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BRIEF REPORT

The bodily fundament of empathy: The role of action, nonaction-oriented, and interoceptive body representations

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Abstract
Mental representations with bodily contents or in various bodily formats have been suggested to play a pivotal role in social cognition, including empathy. However, there is a lack of systematic studies investigating, in the same sample of participants and using an individual differences approach, whether and to what extent the sensorimotor, perceptual, and interoceptive representations of the body could fulfill an explanatory role in the empathic abilities.
To address this goal, we carried out two studies in which healthy adults were given measures of interoceptive sensibility (IS), action (aBR), and nonaction-oriented body representations (NaBR), and affective, cognitive, and motor empathy. A higher tendency to be self-focused on interoceptive signals predicted higher affective, cognitive, and motor empathy levels. A better performance in tasks probing aBR and NaBR predicted, respectively, higher motor and cognitive empathy levels. These findings support the view that the various facets of the empathic response are differently grounded in the body since they diversely involve representations with a different bodily format.
Individual differences in the focus on one's internal body state representation can directly modulate all the components of the empathic experience. Instead, a body representation used interpersonally to represent both one's own body and others' bodies, in particular in its spatial specificity, could be necessary to accurately understand other people's minds (cognitive empathy), while a sensorimotor body representation used to represent both one's own body and others' bodies actions, could be fundamental for the self-awareness of feelings expressed in actions (motor empathy).

Keywords Empathy · Interoception · Body representation · Body schema

Introduction

Empathy is the ability to be sensitive to, understand, and experience the emotions of others through both affective/emotional and cognitive processes (Heydrich et al., 2021; Reniers et al., 2011). It is pivotal for human emotional experience and social interactions since it allows us to make sense of and respond appropriately to other people's behavior (Decety & Jackson, 2006). Empathy may be distinguished into two main dimensions, namely (1) *affective empathy*, which refers to the ability to adapt the emotional experience of others, and (2) *cognitive empathy*, which refers to the ability to understand what another agent feels (Healey & Grossman, 2018).

In addition, *action-based* or *motor empathy,* which occurs when the person mirrors the motor responses of the observed individual, has been suggested to be another relevant component of empathic processing (Blair, 2005).

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Several empirical findings indicate that the ability to empathize with others relies on the simulation of another's experience by activating the same brain areas that are active when the observer experiences that state or feeling (Banissy & Ward, 2007; Gallese, 2003; Gallese & Goldman, 1998; Keysers et al., 2004) and that we use our own bodily experiences and processes to understand our own and others' emotional experience (Damasio, 1999; Havas et al., 2010; Wollmer et al., 2012). These findings suggest that individual differences in sharing and understanding other people's emotions might be linked to individual differences in proprioceptive information feedback processing, action tendency, and interoceptive ability.

In particular, individual differences in the sense of the physiological condition of the body (i.e., interoception) have captured increasing attention, and recent neuroscientific research is targeting interoceptive processing as an intermediary between the body and social cognition, including empathy (for an overview, see Gao et al., 2019). Indeed, there is evidence that individuals with heightened interoceptive capability tend to experience emotions more intensely and have a better understanding of their and others' emotions (Herbert et al., 2011; Shah et al., 2017; Wiens et al., 2000; but see Ainley et al., 2015 for negative findings). In this vein, a link has been suggested between a higher *interoceptive accuracy* (i.e., better performance in a heartbeat perception task) on the one hand and greater empathy for pain (Grynberg & Pollatos, 2015) and better representation of others' mental states in situations where it is reliant upon emotional information (Shah et al., 2017) on the other. Similarly, a study by Fukushima et al., (2011) showed that the central monitoring of the cardiovascular activity of one's own body (i.e., interoceptive accuracy) was significantly involved in processing the affective states of others. Moreover, Mul et al., (2018), in a mixed sample of individuals with and without autism, found that the self-perceived tendency to focus on interoceptive signals measured via questionnaires (i.e., *interoceptive sensibility*) correlated with the ability to recognize and understand others' mental state (i.e., cognitive empathy) and with the ability to share the feelings of others (i.e., affective empathy).

In keeping with these behavioral findings, neuroimaging studies have consistently shown that the anterior insula, the main hub of the interoceptive brain network, is activated during the awareness and understanding of other's feelings, such as in the empathic process (for a metanalysis, see Gu et al., 2013), in line with the idea that there is a learned association between our interoceptive signals and emotions observed in others (Bird & Viding, 2014).

In addition to interoceptive processing, also the malleability of body ownership and the body schema have been shown to be related to empathic abilities and traits (Asai et al., 2011; Farmer & Maister, 2017; Marzoli et al., 2011). For example, Asai et al., (2011) found that people who were more susceptible to the Rubber Hand Illusion had stronger empathic traits, suggesting that people that easier lose their own bodily sense might be more likely to replace their own lost sense of ownership and agency with that of an outside agent.

Taken together, these findings highlight the importance of bodily processing for social cognition, pointing towards novel insights about the embodied perspective of empathy. Yet, a clear understanding of "how" empathy is embodied is missing. According to an exciting point of view, social cognition can be embodied because it is affected by how the body is represented in the mind (Goldman & de Vignemont, 2009). Consequently, body representations, in terms of mental representations with bodily *contents* or in various bodily *formats* (e.g., motoric, somatosensory, and interoceptive formats), can play a pivotal role in empathy. However, there is a lack of systematic studies investigating the relations between different body representations (e.g., in sensorimotor and interoceptive formats) and empathy in the same sample of participants. Thus, following embodied social cognition theories (e.g., Goldman & de Vignemont, 2009), our overarching goal in the current study was to investigate whether and to what extent the sensorimotor, perceptual, and interoceptive representations of the body could fulfill an explanatory role in the empathic abilities.

To address this goal, we carried out two studies investigating the relations between empathy, interoceptive sensibility (IS), and action (aBR) and nonaction-oriented body representations (NaBR) in large samples of healthy adults, using an individual differences approach. We hypothesized that higher IS levels and better NaBR and aBR performance would result in higher empathy. In addition, we predicted that the different empathic components would be differently affected by the tendency to be self-focused on interoceptive signals and by the level of ability in aBR and NaBR.

Study 1: On the relation between interoceptive sensibility (IS) and action-oriented body representations (aBR) with empathy

Methods

Participants

Two hundred and three healthy participants (111 females, aged $M = 27.40$ years, $SD = 9.64$, and 92 males, aged $M = 28.40$ years, $SD = 9.39$) took part in the study. The sample size was determined to be as large as possible, and sensitivity post hoc analyses performed by G*Power 3.1 (Faul et al., 2009) suggest that given the sample sizes (N = 203), we have 99% power to detect a medium-sized effect (r = .50). Participants were asked to complete a self-administered online battery including three questionnaires. All participants had normal or corrected-to-normal vision and no history of neurological or psychiatric conditions.

The study was approved by the local Ethics Committee (Calabria Region Ethical Committee, Catanzaro, Italy) and was performed in accordance with the criteria set laid down in the 1964 Declaration of Helsinki.

Materials and procedure

Assessment of empathy All participants completed the Interpersonal Reactivity Index (IRI, Davis, 1980; Italian version: Albiero et al., 2006), a well-validated and reliable self-report instrument composed of four seven-item subscales tapping four distinct aspects of empathy: Perspective Taking (PT; e.g., "I sometimes try to understand my friends better by imagining how things look from their perspective"), Empathic Concern (EC; e.g., "I often have tender, concerned feelings for people less fortunate than me"), Personal Distress (PD; e.g., "When I see someone who badly needs help in an emergency, I go to pieces"), and Fantasy (FS; e.g., "I really get involved with the feelings of the characters in a novel"). Each item is scored on a 5-point Likert scale ranging from 1 (*does not describe me well*) to 5 (*describes me very well*), with higher scores indicating greater levels of empathy. Perspective taking and FS subscales assess the cognitive component of empathic traits, while EC and PD assess the affective component of empathic traits (Davis, 1983).

IS and aBR assessment All participants also completed the Self-Awareness Questionnaire (SAQ; Longarzo et al., 2015), a 35-item self-report instrument specifically developed to assess the frequency of common bodily feelings, thus probing IS. Items are clustered into two domains, the first related to visceral feelings (*visceral domain*, ViD; e.g., "I feel my heart thudding") and the second related to somatosensory feelings (*somatosensory domain*, SoD; e.g., "I feel my palms sweaty"). Each item is scored on a 5-point Likert scale ranging from 0 (*never*) to 4 (*always*), with higher scores indicating higher IS.

Participants were also given the Florida Praxis Imagery Questionnaire (FPIQ, Ochipa et al., 1997), a 48-item questionnaire used to assess the ability of the individual to imagine complex motor actions (e.g., using scissors), answering questions on the basis of internal representations, and then probing the so defined aBR (or body schema).

The FPIQ includes four subscales: (a) *Kinesthetic,* imagining what joint is moved the most during a specified action; (b) *Position,* imagining the spatial position of a body part when interacting with specific objects; (c) *Action,* imagining the motion of a limb associated with a specific action, and (d) *Object,* imagining an object used during an action (this subscale assesses the ability to imagine objects, without requiring any imagination of body – object interactions; thus, differently from the other subscale, it does not assess the aBR).

Each item has two response options, and a correct answer (scored as one point) indicates that the participant can correctly imagine the action required to arrive at the solution.

Statistical analyses

A Kolmogorov-Smirnov test was applied to verify the normal distribution of data; since the results showed that data were not normally distributed, Spearman correlation coefficients between the SAQ and FPIQ subscale scores on the one hand and the IRI subscale scores on the other were calculated. The alpha value was adjusted by using Bonferroni's correction for multiple comparisons (p < .002; .05/24 = .002).

Multiple linear regression analyses on logarithmically transformed variables were run to estimate the predictive effect of the SAQ domains (i.e., ViD; SoD) and of the FPIQ subscales probing the aBR (i.e., Kinesthetic, Position, Action) on the IRI subscales scores.

Results

Descriptive statistics for each questionnaire are reported in Online Supplementary Material (OSM) 1.

Significant correlations were found between the SAQ and the IRI subscales scores. In particular, the ViD scores significantly correlated with all IRI subscales, except for PT. The SoD scores had a moderate and significant correlation with the FS, PD, and EC subscales, but this last correlation did not survive after the Bonferroni correction. Instead, there were no significant correlations between the FPIQ and the IRI subscales scores. Only the Action subscale scores showed a weak correlation with the PD subscale scores, but this association did not survive after the Bonferroni correction (see Table 1)

The overall regression models were statistically significant for all the IRI subscales (EC: $R^2 = .07$; $F(5,197) = 2.93$, $p = .014$; PD: $R^2 = .18$; $F(5,197) = 8.47$, $p < .001$; PT: $R^2 = .06$, $F(5,197) = 2.40$, $p = .039$; FS: $R^2 = .09$; $F(5,197) = 3.86$, $p = .002$). However, while the ViD scores predicted significantly all the IRI subscales scores and the SoD scores predicted significantly the PD subscale scores, none of the FPIQ subscales was able to predict the IRI subscales scores (see Table 2).

Table 1 Spearman correlation coefficients between the Interpersonal Reactivity Index (IRI) subscales scores on the one hand and the Self-Awareness Questionnaire (SAQ) subscales scores and the Florida Praxis Imagery Questionnaire (FPIQ) subscale scores on the other (Study 1)

			Interoceptive sensibility measures – SAQ		Action-oriented body representation measures – FPIQ			
			ViD	SoD	Kinesthetic	Position	Action	Object
Empathy measures	EC	r_{rho}	**.25**	.16	-.05	.08	-.08	-.09
		p	<.001	.023	.483	.264	.245	.225
	PD	r_{rho}	**.37**	**.32**	-.08	-.04	-.15	-.10
		p	<.001	<.001	.235	.582	.030	.163
	PT	r_{rho}	.12	-.003	.09	.03	-.02	.07
		p	.087	.968	.213	.717	.814	.301
	FS	r_{rho}	**.29**	**.22**	-.11	-.10	-.09	.03
		p	<.001	.002	.136	.157	.225	.680

Significant correlations, after Bonferroni correction, are shown in bold

EC Empathic Concern, *PD* Personal Distress, *PT* Perspective Taking, *FS* Fantasy, *ViD* Visceral Domain, *SoD* Somatosensory Domain

Table 2 Standardized regression coefficients predicting affective and cognitive empathy (Study 1)

	EC			PD			PT			FS		
	Beta	*t*	*p*	*Beta*	*t*	*p*	*Beta*	*t*	*p*	*Beta*	*t*	*p*
ViD	.055	2.82	**.005**	.101	2.35	**.020**	.079	2.87	**.005**	.077	2.46	**.015**
SoD	.008	0.28	.780	.210	3.17	**.002**	-.071	-1.67	.096	.047	0.98	.328
Kinesthetic	.031	0.49	.627	-.125	-0.90	.371	.160	1.79	.075	-.050	-0.50	.620
Position	.043	0.61	.544	-.102	-0.64	.523	.074	0.73	.466	-.167	-1.45	.149
Action	-.027	-0.38	.707	-.239	-1.50	.135	-.108	-1.06	.292	-.108	-0.94	.349

P values for variables predicting empathy measures are shown in bold

Affective empathy: *EC* Empathic Concern, *PD* Personal Distress; *Cognitive empathy*: *PT* Perspective Taking, *FS* Fantasy; *Interoceptive sensibility*: *ViD* Visceral Domain of the Self-Awareness Questionnaire, *SoD* Somatosensory Domain of the Self-Awareness Questionnaire; *Action-oriented body representation*: Kinesthetic, Position and Action subscales of the Florida Praxis Imagery Questionnaire

Interim discussion of Study 1

We investigated whether and how differences in IS and aBR predicted different facets of empathy in healthy adults. We observed that IS, particularly for visceral sensations, predicted both affective and cognitive components of empathy, suggesting that empathic processing relies on the sensibility to one's own interoceptive states. Thus, a more frequent monitoring of one's own internal body states would result in a higher responsivity to others in terms of a tendency to share and understand their emotions and feelings (for similar behavioral findings with interoceptive accuracy measures, see Fukushima et al., 2011; Grynberg & Pollatos, 2015; Shah et al., 2017; for similar behavioral findings with IS measures, see Mul et al., 2018; but see Ainley et al., 2015; Tajadura-Jiménez & Tsakiris, 2014 for negative results using an interoceptive accuracy task).

A number of studies support the idea that empathy might rely also on the activation of the motor representation of the observed action (Gallese, 2003; see also Avenanti et al., 2005; Leslie et al., 2004; Marzoli et al., 2011). In particular, neuroimaging evidence argues that we understand what others feel via a mechanism of action representation that modulates the emotional activity and that the insula plays a pivotal role in the communication between the action representation network and the limbic areas (Carr et al., 2003). Contrary to our expectations, we did not find a significant role of the aBR in cognitive and affective empathy. However, we recognized that the instrument used to assess the aBR (i.e., the FPIQ) has been developed for clinical populations and may not be sensitive enough to interindividual differences in healthy adults. Also, we did not explore the motor component of empathy, which could be more closely related to the body schema, and the NaBR, which could contribute to empathy differently from the aBR. Thus, to overcome the limitations of Study 1, we carried out a second study, including measures used in the healthy population to identify individual differences in aBR, NaBR (see Conson et al., 2020; Nagashima et al., 2019; Palmiero et al., 2019; Raimo et al., 2021a; Raimo et al., 2021b) and motor empathy (Williams et al., 2016).

Study 2: The role of IS, aBR, and nonaction-oriented body representations (NaBR) in affective, cognitive, and motor components of empathy

Methods

Participants

One hundred and sixty-four healthy participants (114 females, aged $M = 29.04$ years, $SD = 11.94$, and 50 males, aged $M = 30.14$ years, $SD = 10.29$) took part in the study. The sample size was determined to be as large as possible, and sensitivity post hoc analyses performed by G*Power 3.1 (Faul et al., 2009) suggest that given the sample sizes (N = 164), we have 99% power to detect a medium-sized effect (r = .50). Participants were asked to complete a self-administered online battery of tasks and questionnaires. All participants had normal or corrected-to-normal vision and had no history of neurological or psychiatric conditions. The study was approved by the local Ethics Committee (Calabria Region Ethical Committee, Catanzaro, Italy) and was performed in accordance with the criteria set laid down in the 1964 Declaration of Helsinki.

Materials and procedure

Assessment of empathy All participants completed the Brief form of the Interpersonal Reactivity Index (B-IRI, Ingoglia et al., 2016), a validated 16-item self-report instrument consisting of four subscales (PT, EC, PD, and FS) replicating the structure hypothesized by Davis (1980, 1983) for the IRI. Each item is scored on a 5-point Likert scale ranging from 1 (*does not describe me well*) to 5 (*describes me very well*), with higher scores indicating greater levels of empathy.

All participants also completed the Action and Feelings Questionnaire (AFQ; Williams et al., 2016), a brief and simple self-report measure tapping action-based empathy (the self-awareness of own and others' actions associated with feelings). It consists of 18 items clustered in two main factors: *Production,* which includes items that refer to the production of actions (e.g., "To make sense of what someone else is doing, I might copy his or her actions"), and *Perception,* which includes items that refer to the experience of perceiving others' actions (e.g., "I tend to pick up on people's body language"). Each item is ranked on a 4-point Likert scale ranging from 0 (*strongly disagree*) to 3 (*strongly agree*), with higher scores indicating higher levels of motor empathy.

IS, aBR and NaBR assessment IS was measured as in Study 1 by using the SAQ.

The aBR (i.e., the body schema) was measured using the Hand Laterality Task (HLT; adapted for the online administration from Raimo et al., 2021c; Parsons, 1987). In this task, participants are asked to make a decision on the laterality of a single hand drawing (48 stimuli, 24 left, and 24 right stimuli), presented at varying degrees of angular rotation (0, 45, 90, 135, 180, 225, 270, and 315°) on the screen. In detail, each stimulus includes a rotated hand drawing presented in the middle of the screen and two response items, that is, a left and a right hand (not rotated), shown in the left and right bottom part of the screen. Participants have to decide whether the rotated hand is a left or a right hand by mentally rotating it and selecting one of the two response items (left/right hand not rotated). The stimulus remained onscreen until participants selected a response item. The task included 48 trials. Response accuracy for each trial was recorded, and the accuracy score corresponded to the sum of correct responses. Individual scores ranged from 0 – 48, with higher scores indicating better performance.

The NaBR (i.e., the body structural representation or visuo-spatial body map) was measured using a modified version of the Frontal Body Evocation task (FBE) (adapted for the online administration from Daurat-Hmeljiak et al., 1978; Raimo et al., 2021c). In this modified version, participants are shown a human body picture on the screen for 10 s. Subsequently they are required to decide if eight specific body parts (i.e., the left and right hands, left and right arms, left and right legs, left and right feet) presented on the screen one at a time are correctly or incorrectly positioned, having only the head or the waist as reference. In particular, each stimulus includes the head/waist (correctly located in the top/middle of the screen), another body part (e.g., the left leg) that could be correctly or incorrectly located, and two response items (i.e., two grey boxes with the labels "correct" and "incorrect") displayed in the left and right bottom part of the screen. Participants have to decide if the body parts are correctly or incorrectly positioned by selecting one of the two response items (correct/incorrect). The stimulus remained onscreen until participants selected a response item. The task included 48 trials. Response accuracy for each trial was recorded, and the accuracy score corresponded to the sum of correct responses. Individual scores ranged from 0 – 48, with higher scores indicating better performance.

To disentangle the contribution of body representations from general cognitive abilities necessary to perform the body representation tasks (i.e., visual processing, mental imagery, visuo-spatial attention, decision making, etc.), participants also completed two control tasks. The Object Laterality Task (i.e., the control task for the aBR task; adapted for the online administration from Raimo et al., 2021c) requires participants to mentally rotate a non-body stimulus. In this task, participants are asked to make a decision on the laterality of a flower with a leaf positioned at the right or left base of the stem (48 stimuli, 24 left and 24 right stimuli), presented at varying degrees of angular rotation (0, 45, 90, 135, 180, 225, 270, and 315°) on the screen. In detail, each stimulus included the rotated flower presented in the middle of the screen and two response items, that is a flower with a leaf positioned at the left of the stem and a flower with a leaf positioned at the right of the stem, shown in the left and right bottom part of the screen. Participants have to decide whether the rotated flower is that with a leaf positioned at the right or at the left base of the stem by mentally rotating it and selecting one of the two response items. The stimulus remained onscreen until participants selected a response item. The task included 48 trials. Response accuracy for each trial was recorded, and the accuracy score corresponded to the sum of correct responses. Individual scores ranged from 0 – 48, with higher scores indicating better performance.

Finally, all participants completed the Christmas Tree Task (i.e., the control task for the NaBR task; adapted from Raimo et al., 2021c), involving the visuo-spatial processing of non-body related stimuli. In this task, participants are shown the picture of a Christmas tree on the screen for 10 s. Subsequently, they are required to decide if eight specific parts of the tree (i.e., the left and right upper branches, left and right mid-upper branches, left and right mid-lower branches, and left and right lower branches with trunks), presented on the screen one at a time, are correctly or incorrectly positioned, having only the star tree topper or the jar as reference. In particular, each stimulus included the star tree topper/the jar (correctly located on the screen), another part of the tree (e.g., the left upper branches) that could be correctly or incorrectly located, and two response items (correct/incorrect) in the bottom of the screen. Participants have to decide if the parts of the tree are correctly or incorrectly positioned by selecting one of the two response items (correct/incorrect). The stimulus remained onscreen until participants selected a response item. The task included 48 trials. Response accuracy for each trial was recorded, and the accuracy score corresponded to the sum of correct responses. Individual scores ranged from 0 – 48, with higher scores indicating better performance.

Statistical analyses

A Kolmogorov-Smirnov test was applied to verify the normal distribution of data. Since the results showed that data were not normally distributed, Spearman correlation coefficients between the SAQ subscales, the HLT and FBE scores on the one hand, and the AFQ and B-IRI subscales scores on the other were calculated. The alpha value was adjusted by using Bonferroni's correction for multiple comparisons (0.05/24 = 0.002).

Stepwise multiple regressions were used to identify the possible predictors of the AFQ and B-IRI subscales scores out of the following variables: ViD, SoD, HLT, and FBE. For the HLT and FBE, the performance in the respective control task was taken into account. In order to perform such analyses, all variables were logarithmically transformed, and the unstandardized residuals of the aBR and NaBR tasks on the control tasks (i.e., the unstandardized residuals of the HLT scores on the Object Laterality Task scores and the unstandardized residuals of the FBE scores on the Christmas Tree Task scores) were calculated.

Results

Descriptive statistics for empathy, IS, aBR, and NaBR measures are reported in OSM 2.

Significant correlations were found between the SAQ subscales scores and the empathy measures (AFQ and B-IRI subscales scores). In particular, the ViD and SoD scores significantly correlated with the Production, FS, PD, and EC subscales, but this last correlation did not survive after the Bonferroni correction.

The HLT scores were significantly associated with the Production and Perception subscales, but this last correlation did not survive after the Bonferroni correction. The FBE scores significantly correlated with the PT subscale scores, but this association did not survive after the Bonferroni correction (see Table 3).

The stepwise linear regression analyses showed that the EC subscale scores (R^2 = .09; $F(1, 162) = 15.67$, $p < .001$) and the PD subscale scores (R^2 = .19; $F(1, 162) = 38.48$, $p < .001$) were significantly predicted by the ViD scores; the PT subscale scores (R^2 = .05; $F(1, 162) = 7.55$, p = .007) were significantly predicted by the FBE unstandardized residuals; the FS subscale scores (R^2 = .22; $F(2, 161) = 22.14$, $p < .001$) were significantly predicted by the ViD subscales scores and the FBE unstandardized residuals; the Production subscale scores (R^2 = .15; $F(2, 161) = 13.95$, $p < .001$) were significantly predicted by HLT unstandardized residuals and the ViD subscale scores; and the Perception subscale scores (R^2 = .05; $F(1, 162) = 8.21$, p = .005) were significantly predicted by HLT unstandardized residuals (see Table 4).

Interim discussion of Study 2

Overall the correlational results, in line with the results of Study 1, showed that participants with higher IS reported higher empathic levels in all components (i.e., affective, cognitive, and motor). These data replicate and expand those of previous behavioral (Fukushima et al., 2011; Grynberg & Pollatos, 2015; Mul et al., 2018; Shah et al., 2017) and neuroimaging (Ernst et al., 2013) studies, which have mainly used interoceptive accuracy measures, underlying the role of the interoceptive processing in empathy.

Notably, our results showed that participants with a better aBR, as evaluated with a task involving the mental rotation of body parts, reported a higher self-awareness of

Table 3 Spearman correlation coefficients between the empathy measures on the one hand and the IS, aBR, NaBR measures on the other (Study 2)

			IS		aBR	NaBR
			ViD	SoD	HLT	FBE
Empathy B-IRI	EC	r_{rho}	.18	.17	.03	.13
		p	.022	.031	.704	.104
	PD	r_{rho}	**.36**	**.26**	.07	-.10
		p	<.001	<.001	.387	.208
	PT	r_{rho}	.08	.08	.11	.16
		p	.29	.29	.159	.037
	FS	r_{rho}	**.35**	**.25**	.06	.14
		p	<.001	.001	.425	.075
Empathy AFQ	Production	r_{rho}	**.33**	**.27**	.18	.02
		p	<.001	<.001	.023	.765
	Perception	r_{rho}	-.05	-.06	**.24**	.12
		p	.544	.392	.002	.140

Significant correlations, after Bonferroni correction, are shown in bold

B-IRI Brief form of the Interpersonal Reactivity Index, *EC* Empathic Concern, *PD* Personal Distress, *PT* Perspective Taking, *FS* Fantasy, *AFQ* Action and Feelings Questionnaire, *IS* interoceptive sensibility, *ViD* Visceral Domain of the Self-Awareness Questionnaire, *SoD* Somatosensory Domain of the Self-Awareness Questionnaire, *aBR* Action-oriented Body Representation, *NaBR* Nonaction-oriented Body Representation, *HLT* Hand Laterality Task, *FBE* Frontal-Body Evocation Task

their own and others' actions associated with feelings (i.e., Perception). This finding supports the results of a previous behavioral study suggesting a link between self-reported empathy and motor identification with imagined agents, as evaluated with a task in which the participants were required to imagine an individual performing a manual action and to indicate the hand used by the imagined individual (Marzoli et al., 2011).

In addition, the results of the regression analyses showed that: the interoceptive (visceral) sensibility levels predicted the affective (i.e., EC, PD), cognitive (i.e., FS), and motor (i.e., Production) components of empathy; the NaBR performance was a predictor of the cognitive (i.e., FS, PT) component of empathy; and the aBR performance was a predictor of the motor component of empathy (i.e., Perception and Production). These findings support the view that the various facets of the empathic response are differently grounded in the body since they diversely involve representations with a different bodily format (Alsmith & de Vignemont, 2012; Goldman & de Vignemont, 2009). Indeed, while the representation of interoceptive information could play a pivotal role in all the emphatic components (i.e., affective, cognitive, and motor), the sensorimotor representation of the body (aBR) would be mainly associated with the motor "state" empathy (see also Marzoli et al., 2011). The visuospatial body map (NaBR) would be mainly associated with cognitive empathy, possibly because it is relevant for correctly mapping an emotion on one's own body to predict the body maps of the same emotional states attributed to another (Sachs et al., 2019).

General discussion

In the present study, we investigated the role of individual differences in IS, aBR, and NaBR in empathy. To this aim, we used well-validated and widely employed self-report questionnaires and specifically developed tasks to measure: empathy components (i.e., affective and cognitive components using the IRI and the B-IRI, motor component using the AFQ), IS levels (using the SAQ), aBR (using the FPIQ and the HLT) and NaBR (using the FBE) in two large samples of healthy participants.

In our first study, we found a significant relationship between affective and cognitive components of empathy and IS levels, especially those referring to visceral sensations, that predicted higher empathy levels. Instead, we did not find a specific role of the aBR, investigated by a questionnaire probing the motor imagery of complex actions, in the cognitive or affective empathy. In this first study, however, we did not evaluate the NaBR and the motor component of empathy.

In the second study conducted on an independent sample of participants, we found that the IS, in particular for the visceral feelings, played a significant role in the interindividual variability in affective, cognitive, and motor components of empathy. In addition, we found a specific role of the NaBR and aBR, respectively, in cognitive and motor empathy. Indeed, we identified the NaBR performance as a factor contributing to the individual difference in the cognitive component of empathy. The aBR performance, instead, was a factor significantly contributing to the interindividual variability in the motor component of empathy, mainly in the tendency to use motor imagery to understand others. Importantly these findings were not affected by

Table 4 Standardized regression coefficients predicting affective, cognitive, and motor empathy (Study 2)

	Predictor	*Beta*	*t*	*p*
B-IRI				
EC	ViD	.30	3.96	<.001
	Excluded variables			
	SoD	.09	0.84	.401
	HLT	.01	0.10	.925
	FBE	.13	1.79	.077
PD	ViD	.44	6.20	<.001
	Excluded variables			
	SoD	.17	1.69	.093
	HLT	-.004	0.59	.556
	FBE	.04	-0.05	.961
PT	FBE	.21	2.75	.007
	Excluded variables			
	ViD	.14	1.80	.074
	SoD	.10	1.34	.182
	HLT	.07	0.93	.352
FS	ViD	.41	5.86	<.001
	FBE	.24	3.49	.001
	Excluded variables			
	SoD	-.05	-0.54	.590
	HLT	.01	0.07	.947
AFQ				
Production	ViD	.36	4.87	<.001
	HLT	.19	2.61	.010
	Excluded variables			
	SoD	.04	0.36	.719
	FBE	-.03	-0.46	.647
Perception	HLT	.22	2.87	.005
	Excluded variables			
	ViD	-.03	-0.33	.741
	SoD	-.07	-0.85	.398
	FBE	.04	0.56	.577

B-IRI Brief Form of the Interpersonal Reactivity Index, *AFQ* Action and Feelings Questionnaire

Affective empathy: *EC* Empathic Concern, *PD* Personal Distress; *Cognitive empathy*: *PT* Perspective Taking, *FS* Fantasy; *Motor empathy*: Production, Perception; *Interoceptive sensibility*: *ViD* Visceral Domain of the Self-Awareness Questionnaire, *SoD* Somatosensory Domain of the Self-Awareness Questionnaire; *Action-oriented body representation*: *HLT* Hand Laterality Task; *Nonaction-oriented body representation*: *FBE* Frontal-Body Evocation Task

The unstandardized residuals of the HLT scores on the Object Laterality Task scores, and the unstandardized residuals of the FBE scores on the Christmas Tree Task scores were used in the regression analyses

individual differences in other cognitive skills used to perform the body representation tasks (e.g., visuo-spatial and mental imagery skills), since we regress out the performance in tasks similar to the ones used to test body representations, but which did not involve body-related stimuli (i.e., control tasks).

Taken together, these results confirm previous suggestions of a link between interoceptive processing and empathy (e.g., Fukushima et al., 2011; Grynberg & Pollatos, 2015; Heydrich et al., 2021; Mul et al., 2018). Importantly, we demonstrated that IS affected all components of empathy (affective, cognitive, and motor) according to the perception-action model of empathy (Preston & De Waal, 2002), positing that interoception (and related neural structures) plays a key role in processing the body sensations underpinning empathy (Ernst et al., 2013; Fukushima et al., 2011). 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). Indeed, previous studies showed as individuals with poor interoceptive skills (i.e., interoceptive accuracy; Garfinkel et al., 2015) have difficulty in identifying their own emotions and, at the same time, in recognizing emotional facial expressions or inferring the mental state of others (Betka et al., 2021; Bornemann & Singer, 2017; Shah et al., 2017). These observations are consistent with the proposal that empathic understanding arises from a simulation (interoceptive prediction) of likely internal bodily state, requiring the integration of subsequent interoceptive afferent signals into emotional representations of both self and other (Singer & Lamm, 2009).

However, it should be acknowledged that some previous studies have reported no or negative links between empathy and interoception (i.e., Ainley et al., 2015; Stoica & Depue, 2020; Tajadura-Jiménez & Tsakiris, 2014). Differences in the kind of interoceptive dimension (i.e., interoceptive accuracy vs. IS) and methodological features (e.g., differences in the kind of interoceptive questionnaires and sample size) could account for the divergence in the findings between the present study and some previous ones. For example, Tajadura-Jiménez and Tsakiris (2014) found no significant association between individual differences in interoceptive accuracy (assessed by means of the heartbeat perception task) and components of empathy in a sample of 28 healthy women. Similar findings were reported by Ainley et al., (2015) in three different experiments using the heartbeat perception task and three measures of empathy (i.e., the IRI, the Questionnaire of Cognitive and Affective Empathy, and the Reading the Mind in the Eyes' Task). However, these studies did not assess interoceptive accuracy considering other submodalities (e.g., thermosensation, affective touch, nociception) that recent evidence suggests being not significantly correlated with the cardiac submodality (see, e.g., Crucianelli et al., 2022), and did not establish whether other interoception dimensions (i.e., IS) were linked to empathy. On the other hand, Stoica and Depue (2020) reported a bidirectional relationship between IS and empathy in a sample of 26 participants. Consistently with our findings, they found a positive association between cognitive empathy and IS; in striking contrast, they reported a negative association with affective empathy. However, this study assessed a different facet of the subjectively reported interoceptive bodily awareness mainly related to cognition and behavior (such as the quality of body sensations, the attitude toward and behavioral reaction to bodily sensations) rather than focusing on one's subjective tendency to perceive bodily sensations. Thus, future studies should further investigate the relationships between interoception and empathy, examining different interoceptive submodalities and the different interoceptive dimensions within the same large sample of healthy individuals.

Beyond interoception, our study showed as empathic abilities were also differently linked to aBR and NaBR. In particular, the aBR (i.e., a representation of the body in a sensorimotor format) affected the motor components of empathy, whereas the NaBR affected the cognitive components of empathy. Notably, in line with a previous exploratory study in a clinical sample (Lee et al., 2021), our findings further underline the role of the aBR, as measured with a motor imagery task, in empathic abilities, supporting the idea that motor simulation is relevant in intention understanding in social situations (Gallese, 2001, 2003, 2016; Gallese et al., 2004; Lewkowicz et al., 2013). In the same vein, previous studies showed as the observation of others' emotional movements involves the Action Observation Network-associated brain structures (i.e., the premotor cortex, the inferior parietal lobule, and the inferior frontal gyrus), suggesting that emotion recognition would be closely related to a mental simulation process that draws on one's own motor representations of such movements (Pichon et al., 2009; Sinke et al., 2010). Interestingly, a recent study by Jospe et al., (2018) found that participants with high empathy levels utilized the simulation process for facial expression recognition more optimally than participants with low empathy levels.

It is interesting to note that the NaBR (i.e., a visuospatial body map or body structural representation) is damaged in autotopagnosic patients (see Guariglia et al., 2002; Semenza, 1988; Sirigu et al., 1991). An intriguing aspect of this body representation disorder is that the difficulties in locating body parts often involve both the own body and others' bodies (for an overview, see Palermo & Di Vita, in press), implying that the same mechanism is used for representing our own body and the body of others (Haggard & Wolpert, 2005). This common body representation used interpersonally to represent both one's own body and others' bodies, in particular in its spatial specificity, could be a basic step toward the human ability to accurately understand other people's minds (Thomas et al., 2006) by mapping the emotions observed in others and those experienced by oneself (Sachs et al., 2019).

Overall, these findings can be read in light of those theories suggesting that people reuse their mental representation in a bodily format in various social-cognitive activities (Alsmith & de Vignemont, 2012; Gallese & Sinigaglia, 2011; Goldman & de Vignemont, 2009), suggesting a possible different role of mental representations with an interoceptive, sensorimotor, and visuo-spatial bodily format in the different aspects of empathy.

Therefore, empathy may be characterized as an umbrella term involving different components (i.e., affective, cognitive, and motor) differently affected by body information processing (see Fig. 1).

Given the implication of impaired empathic abilities in several disorders (e.g., autism and schizophrenia; see Decety & Moriguchi, 2007), a deeper understanding of how embodied processes are involved in the ability to empathize with others may guide in addressing challenges in developing,

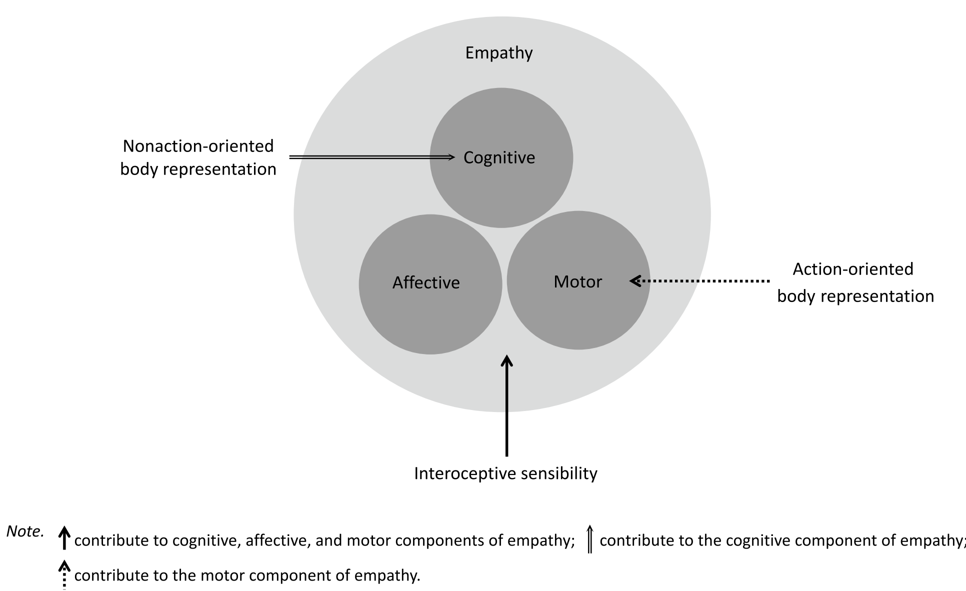

Fig. 1 Schematic representation of a predictive model for empathy that includes the contribution of interoceptive sensibility, action-oriented body representation and nonaction-oriented body representation

implementing, and evaluating tailored interventions in clinical settings.

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Data availability Data are available on request.

Declarations

Informed consent statement All participants gave their informed consent prior to performing the experiment.

Conflict of interest The authors declare no conflicts of interest.

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