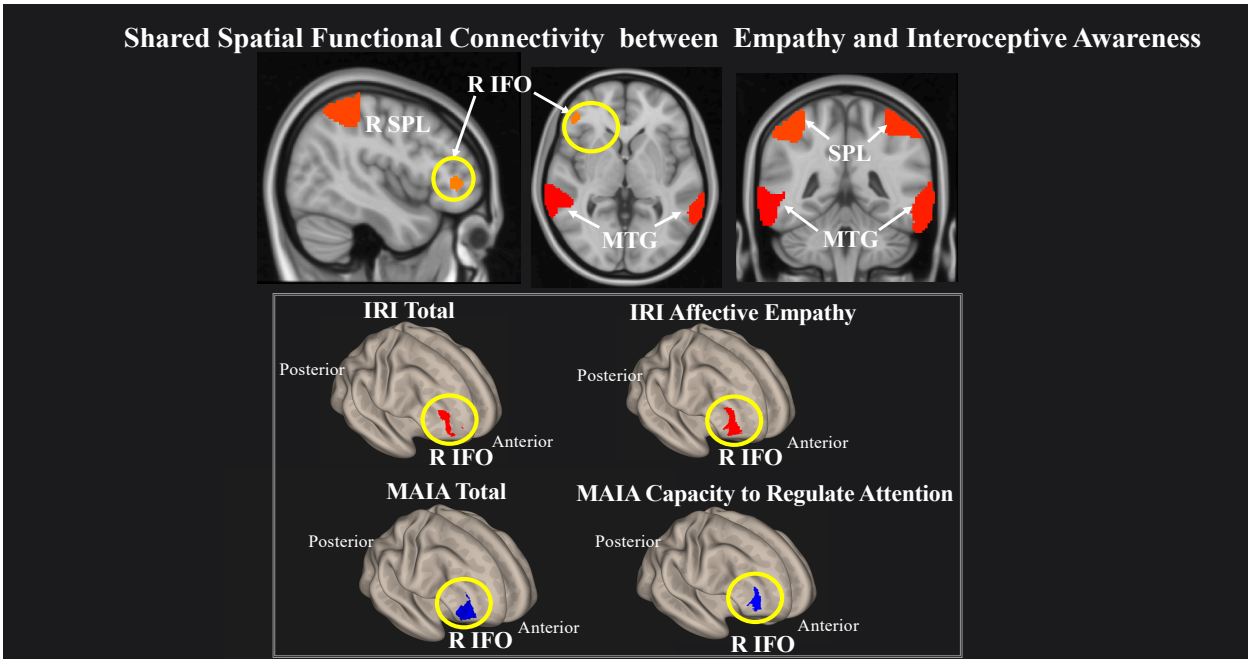
We observed a positive relationship between Cognitive Empathy and the Awareness of Mind Body Integration subscale, r(26) = 0.35, $p=0.06$, although it did not survive multiple comparison correction. In addition, we observed a significant positive relationship between the IRI Perspective Taking (PT) subscale and the MAIA Awareness of Mind Body Integration subscale, r(26) = 0.41, $p<0.01$. Within our sample therefore, we report a positive relationship between Cognitive empathy and IA (influenced by the PT subscale, since Fantasy exhibited no significant relationship).

Therefore, taken together, our behavioral results show a bidirectional relationship between empathy and IA, depending on the facet of empathy interrogated.

3.2 Functional Connectivity Results

3.2.1 Spatial Connectivity

We observed that within a network comprising R inferior frontal operculum (IFO), bilateral superior parietal lobule (SPL) and bilateral middle temporal gyrus (MTG), greater spatial rsFC in



the R IFO was associated with greater overall empathy as measured by the IRI Total, and with greater IRI Affective empathy. Conversely, lower spatial rsFC in the R IFO was associated with increased overall IA as measured by the MAIA Total and increased MAIA Capacity to Regulate Attention (**Figure 2, Table 3**).

Figure 2: Greater spatial rsFC in the right IFO is associated with lower total IA and greater Affective empathy. Statistical maps are thresholded at FDR-corrected cluster-based $p < 0.05$ after voxel threshold at $p < 0.001$.

Table 3
Spatial Network Statistics

Questionnaire Subscale	Region	Laterality	Peak Cluster (X, Y, Z)	size	p-FDR	T stat	Effect Size	90% CI
MAIA Total	IFO	R	46, 48, 2	289	0.04	-6.84	2.7	2, 3.25
Capacity to Regulate Attention	IFO	R	46, 48, 14	407	0.0003	-6.02	2.8	2, 3.25
IRI Total	IFO	R	36, 56, 6	207	0.03	5.26	2.7	1.5, 3
Affective Empathy	IFO	R	40, 48, -4	284	0.02	5.67	2.8	2, 3.5

3.2.2 Temporal Variability

Temporal variability analyses revealed that within a network comprising L IFO, Cerebellum, and R Insula, IRI Personal Distress was negatively related to whole-brain temporal variability (T(22) = -1.04, p=0.02)), while conversely, MAIA Awareness of Body Sensations was positively related (T(22) = 1.48, p=0.001)), (**Figure 3**).

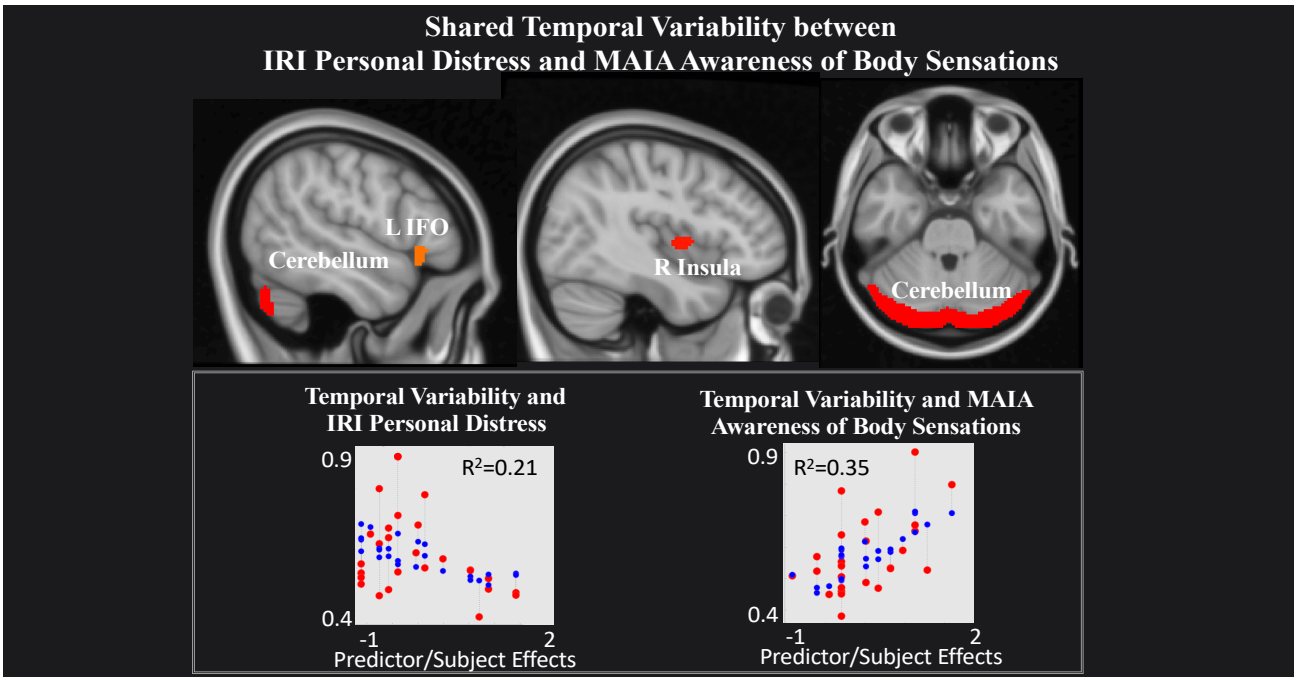


Figure 3: Shared temporal variability between IRI Personal Distress and MAIA Awareness of Body Sensations. Statistical maps are thresholded at FDR-corrected cluster-based $p < 0.05$ after voxel threshold at $p < 0.001$. *Note:* Red dots in graphs represent observed values, Blue dots fitted values.

Lastly, within a network comprising R Precuneus, R MTG, bilateral supramarginal gyrus (SMG) and R IFG, IRI Perspective Taking was positively related to whole-brain temporal variability (T(22) = 1.45, p=0.001), as well as MAIA Mind Body Integration (T(22) = 2.52, p=0.01) (**Figure 4**).

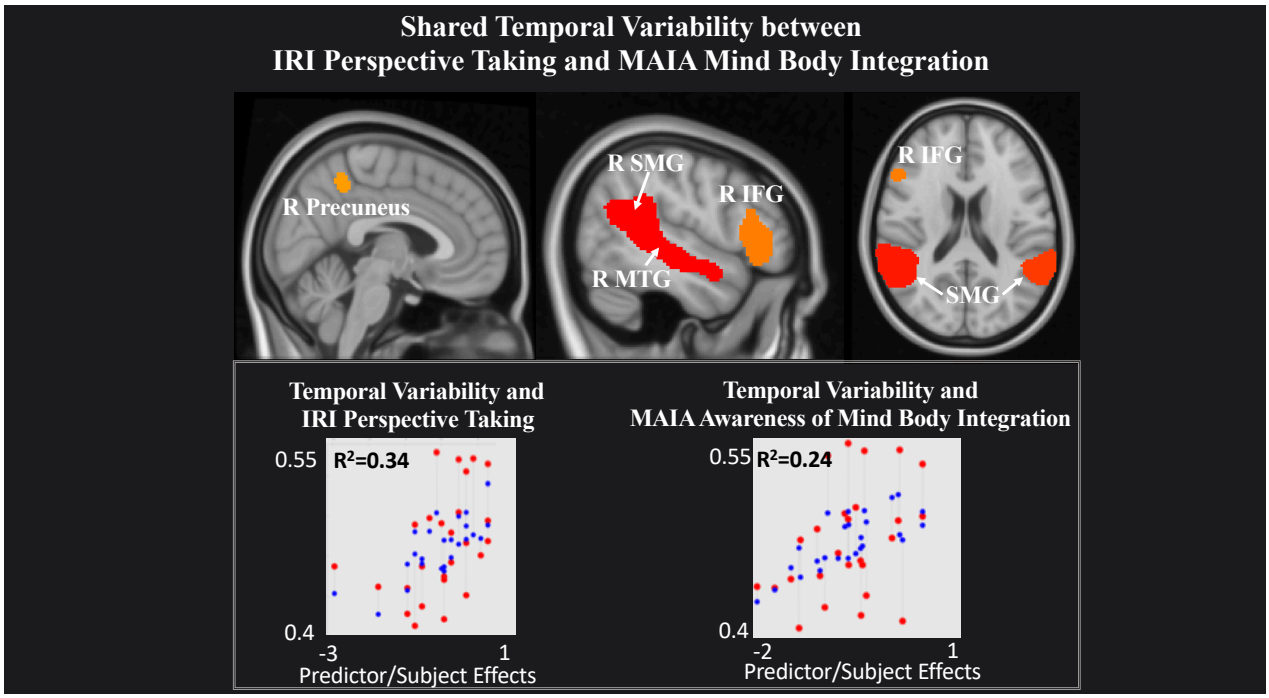


Figure 4: Shared Temporal Variability between IRI Perspective Taking and MAIA Mind Body Integration. Statistical maps are thresholded at FDR-corrected cluster-based $p < 0.05$ after voxel threshold at $p < 0.001$. *Note:* Red dots in graphs represent observed values, Blue dots fitted values.

4. DISCUSSION

Interoceptive awareness and empathy are core social abilities that enable humans to create meaningful social exchanges by accessing one's own internal state in order to understand the experiences of others. Our study employed Independent Component Analysis (ICA) to investigate which empathy facet (Cognitive or Affective) shares spatial connectivity and/or temporal variability with interoceptive awareness (IA) during resting state while healthy adults viewed naturalistic stimuli. We observed a bidirectional behavioral relationship between empathy and IA, depending on the type of empathy interrogated. This bidirectional behavioral relationship also

appeared in the neuroimaging results, such that Affective empathy and IA exhibited an opposite relationship with spatial connectivity within the right IFO of a larger attention network, and similarly, an inverse relationship with temporal variability within an internal sensation network. Whereas, Cognitive empathy and IA both showed a positive relationship with temporal variability within a mentalizing network. These rsFC results indicate that Affective empathy and IA are distributed across similar spatial and temporal neural systems, while Cognitive empathy and IA are only related temporally.

Behaviorally, we observed a negative relationship between the Personal Distress (PD) subscale of the Affective empathy aggregate IRI scale and the total MAIA score, Capacity to Regulate Attention and Trusting Body Sensations subscales. The Capacity to Regulate Attention subscale pertains to various ways of controlling one's attention towards bodily sensations, as part of an active regulatory process; while Trusting Body Sensations reflects the extent to which one views awareness of bodily sensations as helpful for decision making (Mehling et al., 2012). The Empathic Concern (EC) subscale of Affective empathy exhibited no significant relationship, implying that PD is the dominant subscale of the Affective empathy aggregate scale (within our sample) when relating to the MAIA. This distinction is important, considering that previous data suggests EC motivates individuals to pay attention to others' emotions in order to try to comfort them, while conversely, PD drives attention away from others in order to reduce the aversive effects for oneself, perhaps as a form of emotion regulation (Zaki et al., 2014). Indeed, Decety & Jackson, 2004 proposed that PD may arise from the failure of applying sufficient self-regulatory control over the shared emotional state. Echoing previous studies, our study found an inverse relationship between PD and the Capacity to Regulate Attention. Together with the Trusting Body Sensations subscale, our findings suggest increased ability to direct attention internally and rely on this information is linked to a decrease in the discomfort experienced while witnessing another's pain.

Furthermore, we found a positive relationship between the Perspective Taking (PT) subscale of the Cognitive empathy aggregate IRI scale and Awareness of Mind Body Integration of the MAIA. This MAIA subscale represents the integration of several higher level cognitive processes necessary for socially relevant goal-directed behavior (i.e. executive functions (Pribram, 1973)) including: emotional awareness, self-regulation of emotions, and the ability to feel a sense of an embodied self, that is - a sense of the interconnectedness of mental, emotional, and physical

processes as opposed to a disembodied sense of alienation from one's body (Mehling et al., 2012). Thus, our results support previous findings suggesting Cognitive empathy, and in particular PT, is related to a wide array of executive function skills such as working memory, inhibitory control and cognitive flexibility (Aliakbari et al., 2013; Healey & Grossman, 2018; Yan et al., 2020). Taken together with the aforementioned negative relationship between PD and IA, these behavioral results suggest a complex bidirectional association between empathy and IA, contingent on the type of empathy interrogated. To wit, directing attention towards internal bodily sensations may relieve vicarious pain but flexibly employing cognitive-control skills may increase the ability to take another's perspective.

Our spatial functional connectivity results provide further support for this inverse relationship. Within a network of brain regions previously shown to underlie attentional processing (superior parietal lobule (SPL), medial temporal gyrus (MTG) and R inferior frontal operculum (IFO)) (Corbetta & Shulman, 2002; Perrett et al., 1992, 1982, 1985; Wu et al., 2016), we observed that increased rsFC in the R IFO was associated with increased total IRI and Affective empathy on one hand, but reduced total MAIA and Capacity to Regulate Attention on the other hand. Previous studies investigating both personal (Craig, 2009; Critchley, 2005; Damasio, 2005; Gray et al., 2007; Johnson, 2001) and vicarious emotional experience (Jabbi et al., 2007; Singer et al., 2004) show the consistent activation of the AI and frontal operculum, and therefore the IFO is thought of as a continuum between the two structures (Jabbi et al., 2007; Wicker et al., 2003). Because Affective empathy was driven by the PD subscale (within our sample), increased rsFC within the R IFO may relate to intensified personal suffering from witnessing another's pain and decreased awareness of inner body sensations due external attention allocation (perhaps away from oneself and toward another's pain). Our findings reflect previous results showing neural overlap of interoception and empathy in this region (Adolfi et al., 2017; Ernst et al., 2013), and extends these findings by providing rsFC evidence of a double sided association between interoception and empathy.

Our temporal connectivity results offer a complementary perspective that further supports this bidirectional relationship. We observed increased temporal variability was associated with increased MAIA Awareness of Body Sensations subscale, but decreased IRI PD subscale between a network of brain regions previously shown to underlie processing and integration of visceral information (i.e., Cerebellum, L IFO, L AI) (Adamaszek et al., 2017; Baumann & Mattingley,

2012; Bogg & Lasecki, 2015; Schienle & Scharmüller, 2013; J. D. Schmahmann, 2001; Terasawa et al., 2013). Despite the prevailing focus on the AI as a hub for processing body sensations (Kuehn et al., 2016; Pollatos et al., 2007; Singer et al., 2009; Terasawa et al., 2013), additional brain regions are also commonly implicated in interoceptive experience. For example, fMRI studies identify the involvement of the IFO and cerebellum, reinforcing the notion that interoceptive processing (and perhaps especially nociceptive information) may occur through multiple neural pathways (Garcia-Larrea, 2012; Peiffer et al., 2008; Rapps et al., 2008). In the same vein, observing distress in others without actually experiencing it may rely on high-order cognitive functions to access minor changes in physical state, as a tool to modulate negative stimulus input. The implication of the cerebellum in a shared network underlying PD and interoception processing is not surprising, since the cerebellum serves as an integral node in the distributed cortical–subcortical neural circuitry supporting social cognitive operations (Jeremy D. Schmahmann & Pandya, 1995). Taken together, we interpret the findings to suggest that enhanced information integration between this network of brain regions underlying interoceptive experience is related to both increased sensitivity of internal sensation, but in addition, to decreased suffering arising from witnessing another's pain.

Lastly, we observed a positive relationship between both the IRI PT subscale and the MAIA Awareness of Mind Body Integration subscale and temporal variability within a network of brain regions previously associated with the process of mentalizing – the precuneus, IFG, SMG and MTG (Mar, 2011; Northoff et al., 2006; Schurz et al., 2014; Spreng et al., 2009; Vogeley et al., 2001). Mentalizing (Frith et al., 1991), also referred to as Theory of Mind (TOM) (Premack & Woodruff, 1978), signifies the ability to attribute mental states to another individual, allowing the observer to predict intent and direct their behavior appropriately. Researchers agree that mentalizing differs from the vicarious sharing of emotion since it is a more complex form of psychological inference by which observation, memory, knowledge, and reasoning are combined to provide insight into the thoughts and feelings of others (Decety & Jackson, 2004; van der Heiden et al., 2013). Therefore, its connection with MAIA's Awareness of Mind Body Integration scale is not surprising, since both concepts require not only affective experience, but also comprehension and integration of that actual state of mind. We therefore suggest that improved processing between brain regions underlying the mentalizing network may relate not only to a better ability to take someone's perspective but also an improved sense of mind-body interconnectedness.

In conclusion, the current research provides novel information about the relationship between internal body sensation awareness and empathy. In contrast to previous studies which used task-based fMRI to assess the neurobiology of these two constructs separately, we used a rsFC approach to test whether distinct empathy facets are spatially and/or temporally are to IA. We demonstrate a complex bidirectional relationship between empathy and IA, depending on the type of empathy interrogated. Specifically, Affective empathy and IA are distributed across similar spatial and temporal neural systems, while Cognitive empathy and IA are only related temporally. In regard to Affective empathy, on the spatial domain, increased vicarious emotional experience and decreased IA were associated with increased rsFC within the R IFO; while on the temporal domain, increased IA and reduced personal discomfort arising from witnessing another's pain were related to enhanced information processing within an internal sensation network. Concerning Cognitive empathy, perspective-taking ability and a sense of mind-body connectedness related to improved processing between brain regions subserving a mentalizing network. Importantly, we show that the ability to feel and understand another's emotional state is related to the awareness of internal body changes, and that this relationship is not task-dependent, but is reflected in the brain's intrinsic neuroarchitecture. Our findings could have implications for understanding differences in empathic and interoceptive functioning without needing to probe participants with specialized tasks or questionnaires, particularly in clinical populations.

Our study's findings should be considered along with its limitations. The lack of inclusion of an alexithymia measurement may be problematic. In previous studies, empathy and IA have been suggested to be mediated by alexithymia, or the impairment of the ability to identify and describe feelings and emotions (Bird et al., 2010; Decety & Moriguchi, 2007; Moriguchi & Komaki, 2013). It is also important to note that due to the nature of the analyses used, the findings of this study do not represent causal relationships. That is, the results represent a correlational relationship between a questionnaire-based measure of IA or empathy and functional connectivity. Our sample was unfortunately not large enough for a gender-specific analysis, as evidence suggests there are differences in the capacity for empathy between males and females (Christov-Moore et al., 2014). Future research should be conducted in this regard. Similarly, in using an undergraduate sample, the generalizability of these findings is limited.

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