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Interactions between interoception and perspective-taking: Current state of research and future directions

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Abstract

Interoception, the sense of the physiological state of the body, and perspective-taking, the ability to take another's point of view, are two fundamental components contributing to our perception and interaction with the external world. However, whether the perception of our inner body influences how we perceive the external world and other people remains poorly understood. Here, we review recent behavioural and neuroimaging evidence investigating the links between dimensions of interoception (i.e., accuracy, sensibility and awareness) and perspective-taking (i.e., affective, cognitive and visual). So far, only a limited subset of these dimensions has been investigated together and the results suggest that interoceptive abilities may only interact with perspective-taking when embodied mental transformations are required. Furthermore, mainly the emotional aspects of perspective-taking are related to interoception, influencing the ability to empathise with others. Future research should systematically investigate the links between all dimensions of interoception and perspective-taking to provide full understanding of the specific role interoception has on how we perceive the world and take another's point of view.

Keywords: interoception; interoceptive accuracy; interoceptive sensibility; interoceptive awareness; affective perspective-taking; cognitive perspective-taking; visuo-spatial perspective-taking; Theory of Mind; empathy

1. Introduction

Our comprehension of the world is driven by both internal and external stimuli and the two influence each other. For a long time, research on human behaviour and perception has primarily concerned information coming from the external world (i.e. exteroception), neglecting the substantial amount of perceptual information arising from within the body. More recently, interest in the impact of afferent information arising from within the body on perception has grown considerably. Behaviour typically requires internal control mechanisms such as hormone release, adjustments of sympathetic or parasympathetic activity as well as motor commands (Petzschner et al., 2021). Similarly, a strong integration of external and internal sensations is necessary for a unified perception. To allow for this, organisms must respond to the challenge of maintaining their physiological integrity in an ever-changing external environment (Petzschner et al., 2021).

Interoception refers to the sense of the physiological condition of the body (Ceunen et al., 2016) and includes feelings such as pain, temperature, itch, affective touch, muscular activity, visceral sensations, vasomotor activity, hunger, thirst and air hunger (Chen et al., 2021). More recently interoception has been defined as “the process by which the nervous system senses, interprets, and integrates signals originating from within the body, providing a moment-by-moment mapping of the body’s internal landscape across conscious and unconscious levels” (Khalsa et al., 2018). Interoceptive processing is crucial for the representation of the self as agentive, continuous and invariant over time (Craig, 2010). For these reasons, interoception appears to be linked to mechanisms of embodiment (Herbert and Pollatos, 2012). Embodiment refers to the idea that many aspects of cognition are shaped by our body, in particular, it implies that we use bodily experience to understand our own emotional experience and the experiences of others (Ferrari and Coudé, 2018). At the crossroad between spatial cognition and bodily sensation research, some scientists have proposed that the integration of various visceral/internal signals in the brain generates a body-centred reference frame (Park and Tallon-Baudry, 2014; Babo-Rebelo et al., 2016), which is used to tag mental processes as being self-related (Babo-Rebelo and Tallon-Baudry, 2018). For example, the amplitude of heartbeat-evoked responses (i.e. neural responses to heartbeats, Coll et al., 2021) differs between imagining oneself or someone else (Babo-Rebelo et al., 2019).

The ability to perceive visceral changes in the body, referred to as Interoceptive Accuracy (IAcc), is typically assessed with cardiac detection or discrimination tasks. Heartbeat detection procedures usually require participants to count the number of times they feel their heart beating during different time periods (i.e. the “heartbeat counting task”, Schandry, 1981), while heartbeat discrimination procedures involve differentiating the timing of individual heartbeats from external stimuli (Whitehead et al., 1977). More recently, Garfinkel et al. (2015) distinguished three dimensions for the assessment of interoceptive abilities: (i) interoceptive accuracy (performance on objective behavioural tests of heartbeat detection or discrimination); (ii) interoceptive sensibility (subjective measure assessed using questionnaires); (iii) interoceptive awareness (metacognitive awareness of interoceptive accuracy). These three dimensions were found to be partially distinct and dissociable. In addition to the perception of one’s own cardiac signals, interoception also includes the perception of internal bodily states such as gastric signals (van Dyck et al., 2016), temperature, itching and pain (Ceunen et al., 2016).

Interoception contributes to a feeling that our conscious experiences are bound to the self, referred to as 'bodily self-awareness'. Bodily self-awareness includes the perception of visceral signals coming from our own body (i.e. interoception), the identification with one's body (i.e. body-ownership), the feeling of the body in space and the sense of agency (Blanke et al., 2015). Recent studies highlighted the strong interaction between interoceptive and exteroceptive abilities (Azzalini et al., 2019; Herman et al., 2020), and in particular their importance for self-other distinction. Exteroceptive abilities include all the signals (e.g. tactile and visual cues) involving a human body or body parts normally presented in space and surrounding the person's body (Blanke et al., 2015).

An example illustrating the crosstalk between exteroceptive and interoceptive abilities is the Rubber Hand Illusion (RHI). When synchronous exteroceptive visuo-tactile stimulation between a rubber hand and the participant's hidden hand is delivered, many report subjective feelings of ownership for the rubber hand (Botvinick and Cohen, 1998). The RHI has now become a robust measure of the sense of body-ownership and self-other boundaries. Participants with lower interoceptive accuracy, as measured by the heartbeat counting task (Schandry, 1981), reported a greater experience of the RHI, compared to individuals with higher interoceptive accuracy (Tsakiris et al., 2011; but for recent counter findings see Horváth et al., 2020). This finding is in line with the hypothesis that those with higher interoceptive accuracy have a stronger sense of self, centered on their internal bodily states (Palmer and Tsakiris, 2018).

Furthermore, multisensory integration of exteroceptive and interoceptive signals modulates the experience of body ownership in the RHI (Suzuki et al., 2013). By combining computer-generated augmented reality with feedback of cardiac information, Suzuki et al., (2013) implemented a "cardiac rubber hand illusion task" in which a rubber hand appeared to be pulsing in synchrony with the cardiac rhythm of the participant. Synchronous cardio-visual feedback presented on the rubber hand induced an enhanced experience of ownership of the virtual hand.

To examine more implicit aspects of self-other boundaries and their relationships with interoceptive accuracy, Imafuku et al. (2020) focused on the phenomenon of spontaneous facial mimicry. Results showed that observing another person's facial expression led to involuntary facial movements that matched the perceived facial configuration. Participants with higher interoceptive accuracy showed higher spontaneous facial mimicry in a certain social context (direct eye gaze), suggesting a greater blurring of self-other boundaries. This implies that interoception is related not only to the perceived boundary of the self, but also to social cues. In regard to previous findings with the RHI (Tsakiris et al, 2011), these mixed results suggest that several mechanisms are involved when distinguishing our own feelings and behaviours from that of others, such as perspective-taking (Steinbeis, 2016).

Perspective-taking is a multidimensional construct referring to the ability to take another person's 'point of view' and is often characterized along three dimensions: (i) cognitive perspective-taking, defined as the ability to infer the thoughts or beliefs of another agent; (ii) affective perspective-taking, defined as the ability to infer the emotions or feelings of another agent (Healey and Grossman, 2018); iii) visuo-spatial perspective-taking, defined as the ability to understand the visuo-spatial experience of another agent (Proulx et al., 2016). Cognitive, affective and visuo-spatial perspective-taking are all thought to interact in order to contribute to social cognition (Hamilton et al., 2014).

Perspective-taking refers to how an individual perceives or interprets incoming information but can also refer to how the information can be imagined or remembered from different perspectives. For example, studies on autobiographical memory showed that events from an individual's life can be remembered using different viewpoints. An event may be recalled from a first-person perspective (i.e. field mode) or from the perspective of an external observer (i.e., observer mode; Rice and Rubin, 2009; Robinson and Swanson, 1993). Interestingly, reliving past events from an external observer perspective decreases bilateral insula and somatic motor activity that are central for monitoring our bodies' internal states (i.e. interoception, Eich et al., 2009).

Interoception provides a key mechanism for the representation of the self and could therefore also be important for cognitive, affective and visual-spatial perspective-taking. Indeed, the strong links between exteroceptive and interoceptive processing, and the relationship between perspective-taking and the sense of body ownership (Tsakiris, 2017) suggest a role of interoception in perspective-taking (Palmer and Tsakiris, 2018).

Recent studies have started to investigate the links between interoception and perspective-taking, however the extent to which these two multidimensional constructs interact remains unclear. Bringing together the disparate findings collected so far may be crucial to better understand how perceiving internal sensations may affect the ability to take another's point of view, at both the emotional, cognitive and visuo-spatial levels; and how this can be affected in different psychiatric disorders. The present review aims to provide an overview of the current research on interoception and the different dimensions of perspective-taking. The possible commonalities in the underlying neural mechanisms, as well as how both abilities can be impaired in the same clinical populations, is presented. Finally, suggestions for future avenues of research are discussed.

It should be underlined here that in the perspective-taking literature, terminology and operational definitions can differ when referring to the same construct, or different constructs can also share the same terminology. For example, the terms perspective-taking and Theory of Mind (ToM) are often used interchangeably. ToM is defined as a person's cognitive ability to understand another person's mental states, such as thoughts, beliefs, desires and intentions (Happé et al., 2017), and requires both cognitive and affective perspective-taking abilities (Hynes et al., 2006). Furthermore, there is a distinction between *cognitive* and *affective* empathy (Zaki and Ochsner, 2012). While affective empathy refers to the ability to adopt the emotional experience of others, cognitive empathy corresponds to the ability to understand what another agent feels (Healey and Grossman, 2018). Both cognitive and affective empathy require perspective-taking abilities, but the main difference between the two processes is that affective empathy not only concerns emotion recognition but also adopting another person's emotion (Healey and Grossman, 2018).

Authors, year, N	Levels of PT	PT tasks	Interoceptive tasks	Primary research question	Major finding
Ainley et al., 2015 [N=86 (E1) N=34 (E2) N=97 (E3) N=60 (E4)]	Affective PT, Cognitive PT, VPT	E1- Interpersonal Reactivity Index[1] E2 - Questionnaire of Cognitive and Affective Empathy[2] E3 - Reading the Mind in the Eyes' task[3] E4 - The Director task[4]	Heartbeat counting task[14] = IAcc	Investigate the possible associations between interoception and different levels of PT	There were no significant associations between IAcc and measures of empathy, ToM and VPT
Shah et al., 2017 (N=72)	Affective PT, Cognitive PT	Movie for the Assessment of Social Cognition[5]	Heartbeat counting task[14] = IAcc Time estimation task[15]	Investigate whether IAcc predicted performance on the representation of mental states in general or only when understanding emotions is required	Greater IAcc was associated with better performance on items requiring the representation of another's emotion
von Mohr et al., 2020 (N=46)	Affective PT, Cognitive PT	Cardiac audio-visual EEB task	Heartbeat counting task[14] = IAcc	Investigate how cardiac interoceptive impact, manipulated by presenting affective stimuli across different phases of the cardiac cycle modulates the tendency to use one's own emotional state when relating to others	Individuals with higher IAcc showed an increased EEB when the other's emotional state was presented at the point of maximum interoceptive impact (i.e., at systole)
Shaw et al., 2020 (N=290)	Affective PT, VPT	Interpersonal Reactivity Index[1] Adaptation of the Multifaceted Empathy Test[6] The Director task[4]	Heartbeat counting task[14] = IAcc	Investigate relationships among various components of social cognition (e.g., self-other distinction and VPT) and socio-emotional processes (e.g., affective empathy, emotion regulation and interoception)	Self-other distinction and VPT may influence socio-emotional processes such as affective empathy, emotion regulation and interoception
Heydrich et al., 2021 (N=20)	Affective PT, VPT	Empathy Quotient [7] Own-body transformation task[8]	Cardio-visual paradigm[16]	Investigate whether VPT abilities could change through the manipulation of interoceptive cues and if this effect could depend on empathy	Participants with high empathy showed better performance in the VPT task during synchronous versus asynchronous cardio-visual stimulation
Ernst et al., 2013 (N=18)	Affective PT	Japanese and Caucasian facial expressions of emotions[9]	Heartbeat counting task[14] = IAcc	Investigate how a period of IAcc task modulates neural activity during subsequent empathy, using fMRI	A preceding IAcc task enhanced neural activity during empathy in bilateral anterior insula and other cortical midline regions
Grynberg and Pollatos, 2015 (N=93)	Affective PT	Pictures showing painful and non-painful situations	Heartbeat counting task[14] = IAcc	Investigate whether interoception shapes affective and cognitive empathy	Higher IAcc was associated with cognitive empathy, affective empathy, and arousal, but not with distress, in response to painful pictures
Terasawa et al., 2014 (N=30)	Affective PT	Social Anxiety Disorder Scale[10] Manifest Anxiety Scale[11] Emotional sensitivity task[12]	Heartbeat counting task[14] = IAcc Time estimation task[15]	Investigate whether interoception modulates emotional experience	Participants with higher IAcc were more sensitive to the emotions of others, especially for sadness
Dirupo et al., 2020 (N=50)	Affective PT	Video-clips of Pain and Disgust Expressions	Heartbeat counting task[14] = IAcc Confidence rating in Heartbeat counting task performance = IAw Time estimation task[15]	Investigate whether individual interoceptive abilities influence the ability to understand other people's unpleasant emotional/affective states.	Individuals that were more accurate in tracking their heartbeats were more prone to judge facial expressions as more unpleasant
Stoica and Depue, 2020a (N=26)	Affective PT	Interpersonal Reactivity Index[1]	Multidimensional Assessment of Interoceptive Awareness[17] =IS	Investigate whether empathy and interoception share spatial and/or temporal functional connectivity	Resting-state fMRI spatial connectivity and temporal variability data were correlated with empathy levels and IS. Improved processing between part of the salience network regions was related to an improved ability to take other's perspective
Stoica and Depue, 2020b (N=26)	Affective PT	Interpersonal Reactivity Index[1]	Multidimensional Assessment of Interoceptive Awareness[17] =IS	Investigate which dimension of empathy is functionally related to interoception	Affective empathy and IS were inversely related to increased resting-state functional connectivity within the right inferior frontal operculum, and to blood oxygenation variability between interoceptive network regions
Erle, 2019 (N=101)	VPT	Level 2 VPT task[13]	Heartbeat counting task[14] = IAcc Confidence rating in Heartbeat counting task performance = IAw	Investigate the possible links between interoception and VPT	IAcc was related to faster and more accurate VPT performance. No relationship with IAw and VPT was found

Note. IAcc: interoceptive accuracy; IS: interoceptive sensibility; IAw: interoceptive awareness; PT: perspective-taking; VPT: visuo-spatial perspective-taking; ToM: Theory of Mind; EEB: emotional egocentricity bias.
1. Davis, 1983; 2. Reniers et al., 2011; 3. Baron-Cohen et al., 2001; 4. Santiesteban et al., 2012; 5. Dziobek et al., 2006; 6. Dziobek et al., 2008; 7. Baron-Cohen and Wheelwright, 2004; 8. Parsons, 1987; 9. Matsumoto and Ekman, 1988; 10. Kaiya, 2009; 11. Taylor et al., 1985; 12. Terasawa et al., 2014; 13. Kessler and Thomson, 2010; 14. Schandry, 1981; 15. Dunn et al., 2010; 16. Aspell et al., 2013; 17. Mehling et al., 2012.

Table 1
Characteristics of the studies investigating the links between interoception and perspective-taking, highlighting which dimensions of perspective-taking were investigated and which perspective-taking and interoceptive tasks were used.

Due to the close similarity in the definition and in order to simplify the terminology, in this review, the term 'affective perspective-taking' is used to refer to affective empathy as well. A recent review concluded that empathy and 'cognitive perspective-taking' recruit distinct neural circuits and can be distinguished from each other even early during development and across the life span (Stietz et al., 2019) highlighting the need to dissociate empathy from the cognitive mechanisms of understanding others (i.e. 'cognitive perspective-taking').

The literature search was performed up to June 2021. Given the multitude of terminology used in the field, the search included terms associated with the different dimensions of perspective-taking (i.e. cognitive, affective and visuo-spatial) and interoception (i.e. interoceptive accuracy, interoceptive sensibility, interoceptive awareness), as well as empathy and ToM. This search was supplemented by manual searches of reference lists cited in the original and review articles. Only reports published in English were included. The final reference list was generated on the basis of relevance to the topics covered in this review. Characteristics of the studies found in this search are reported in Table 1.

2. The role of interoception in perspective-taking

2.1. Interoception, cognitive and affective perspective-taking

Interoception is thought to be involved in emotion processing as the physiological condition of the body may act as the basic substrate for feeling states and emotions (Bechara and Damasio, 2005). In support of this hypothesis, functional neuroimaging studies have highlighted areas of overlap between the neural substrates of emotion and interoception (Critchley and Garfinkel, 2017). Moreover, a possible link between interoceptive processing, affective (i.e. empathy) and cognitive (i.e. ToM) perspective-taking has been hypothesized.

Studies have investigated the role of interoception in empathy, both at the affective and cognitive levels. Terasawa et al. (2014) examined whether interoception [measured by the heartbeat counting task (Schandry et al., 1981), followed by a time estimation task as a control] modulated emotional experience by using morphed facial expressions. In the task, participants saw morphed photos with the following facial expressions: angry, sad, disgusted, happy. They were asked to choose the most appropriate option for the emotion that had been elicited by the stimulus. Results indicated that participants with higher interoceptive accuracy were more sensitive to the emotions of others, especially for expressions of sadness. Furthermore, the false identification of sad faces was related to social anxiety.

Grynberg and Pollatos (2015) investigated whether interoception shapes affective and cognitive empathy for pain and other forms of affective responses in a sample of healthy participants. In that study, one hundred pictures showing both painful and non-painful situations were used. Participants had to: (i) report the valence of their feelings and the degree of arousal they felt in response to the person in pain or non-pain situations; (ii) estimate how painful the depicted situation was; (iii) rate how compassionate and how distressed they felt in response to the person in pain or non-pain depicted in the picture. Interoception was measured by using a heartbeat counting task (Schandry et al., 1981). Higher interoceptive accuracy was associated with higher ratings of the intensity of the person's pain (cognitive empathy), with higher reports of compassion (affective empathy) and arousal, but not with distress, in response to painful pictures. According to the authors, these results are in line with reports of higher arousal in response to emotional stimuli in good heartbeat perceivers (i.e. high interoceptive accuracy; see also Pollatos et al., 2007).

However, Ainley et al. (2015) reported contrasting results. Interoception was similarly measured using a heartbeat counting task, however no significant associations between interoception and empathy (both at the cognitive and affective levels) were found. These contrasting findings may be due to the fact that Terasawa et al. (2014) and Grynberg and Pollatos (2015) differentiate empathy linked to specific emotional states (e.g. pain, sadness), which was not done in Ainley et al. (2015). Thus, it might be the case that the link between interoception and empathy is stronger for specific emotional states (e.g. sadness and pain). To further investigate this hypothesis, Dirupo and colleagues (2020) studied whether individual interoceptive abilities influence the ability to understand another's affective state. In that study, participants watched video-clips of naturalistic facial expressions in response to painful (thermal) and disgusting (olfactory) events. Participants were required to classify the video-clips according to the emotional state they induce (pain, disgust, neutral) and to rate the unpleasantness felt by the person in the video. IAcc was measured with a heartbeat counting task (Schandry et al., 1981) and confidence ratings about their estimation (i.e. interoceptive awareness). Subsequently, participants underwent a control task to account for potential confounds related to personal beliefs about one's cardiac response and time estimation (Desmedt et al., 2020). Individuals with higher IAcc were more likely to judge facial expressions as more unpleasant. However, when asked to discriminate between pain and disgust, participants' performance was not influenced by their interoceptive abilities. Overall, this study supports the view from embodied accounts that interoception promotes individual receptivity to others' affect, especially with unpleasant emotions.

Studies on interoception and cognitive perspective-taking have focused on identifying how processing of internal visceral and autonomic information (interoception) could contribute to the understanding of another's intentions. Ondobaka et al. (2017) proposed that knowledge of the interoceptive causes of our own behaviour (motor and autonomic) helps us predict and infer another's behaviour (i.e. ToM). From the active inference perspective, the authors suggest that knowing the contents of another's mind could also be demystified based on the behaviour that we would have produced in a similar situation. These hypotheses were based on the 'Predictive Coding' framework, according to which the brain generates hypotheses about the world and tests their predictive validity against incoming sensory evidence (Friston, 2005). Ondobaka et al. (2017) therefore proposed that not only are our own mental states inferred from interoceptive states, but also that understanding another's mental states (ToM) entails interoceptive predictions. In line with this framework, Shah et al. (2017) tested whether interoceptive accuracy predicts performance on the representation of mental states in general, or if it is linked only to those situations in which understanding emotion is crucial for accurate mental state representation. A sample of healthy participants completed the Movie for the Assessment of Social Cognition (MASC, Dziobek et al., 2006) in which they watched a social event requiring accurate mental state inferences to understand the story. Performance was quantified separately for questions requiring representation of another's emotion (e.g., “What is Sandra feeling?”) and for those which did not require the representation of emotional states (e.g., “What is Michael thinking?”). Interoceptive accuracy was assessed with the Heartbeat counting task (Schandry, 1981) followed by a time estimation task as a control measure. Results showed that greater interoceptive accuracy was associated with better performance on items requiring the representation of another's emotion, but not when representation of emotional states was not required. These findings thus suggest that interoception contributes to accurate representation of mental states in situations where this process is reliant upon emotional information. However, interoception seems to be not strictly necessary for the representation of mental states *per se*.

Recently, von Mohr et al. (2019) went one step further and investigated how cardiac interoceptive accuracy modulates the tendency to use one’s own emotional state when judging the emotional state of others (emotional egocentricity bias); as well as how manipulating the presentation of affective stimuli across different phases of the cardiac cycle (cardiac interoceptive impact) influences this relationship. Results showed that healthy participants with higher interoceptive accuracy displayed an increased emotional egocentricity bias when another’s emotional state was presented at the point of maximum interoceptive impact (i.e., at systole, Garfinkel et al., 2014), whereas the opposite effect was observed for individuals with lower interoceptive accuracy. Taken together, these findings are in line with the hypothesis that individuals with lower interoceptive accuracy are more likely to switch to another person’s emotional perspective given their tendency to blur self-other boundaries (Palmer and Tsakiris, 2018). Therefore, interoception may be more relevant for emotional aspects of social cognition which influence the ability to empathise with others.

2.2 Interoception and visuo-spatial perspective-taking

In addition to the emotional aspects linked to understanding another's perspective, interoception may also shape the ability to distinguish between one’s own and another’s visual-spatial perspective. Visuo-spatial perspective-taking (VPT) has been described as the ability to understand the visuo-spatial and mental experience of another agent (Proulx et al., 2016). VPT is often characterized as having two levels (Flavell et al., 1981): (i) level-1 VPT is the ability to understand that another agent can see things differently compared to one’s own point of view; (ii) level-2 VPT is the ability to judge what a visual scene looks like from another’s point of view. Level-1 VPT can involve implicit, automatic processing of a target’s perspective as well as effortful and controlled ascription of a target’s mental state (Todd et al., 2017). Level-2 VPT is thought to be an embodied process during which the perspective-taker mentally simulates a movement of his or her body into the location of the target (Kessler and Rutherford, 2010; Surtees et al., 2013). VPT processes are differently used depending on the tasks and goals at hand. In particular, some underlying VPT mechanisms allow us to transform our perspective to describe the visuospatial aspects of a scene perceived from a different viewpoint, while others allow us to compute the line of sight of a third agent (Michelon and Zacks, 2006).

The first study investigating the potential relationship between VPT and interoceptive accuracy used a level-1 VPT task (Ainley et al., 2015), assessing the ability to understand what another can and cannot see. This task, named the "Director Task" (Santiesteban et al., 2012), requires participants to move objects around a grid of shelves according to verbal instructions from a 'Director'. Sometimes, the grid display affords two competing perspectives: the participants' viewpoint from the front of the display differs from the Director's vantage point from the rear. Under these conditions, the participants must ignore their own self-perspective and act according to their inference of the Director's perspective. Interoceptive accuracy was assessed using the heartbeat counting task (Schandry, 1981). Contrary to their expectations, Ainley et al. (2015) did not find any associations between interoceptive accuracy and the results obtained in the Director task.

The possible relationships between interoceptive accuracy, level-1 VPT and other dimensions of perspective-taking were investigated by Shaw et al. (2020). Similarly to Ainley et al. (2015), level-1 VPT was assessed using the "Director Task" (Santiesteban et al., 2012) and interoceptive accuracy was investigated with the heartbeat counting task (Schandry, 1981). Structural equation modelling analysis showed that a hierarchical pattern of relationships among various components of social cognition (e.g., self-other distinction and visual perspective-taking) may influence socioemotional processes (e.g., affective empathy, emotion regulation and interoception). However, no direct associations between level-1 VPT and interoception were found.

Furthermore, Erle (2019) investigated how interoception is related to a level-2 VPT test, assessing the ability to understand how someone else sees things. Participants completed a behavioural level-2 VPT task in which they saw a person (the "target") sitting at a table with two objects on a computer screen. They had to mentally "grab" one of the objects from the target's perspective, using two response keys. Interoceptive accuracy was quantified by the heartbeat counting task (Schandry, 1981). Moreover, interoceptive sensibility was measured by the subjective confidence in the estimated number of heartbeats. Faster VPT performance was related to higher interoceptive accuracy but was unrelated to interoceptive sensibility.

Thus, the relationship between interoception and non-emotional forms of perspective-taking appears to be more controversial. Some findings suggest that interoceptive accuracy is not related to understanding the non-emotional contents of another's thoughts (Shah et al., 2017) or to ignoring one's own visual point of view in favor of another's (Ainley et al., 2015). However, other findings (Erle, 2019) suggest that visual perspective-taking is indeed related to interoceptive accuracy, supporting an embodied cognition account of visual perspective-taking. The disparate findings may relate to the requirement of level-1 vs. level-2 perspective-taking in the tasks used. The task of Ainley et al. (2015) as well as Shaw et al. (2020) assessed level-1 perspective-taking, while Erle (2019) measured level-2 perspective-taking. Only level-2 perspective-taking is thought to be an embodied process, which suggests that interoceptive processes may interact with perspective-taking only when there is a requirement to engage in embodied transformations of one's body in space (i.e. imagined self-rotation).

More recently, Heydrich et al. (2021) investigated how embodied transformations of one's body are influenced by interoceptive cues as well as empathic abilities. A cardio-visual paradigm (Aspell et al., 2013) was used to assess whether VPT abilities are affected by systematic manipulations of interoceptive cues as well as an individual's empathic ability. In an adapted version of the own-body transformation task, participants were instructed to mentally adopt the perspective and position of a virtual body presented on a computer screen (see Parsons, 1987). The virtual body was surrounded by a flashing silhouette which appeared either synchronously or asynchronously with the timing of participants' heartbeats. Participants with high empathy had better performance in the VPT task during synchronous versus asynchronous cardio-visual stimulation. Moreover, empathy was positively associated with the difference in reaction times between the asynchronous and synchronous conditions (i.e. the synchrony effect). These results suggest that synchronous cardio-visual stimulation facilitates adopting the virtual body's perspective. Moreover, this effect was influenced by empathy (i.e. affective perspective-taking), thus suggesting that interoception and both emotional and non-emotional perspective-taking abilities are strongly linked.

3. Do interoception and perspective-taking share neural correlates?

In a meta-analysis of functional Magnetic Resonance Imaging (fMRI) studies of cardiac interoception, Schulz (2016) corroborated the involvement of an extended network including the posterior right and left insula, right claustrum, precentral and medial frontal gyri. Functional neuroimaging data also indicate that the anterior insula could represent a hub between brain networks involved in externally directed attention to stimuli in the environment and internally directed attention to one's body (Menon and Uddin, 2010). Thus, the anterior insula could not only be an area of body awareness, but it may mediate representations of the outside world and the body's internal state (Farb et al., 2013). Moreover, a right-hemispheric dominance of interoceptive processing has been reported, with the posterior insula presumably serving as the major gateway for cardiac interoception (Critchley et al., 2004). In particular, the posterior insula first supports the convergence of sensory and affective signals about the body that are then represented in the mid and anterior insula, which integrate interoceptive information with other contextual information (Critchley et al., 2004; Evrard and Craig, 2015). The anterior insula–cingulate network is also credited with the specific function of self-recognition (Devue et al. 2007) and it is crucial for integrating all subjective feelings related to the body, especially to its homeostatic conditions, into emotional experiences and conscious awareness of the environment and the self (Craig, 2009).

Regarding perspective-taking, studies on functional lateralization emphasize the importance of right temporo-parietal junction (TPJ) activation in ToM tasks (e.g. Saxe and Wexler, 2005). Furthermore, Wang et al. (2016) concluded that the right TPJ is a crucial network hub for transforming the embodied self into another's viewpoint. However, Jenkins and Mitchell (2010) reported bilateral activation of the TPJ and Santiesteban et al. (2015) reported a bilateral TPJ involvement in a MEG-TMS study. Thus, the functional lateralization of perspective-taking is not well defined. Moreover, the TPJ is a multimodal cortical region, receiving inputs from thalamic, limbic, somatosensory, visual and auditory areas (Bzdok et al., 2013). Transient changes in brain activity locked to heartbeats (Heartbeat-evoked potentials, HEPs) can also provide information about the mechanisms of self-other distinction. To test the hypothesis that an internal mechanism based on the neural monitoring of heartbeats could distinguish between self and another, Babo-Rebelo et al. (2019) showed that the amplitude of heartbeat-evoked responses, in the precuneus and bilateral mid/posterior cingulate regions, differed between imagining oneself and imagining a friend (Babo-Rebelo et al., 2019). Furthermore, neural responses to heartbeats in the posterior cingulate cortex were found to vary with changes in bodily self-consciousness induced by a body illusion (Park and Tallon-Baudry, 2014).

To date, few studies have simultaneously investigated a possible relationship between the neural correlates of interoception and perspective-taking. In Ernst et al. (2013), the participants had to judge if they could empathize with pictures showing facial expressions. Completing an interoceptive accuracy task before an empathy task significantly enhanced neural activity of the bilateral anterior insula, anterior and posterior midline regions such as the cingulate cortex and the precuneus, suggesting a close relationship between interoception and empathy. However, the empathy task used by the authors did not assess the ability to understand what another agent feels, but it required participants to judge if they could empathize with pictures of facial expressions. Recently, Stoica and Depue (2020a) found that resting-state fMRI spatial connectivity and temporal variability data were correlated with participants' self-reported empathy levels and interoceptive sensibility. Interestingly, improved processing between brain regions part of the 'salience network' (e.g. anterior insula, anterior midcingulate cortex) was related to an improved ability to take someone's perspective. Stoica and Depue (2020b) also investigated which dimension of empathy (i.e. cognitive or affective) shared resting-state functional connectivity with self-reported interoceptive sensibility (as defined by Garfinkel et al., 2015). They found that affective empathy and interoceptive sensibility were inversely related to increased resting-state functional connectivity within the right inferior frontal operculum, and also inversely related to blood oxygenation variability between brain regions of an interoceptive network. On the other hand, cognitive empathy and interoceptive sensibility shared only blood oxygenation variability. According to the authors their results suggest a relation between the ability to feel and understand another's emotional state and one's awareness of or sensibility towards internal body changes, which is reflected in the brain's intrinsic neuroarchitecture.

Studies of stroke patients can also help to better understand the possible overlap between the neural networks involved in interoception and perspective-taking. Impaired performance on a task of interoceptive accuracy correlated with damage to the left anterior cingulate cortex and fronto-insular cortex in patients with non-hemorrhagic fronto-insular stroke (Garcìa-Cordero et al., 2016). Similarly, lower scores on an interoceptive sensibility questionnaire were associated with insula lesions and its connections to the amygdala and putamen (Grossi et al., 2014). Lesions of the posterior insula, inferior and middle frontal gyri and of dorsal frontal white matter were also associated to impaired performance in cognitive (i.e. ToM) and visual perspective-taking tasks in patients with anosognosia for hemiplegia following right-hemisphere strokes (Besharati et al., 2016). A recent study by Terasawa et al. (2021) examined the change in interoception and emotion after insular resection and found that removal of the insula affects the recognition of emotions such as anger and happiness through interoceptive processing. However, no lesion study to date has investigated the possible interconnection between interoceptive and perspective-taking networks. Some evidence with healthy participants has shown that performing an interoceptive accuracy task increases cortical activity in areas associated with empathy (i.e. the anterior insula and the anterior cingulate cortex; Ernst et al., 2013) and the TPJ is functionally connected to the insular cortex (Araujo et al., 2015; Kucyi et al., 2012). Studies specifically examining brain damage and its ensuing effects on both interoception and perspective-taking are necessary in order to determine crucial networks involved in both processes.

4. Interoceptive and perspective-taking specificities in clinical populations

Interoceptive and perspective-taking abilities may be simultaneously impaired in many psychiatric, neurodevelopmental and neurodegenerative conditions, but no study to date has investigated the impact of these two constructs together in clinical samples.

For example, there is a growing interest in interoceptive alterations in anxiety disorders as well as in trait anxiety (for a review see Paulus and Stein, 2010). Most studies of trait anxiety reported an association between higher cardiac interoceptive accuracy and higher levels of anxiety assessed with self-reported questionnaires (Domschke et al., 2010). Moreover, interoceptive accuracy, assessed with the Heartbeat Discrimination Task (Whitehead et al., 1977), was positively associated with individual trait anxiety and other related traits such as negative affect, emotional intensity, introversion and behavioural inhibition (Lyyra and Parviainen, 2018).

A recent study (Palser et al., 2018a) found that the positive association between interoceptive sensibility and trait anxiety was partially mediated by alexithymia, a personality trait characterized by a subclinical difficulty in identifying and describing one’s own emotions (Nemiah et al., 1976). Therefore, those most at risk for clinically significant levels of trait anxiety have both significantly higher levels of interoceptive sensibility and alexithymia. It has been also hypothesized that trait anxiety may influence empathic responses with an inverse relationship between empathy and anxiety, as empathy requires sensitivity to another’s needs, while anxiety may be more associated with self-focused worry (Deardorff et al., 1977). In line with this, Negd et al. (2011) experimentally induced anxiety through an unpleasant electro-tactile stimulus and found that it was associated with decreased empathy-related feelings.

Similar results were found for level-1 visual perspective-taking, where experiencing anxiety impaired the spontaneous calculation of what another social agent can see (Todd and Simpson, 2016). Similarly, adolescents with higher social anxiety traits were less accurate at taking another’s perspective in the Director Task (Santiesteban et al., 2012) compared to those with low social anxiety traits (Pile et al., 2017). A strong grounding in one's natural spatial perspective was also found to be associated with lower interpersonal anxiety and higher social intelligence (Job et al., 2021). Together these findings suggest that trait anxiety could be associated with higher levels of interoception and an impaired ability to take another person's point of view. However, studies on anxiety disorders including generalized anxiety disorder, panic disorder, social anxiety, specific phobias and agoraphobia showed findings as heterogeneous as the differentiation of anxiety conditions (Domschke et al., 2010). For example, anxiety disorder patients who experienced panic attacks, did not show differences in interoceptive accuracy compared with healthy controls but exhibited more worries and catastrophic thoughts about somatic sensations (Yoris et al., 2015). No evidence for higher interoceptive accuracy was found in patients with pathological health anxiety either (Krautwurst et al., 2016).

Dysfunctional perspective-taking abilities in anxiety disorders were found for cognitive and affective perspective-taking (Hezel and McNally, 2014). Tone and Tully (2014) proposed a model in which an excessive empathic sensitivity, together with interpersonal guilt, contributed to increased risk of developing *internalizing* psychiatric disorders, such as anxiety. Moreover, a study on autobiographical memory showed that individuals with social anxiety are more likely to take an external observer perspective compared to control participants when recalling anxious situations (Wells and Papageorgiou, 1999), in line with the view that social phobics are prone to generating negative impressions of how they appear to others. Taking an external observer perspective in recalling past events is also associated with insular deactivation, a key area for interoceptive processing (Eich et al., 2009; Craig et al., 2002). However, no studies to date have investigated the possible alteration of visual perspective-taking in anxiety, so this deserves further investigation.

Changes in affective, cognitive and visual perspective-taking have been found in Autism Spectrum Disorders (ASD; Harmsen, 2019; Conson et al., 2015; Cardillo et al., 2020). ASD is a neurodevelopmental condition characterized by lifelong difficulties in social and emotional functioning with restricted and stereotyped patterns of behaviour, interests and activities (Frith and Frith, 2006). Recent studies suggested that interoceptive abilities are impaired in both autistic children and adults (Palser et al., 2018b; Garfinkel et al., 2016). Specifically, Garfinkel et al. (2016) found a dissociation between a reduced interoceptive accuracy (quantified using heartbeat counting and detection tasks) and an exaggerated interoceptive sensibility (subjective sensitivity to internal sensations measured with self-report questionnaires) in ASD participants. Interestingly, socio affective ASD features appeared to be related to interoceptive sensibility, while repetitive restricted behaviors to interoceptive accuracy in ASD children (Palser et al., 2020). Moreover, a lower interoceptive accuracy was related to autistic traits, lower empathy and alexithymia in a sample of autistic adults compared to those with typical development (Mul et al., 2018).

Disturbed interoceptive and perspective-taking abilities can also be found in some neurodegenerative disorders. For example, lower performance on interoceptive accuracy tasks was found in non-demented Parkinson's disease patients (Ricciardi et al., 2016; Santangelo et al., 2018). Parkinson's disease is characterized by a large spectrum of non-motor symptoms ranging from cognitive to behavioural disturbances (Chaudhuri et al., 2006). Alterations of affective and cognitive perspective-taking (i.e. empathy and ToM) are typically reported in

Parkinson's disease patients (for a meta-analysis see Coundouris et al., 2020), but no study to date investigated a possible dysfunction of visual perspective-taking.

Finally, interoceptive dysfunctions have been reported in anorexia nervosa and other body image disturbances (for a review see Badoud and Tsakiris, 2017). For example, Pollatos and Georgiou (2016) demonstrated a link between reduced IAcc and negative body image (i.e. higher body dissatisfaction) in anorexic patients; while Khalsa et al. (2015) suggested that in anorexia nervosa there is a dysregulated ability to adequately predict and cognitively represent and regulate what is happening in the physiological state of the body. Anorexia nervosa is also characterized by cognitive perspective-taking deficits that can contribute to poor insight, treatment resistance, and social impairment (Bora and Köse, 2016). However, many inconsistent findings remain, and no study to date investigates both deficits simultaneously.

Taken together, the circumstantial evidence to date suggests the need to directly investigate the common processes and neural mechanisms underlying the various dimensions of interoception and perspective-taking in non-clinical as well as in clinical populations.

5. Areas of investigation and future perspectives

The aim of this review was to clarify how the perception of signals originating from within the body (i.e. interoception) underlies different levels of perspective-taking and to provide new perspectives about the embodied nature of the two processes. A summary graphic of the possible interactions between dimensions of interoception and perspective-taking is shown in Figure 1.

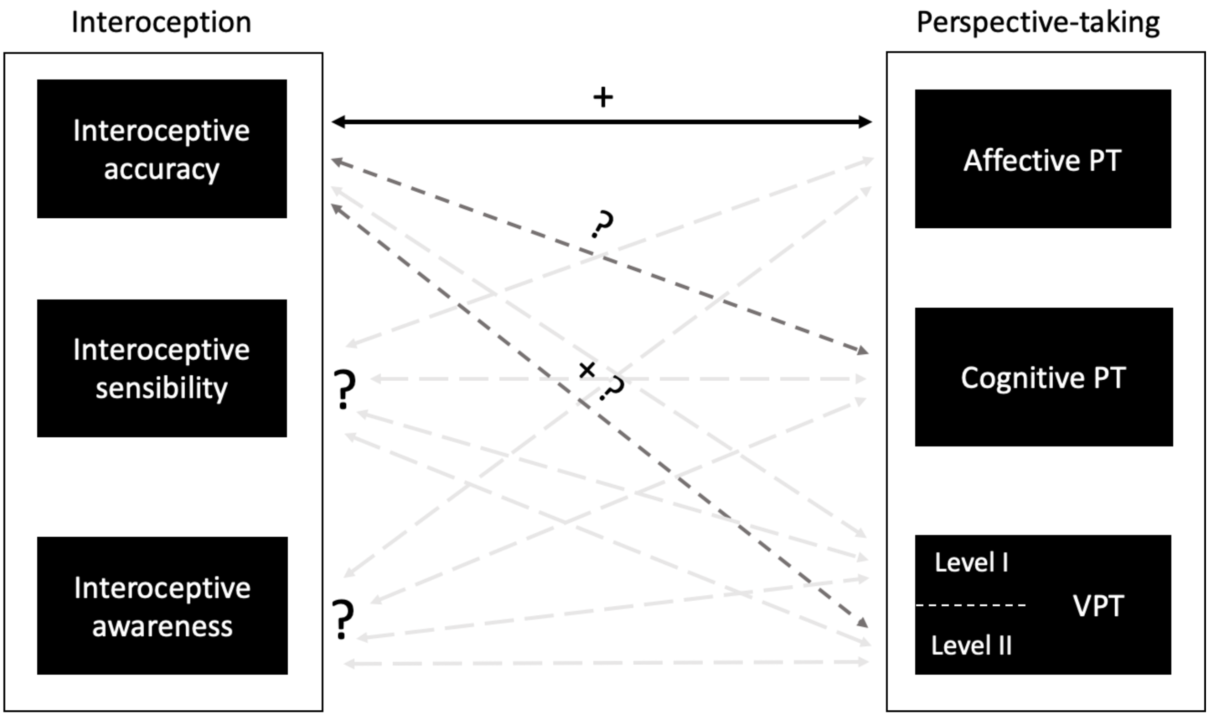

Figure 1. **Schema of the possible links between interoception and perspective-taking (PT) taken from existing literature.** The solid line indicates a strong relationship (Grymberg and Pollatos, 2015; Shah et al., 2017; Terasawa et al., 2015); the dashed lines indicate possible bonds that require further

clarification (for cognitive PT: Grymberg and Pollatos, 2015; von Mohr et al., 2019; For visual PT: Erle, 2019); the lighter dashed lines mean that no studies were conducted so far. The plus sign indicates a positive association while the lines with the question mark are for inconsistency between findings. Affective PT includes empathy, Cognitive PT includes Theory of Mind. VPT: visuo-spatial perspective-taking.

Interoceptive abilities appear to be closely connected to affective aspects of perspective-taking (e.g. empathy, Dirupo et al., 2020; Grynberg and Pollatos, 2015; Shah et al., 2017; Terasawa et al., 2015). The perception of internal signals appears to be associated with a greater ability to share and understand another person's emotional states (i.e. empathy).

In particular, greater interoceptive accuracy appears to be linked to empathy for specific emotional states, such as pain, sadness or disgust (Dirupo et al., 2020; Grynberg and Pollatos, 2015). Regarding cognitive perspective-taking (e.g. ToM), the ability to infer the mental states of others appears to be biased in individuals with higher interoceptive accuracy (von Mohr et al., 2019). This is in line with the hypothesis that individuals with higher interoceptive accuracy may be less able to update beliefs about another person’s emotional state given their stronger perceived boundaries between internal states and the external world (Palmer and Tsakiris, 2018).

An involvement of interoceptive processes in visual perspective-taking is largely unknown, with only one study (Erle, 2019) identifying a significant relationship. More efficient level-2 visual perspective-taking could be linked to higher interoceptive accuracy as both are embodied processes. Thus, the ability to perceive one’s own body from within (IAcc) might benefit from the ability to distinguish between one’s own and another’s visual perspective. Moreover, Heydrich et al. (2021) suggested that interoception and both emotional and non-emotional aspects of perspective-taking are strongly linked, suggesting that perspective-taking strongly depends on the activation of multisensory signals from one’s own body. The functional interactions between neural networks related to interoception (e.g. insular and cingulate cortex) and perspective-taking (e.g. bilateral TPJ) could also support the above-mentioned hypothesis.

Links between interoception and perspective-taking can also be found in studies with clinical populations. For example, high interoception was found to be positively associated with levels of arousal and anxiety, which could be characterized by an excessive and maladaptive empathic sensitivity (Tone and Tully, 2014). Moreover, dysfunctions in both constructs might be also found in psychiatric, neurological and developmental disorders (e.g. Anorexia nervosa, Parkinson’s disease, Autism Spectrum Disorders). This suggests that interoceptive training could have a positive impact on patients’ quality of life, where an improved ability to represent the interoceptive states of oneself and of others could result in more accurate mental state inferences and in a better understanding of another’s point of view (i.e. improved perspective-taking). However, direct evidence to support these assumptions is needed due to the lack of studies and poor consistency between them.

Several limitations can be highlighted. Firstly, most of the studies taken into account for this review used a unidimensional approach to assess interoceptive abilities. As suggested by Garfinkel et al. (2015), a differentiation between objective, subjective and metacognitive aspects of interoception is needed. In fact, different dimensions of interoception may be independent and could contribute differently to cognitive and affective processes (Garfinkel and Critchley, 2013). Currently, studies focusing on interoception and perspective-taking have exclusively used the heartbeat counting task as a measure of cardiac interoceptive accuracy (Schandry, 1981). Only two studies (Dirupo et al., 2020; Erle, 2019) assessed confidence ratings in heartbeat counting task performance (to measure interoceptive awareness), without significant results.

Moreover, the validity of the heartbeat counting task was recently questioned (Ring and Brener, 2018). Participants may perform the task by estimating, rather than counting, their felt heartbeats or just estimate the seconds elapsed in the time intervals (Desmedt et al., 2020). Therefore, the need to use adequate control measures (e.g. time estimation) and adapted instructions has been recently highlighted (Desmedt et al., 2020). However, a time estimation control task was administered in only three of the studies presented in this review (Dirupo et al., 2020; Shah et al., 2017; Terasawa et al., 2015). Future studies should seek to address these criticisms as well as to include measures of all aspects of cardiac interoception.

Future studies should investigate further the relationships between interoception and spatial perspective-taking (defined broadly as the ability to understand where something is located relative to someone else, Surtees et al., 2013), including but not limited to visuo-spatial perspective-taking. Indeed, studies to date have focused on the visual domain, but one should also explore other modalities, such as touch. One potential avenue is to use the Graphesthesia task (Arnold et al., 2016, 2017), which provides an ideal tool to investigate the embodied nature of spatial perspective-taking, in the tactile domain.

A further possible link with embodiment might be found by investigating the role of the vestibular system in the relationship between interoception and perspective-taking. Recent studies highlighted the role of the vestibular system in multisensory integration and embodiment (Lenggenhager and Lopez, 2015). At a functional level, both vestibular and interoceptive systems provide information about self-motion and gravitational forces exerted on the body and both appear to be involved in emotional processes and our sense of a bodily self (Nakul et al., 2020). In particular, one study suggested a possible role of the vestibular system in the integration between interoceptive and exteroceptive information (Ponzo et al., 2018). However, no difference has been found between patients with bilateral vestibulopathy and controls regarding interoceptive accuracy, confidence and body awareness (Nakul et al., 2020). Moreover, possible vestibular contributions to several sensorimotor bases of social cognition has been suggested, but they need further investigation (Deroualle and Lopez, 2014).

Finally, studies on non verbal self-referential processing, which includes somatic and inner bodily self-consciousness, suggested that the TPJ, together with the anterior insula and the extrastriate body area, plays a key role in embodiment and self-awareness (Salgues et al., 2021). Interestingly, right posterior TPJ was found to be involved during emotional contexts requiring perspective-taking abilities, whereas a more anterior region seems to be involved during third-person perspective-taking in neutral contexts (Frewen et al., 2020; Ruby and Decety, 2004). For these reasons, future studies should also investigate the links between interoception and perspective-taking taking into account self-referential mechanisms.

In conclusion, the findings reviewed here highlight that interoception may be more relevant for emotional aspects of perspective-taking, which influence the ability to empathise with others. Despite the relatively few studies, a view is emerging that interoceptive information may be important for those aspects of perspective-taking that require embodied processes. These possible interactions have several implications for future research and clinical applications, such as the possibility to implement tailored interventions (e.g. biofeedback paradigms, Sugawara et al., 2020) with a positive impact on patients' quality of life.

References

Ainley, V., Maister, L., Tsakiris, M., 2015. Heartfelt empathy? No association between interoceptive awareness, questionnaire measures of empathy, reading the mind in the eyes task or the director task. Front. Psychol. 6, 554. https://doi.org/10.3389/fpsyg.2015.00554

Araujo, H.F., Kaplan, J., Damasio, H., Damasio, A., 2015. Neural correlates of different self domains. Brain Behav. 5, e00409. https://doi.org/10.1002/brb3.409

Arnold, G., Spence, C., & Auvray, M., 2016. Taking someone else's spatial perspective: Natural stance or effortful decentring?. Cognition. *148*, 27–33. https://doi.org/10.1016/j.cognition.2015.12.006

Arnold, G., Spence, C., & Auvray, M., 2017. A unity of the self or a multiplicity of locations? How the graphesthesia task sheds light on the role of spatial perspectives in bodily self-consciousness. *Consciousness & Cognition*, *56*, 100-114. doi: 10.1016/j.concog.2017.06.012

Aspell, J. E., Heydrich, L., Marillier, G., Lavanchy, T., Herbelin, B., Blanke, O. 2013. Turning body and self inside out: visualized heartbeats alter bodily self-consciousness and tactile perception. Psychol. Sci. 24, 2445–2453. https://doi.org/10.1177/0956797613498395

Azzalini, D., Rebollo, I., Tallon-Baudry, C. 2019. Visceral Signals Shape Brain Dynamics and Cognition. Trends Cogn. Sci. 23, 488–509. https://doi.org/10.1016/j.tics.2019.03.007

Babo-Rebelo, M., Richter, C. G., Tallon-Baudry, C., 2016. Neural responses to heartbeats in the default network encode the self in spontaneous thoughts. J. Neurosci. 36,7829–7840. https://doi.org/10.1523/JNEUROSCI.0262-16.2016

Babo-Rebelo, M., Tallon-Baudry, C., 2018. Interoceptive signals, brain dynamics and subjectivity. In: Tsakiris, M., De Preester, H. (Eds.), The Interoceptive Mind. Oxford University Press, Oxford, 368.

Babo-Rebelo, M., Buot, A., Tallon-Baudry, C., 2019. Neural responses to heartbeats distinguish self from other during imagination. NeuroImage. 191,10–20. https://doi.org/10.1016/j.neuroimage.2019.02.012

Badoud, D., Tsakiris, M., 2017. From the body's viscera to the body's image: Is there a link between interoception and body image concerns? Neurosci. Biobehav. Rev. 77, 237–246. https://doi.org/10.1016/j.neubiorev.2017.03.017

Bechara, A., Damasio, A. R., 2005. The somatic marker hypothesis: a neural theory of economic decision. Games and Economic Behaviour 52, 336–372. https://doi.org/10.1016/j.geb.2004.06.010

Besharati, S., Forkel, S. J., Kopelman, M., Solms, M., Jenkinson, P. M., Fotopoulou, A., 2016. Mentalizing the body: spatial and social cognition in anosognosia for hemiplegia, Brain. 139, 971–985. https://doi.org/10.1093/brain/awv390

Blanke, O., Slater, M., Serino, A., 2015. Behavioral, neural, and computational principles of bodily self-consciousness. Neuron. 88, 145–166.https://doi.org/10.1016/j.neuron.2015.09.029

Bora, E., Köse, S., 2016. Meta-analysis of theory of mind in anorexia nervosa and bulimia nervosa: A specific İmpairment of cognitive perspective taking in anorexia nervosa? Int. J. Eat. Disord. 49, 739–740. https://doi.org/10.1002/eat.22572

Botvinick, M., Cohen, J. D., 1998. Rubber hands ‘feel’ touch that eyes see. Nature. 391, 756. https://doi.org/10.1038/35784.

Bzdok, D., Langner, R., Schilbach, L., Jakobs, O., Roski, C., Caspers, S., Laird, A. R., Fox, P. T., Zilles, K., Eickhoff, S. B., 2013. Characterization of the temporo-parietal junction by combining data-driven parcellation, complementary connectivity analyses, and functional decoding. NeuroImage. 81, 381–392. https://doi.org/10.1016/j.neuroimage.2013.05.046

Cardillo, R., Erbì, C., Mammarella, I. C., 2020. Spatial Perspective-Taking in Children With Autism Spectrum Disorders: The Predictive Role of Visuospatial and Motor Abilities. Front. Hum. Neurosci. 14, 208. https://doi.org/10.3389/fnhum.2020.0020

Ceunen, E., Vlaeyen, J. W., Van Diest, I., 2016. On the Origin of Interoception. Front. Psychol. 7, 743. https://doi.org/10.3389/fpsyg.2016.00743

Chaudhuri, K. R., Healy, D. G., Schapira, A. H., 2006. Non-motor symptoms of Parkinson's disease: diagnosis and management. Lancet Neurol. 65, 235–245. https://doi.org/10.1016/S1474-4422(06)70373-8

Chen, W. G., Schloesser, D., Arensdorf, A. M., Simmons, J. M., Cui, C., Valentino, R., Gnadt, J. W., Nielsen, L., Hillaire-Clarke, C. S., Spruance, V., Horowitz, T. S., Vallejo, Y. F., Langevin, H. M., 2021. The Emerging Science of Interoception: Sensing, Integrating, Interpreting, and Regulating Signals within the Self. Trends. Neurosci. 44, 3–16. https://doi.org/10.1016/j.tins.2020.10.007

Coll, M., Hobson, H., Murphy, J., 2021. Systematic review and meta-analysis of the relationship between the heartbeat-evoked potential and interoception. Neurosci. Biobehav. Rev. S0149-7634, 30688–6. https://doi.org/10.1016/j.neubiorev.2020.12.012

Conson, M., Mazzarella, E., Esposito, D., Grossi, D., Marino, N., Massagli, A., Frolli, A., 2015. “Put Myself Into Your Place”: Embodied Simulation and Perspective Taking in Autism Spectrum Disorders. Autism Res. 8, 454–466. https://doi.org/10.1002/aur.1460

Coundouris, S. P., Adams, A. G., Henry, J. D., 2020. Empathy and theory of mind in Parkinson's disease: A meta-analysis. Neurosci. Biobehav. Rev. 109, 92–102. https://doi.org/10.1016/j.neubiorev.2019.12.030

Craig, A. D., 2009. How do you feel--now? The anterior insula and human awareness. Nat. Rev. Neurosci. 10, 59–70. https://doi.org/10.1038/nrn2555

Craig, A. D., 2010. The sentient self. Brain Struct. Funct. 214, 563–577. http://dx.doi.org/10.1007/s00429-010-0248-y

Critchley, H. D., Wiens, S., Rotshtein, P., Ohman, A., Dolan, R. J., 2004. Neural systems supporting interoceptive awareness. Nat. Neurosci. 7, 189–195. https://doi.org/10.1038/nn1176

Critchley, H. D., Garfinkel, S. N., 2017. Interoception and emotion, Curr. Opin. Psychol. 17, 7–14. https://doi.org/10.1016/j.copsyc.2017.04.020.

Deardorff, P. A., Kendall, P. C., Finch, A. J., Jr., Sitarz, A. M., 1977. Empathy, locus of control and anxiety in college students. Psychol. Rep. 40, 1236–1238. https://doi.org/10.2466/pr0.1977.40.3c.1236.

Deroualle, D., Lopez, C., 2014. Toward a vestibular contribution to social cognition. Front. Integr. Neurosci. 8, 16. https://doi.org/10.3389/fnint.2014.00016

Desmedt, O., Corneille, O., Luminet, O., Murphy, J., Bird, G., Maurage, P., 2020. Contribution of Time Estimation and Knowledge to Heartbeat Counting Task Performance under Original and Adapted Instructions. Biol. Psychol. 154, 107904. https://doi.org/10.1016/j.biopsycho.2020.107904

Devue, C., Collette, F., Balteau, E., Degueldre, C., Luxen, A., Maquet, P., Brédart, S., 2007. Here I am: the cortical correlates of visual self-recognition. Brain Res. 1143, 169–182. https://doi.org/10.1016/j.brainres.2007.01.055

Dirupo, G., Corradi-Dell'Acqua, C., Kashef, M., Debbané, M., Badoud, D., 2020. The role of interoception in understanding others' affect. Dissociation between superficial and detailed appraisal of facial expressions. Cortex. 130, 16–31. https://doi.org/10.1016/j.cortex.2020.05.010

Domschke, K., Stevens, S., Pfleiderer, B., Gerlach, A. L., 2010. Interoceptive sensitivity in anxiety and anxiety disorders: an overview and integration of neurobiological findings. Clin. Psychol. Rev. 30, 1–11. https://doi.org/10.1016/j.cpr.2009.08.008

Dziobek, I., Fleck, S., Kalbe, E., Rogers, K., Hassenstab, J., Brand, M., Kessler, J., Woike, J. K., Wolf, O. T., Convit, A., 2006. Introducing MASC: a movie for the assessment of social cognition. J. Autism Dev. Disord. 36, 623–636. https://doi.org/10.1007/s10803-006-0107-0

Eddy, C. M., 2016. The junction between self and other? Temporo-parietal dysfunction in neuropsychiatry. Neuropsychologia. 89, 465–477. https://doi.org/10.1016/j.neuropsychologia.2016.07.030

Eich, E., Nelson, A. L., Leghari, M. A., Handy, T. C., 2009. Neural systems mediating field and observer memories. Neuropsychologia. 47(11), 2239–2251. https://doi.org/10.1016/j.neuropsychologia.2009.

Erle, T. M., 2019. Level-2 visuo-spatial perspective-taking and interoception – More evidence for the embodiment of perspective-taking. PLoS One. 14, e0219005. https://doi.org/10.1371/journal.pone.0219005

Ernst, J., Northoff, G., Heinz, B., Seifritz E., Grimm S., 2013. Interoceptive Awareness Enhances Neural Activity During Empathy. Hum. Brain Mapp. 34, 1615–1624. https://doi.org/10.1002/hbm.22014

Evrard, H. C., Craig, A. D., 2015. "Insular cortex," in Brain Mapping: An Encyclopedic Reference, ed. A.W. Toga (Cambridge, MA: Academic Press), 387–393.

Farb, N. A., Segal, Z. V., Anderson, A. K., 2013. Attentional modulation of primary interoceptive and exteroceptive cortices. Cereb. Cortex. 23, 114–126. https://doi.org/10.1093/cercor/bhr385

Ferrari, P. F., Coudé, G., 2018. Mirror neurons, embodied emotions, and empathy. In K. Z. Meyza E. Knapska (Eds.), Neuronal correlates of empathy: From rodent to human (p. 67–77). Elsevier Academic Press. https://doi.org/10.1016/B978-0-12-805397-3.00006-1

Flavell, J. H., Everett, B. A., Croft, K., Flavell, E. R., 1981. Young children's knowledge about visual perception: Further evidence for the Level 1–Level 2 distinction. Dev. Psychol. 17, 99–103. https://doi.org/10.1037/0012-1649.17.1.99

Frewen, P., Schroeter, M. L., Riva, G., Cipresso, P., Fairfield, B., Padulo, C., Kemp, A. H., Palaniyappan, L., Owolabi, M., Kusi-Mensah, K., Polyakova, M., Fehertoi, N., D'Andrea, W., Lowe, L., Northoff, G., 2020. Neuroimaging the consciousness of self: Review, and conceptual-methodological framework. Neurosci. Biobehav. Rev. 112, 164–212. https://doi.org/10.1016/j.neubiorev.2020.01.023

Friston, K., 2005. A theory of cortical responses. Philos. Trans. R. Soc. Lond. B Biol. Sci. 360, 815–836. https://doi.org/10.1098/rstb.2005.1622

Frith, C. D., Frith, U., 2006. The neural basis of mentalizing. Neuron. 50, 531–534. https://doi.org/10.1016/j.neuron.2006.05.001

García-Cordero, I., Sedeño, L., de la Fuente, L., Slachevsky, A., Forno, G., Klein, F., Lillo, P., Ferrari, J., Rodriguez, C., Bustin, J., Torralva, T., Baez, S., Yoris, A., Esteves, S., Melloni, M., Salamone, P., Huepe, D., Manes, F., García, A. M., & Ibañez, A., 2016. Feeling, learning from and being aware of inner states: interoceptive dimensions in neurodegeneration and stroke. Philos. Trans. R. Soc. Lond. B Biol. Sci. 371, 2016006. https://doi.org/10.1098/rstb.2016.0006

Garfinkel, S. N., Critchley, H. D., 2013. Interoception, emotion and brain: new insights link internal physiology to social behaviour. Commentary on: "Anterior insular cortex mediates bodily sensibility and social anxiety" by Terasawa et al. (2012). Soc. Cogn. Affect. Neurosci. 8, 231–234. https://doi.org/10.1093/scan/nss140

Garfinkel, S. N., Minati, L., Gray, M. A., Seth, A. K., Dolan, R. J., Critchley, H. D., 2014. Fear from the heart: sensitivity to fear stimuli depends on individual heartbeats. J. Neurosci. 34, 6573–6582. https://doi.org/10.1523/JNEUROSCI.3507-13.2014

Garfinkel, S. N., Seth, A. K., Barrett, A. B., Suzuki, K., Critchley, H. D., 2015. Knowing your own heart: Distinguishing interoceptive accuracy from interoceptive awareness. Biol. Psychol. 104, 65–74. https://doi.org/10.1016/j.biopsycho.2014.11.004

Garfinkel, S. N., Tiley, C., O'Keeffe, S., Harrison, N. A., Seth, A. K., Critchley, H. D., 2016. Discrepancies between dimensions of interoception in autism: Implications for emotion and anxiety. Biol. Psychol. 114, 117–126. https://doi.org/10.1016/j.biopsycho.2015.12.003

Grossi, D., Di Vita, A., Palermo, L., Sabatini, U., Trojano, L., Guariglia, C., 2014. The brain network for self-feeling: a symptom-lesion mapping study. Neuropsychologia. 63, 92–98. https://doi.org/10.1016/j.neuropsychologia.2014.08.004

Grynberg, D., Pollatos, O., 2015. Perceiving one's body shapes empathy. Physiol. Behav. 140, 54–60. https://doi.org/10.1016/j.physbeh.2014.12.026

Hamilton, A. F., Kessler, K., Creem-Regehr, S. H., 2014. Perspective taking: Building a neurocognitive framework for integrating the "social" and the "spatial." Front. Hum. Neurosci. 8, 403. https://doi.org/10.3389/fnhum.2014.00403

Happe, F., Cook, J. L., Bird, G., 2017. The structure of social cognition: In(ter)dependence of sociocognitive processes. Annu. Rev. Psychol. 68, 243–267. https://doi.org/10.1146/annurev-psych-010416-044046

Harmsen, I. E., 2019. Empathy in Autism Spectrum Disorder. J. Autism Dev. Disord. 49, 3939–3955. https://doi.org/10.1007/s10803-019-04087-w

Healey, M. L., Grossman, M., 2018. Cognitive and Affective Perspective-Taking: Evidence for Shared and Dissociable Anatomical Substrates. Front. Neurol. 9, 491. https://doi.org/10.3389/fneur.2018.00491

Herbert, B., Pollatos, O., 2012. The body in the mind. On the relationship between interoception and embodiment. Top. Cogn. Sci. 4, 692–704. https://doi.org/10.1111/j.1756-8765.2012.01189.x

Herman, A.M., Palmer, C., Azevedo, R.T., Tsakiris M., 2020. Neural divergence and convergence for interoceptive and somatosensory attention and detection. Cortex. 135, 186–206. https://doi.org/10.1016/j.cortex.2020.11.019

Heydrich, L., Walker, F., Blättler, L., Herbelin, B., Blanke, O., Aspell, J. E., 2021. Interoception and Empathy Impact Perspective Taking. Front. Psychol. 11, 599429. https://doi.org/10.3389/fpsyg.2020.599429

Hezel, D. M., McNally, R. J., 2014. Theory of mind impairments in social anxiety disorder. Behav. Ther. 45, 530–540. https://doi.org/10.1016/j.beth.2014.02.010

Horváth, Á., Ferentzi, E., Bogdány, T., Szolcsányi, T., Witthöft, M., Köteles, F., 2020. Proprioception but not cardiac interoception is related to the rubber hand illusion. Cortex.132, 361–373. https://doi.org/10.1016/j.cortex.2020.08.026

Hynes, C. A., Baird, A. A., Grafton, S. T., 2006. Differential role of the orbital frontal lobe in emotional versus cognitive perspective-taking. Neuropsychologia. 44, 374–383. https://doi.org/10.1016/j.neuropsychologia.2005.06.011

Imafuku, M., Fukushima, H., Nakamura, Y., Myowa, M., Koike, S. 2020. Interoception is associated with the impact of eye contact on spontaneous facial mimicry. Sci. Rep. 10, 19866. https://doi.org/10.1038/s41598-020-76393-8

Ionta, S., Heydrich, L., Lenggenhager, B., Mouthon, M., Fornari, E., Chapuis, D., Gassert, R., Blanke, O., 2011. Multisensory mechanisms in temporo-parietal cortex support self-location and first-person perspective. Neuron. 70, 363–374. https://doi.org/10.1016/j.neuron.2011.03.009

Jenkins, A. C., Mitchell, J. P., 2010. Mentalizing under uncertainty: Dissociated neural responses to ambiguous and unambiguous mental state inferences. Cereb. Cortex. 20, 404–410. https://doi.org/10.1093/cercor/bhp109

Job, X., Kirsch, L. P, Inard, S., Arnold, G., Auvray, M., 2021. Spatial perspective taking is related to social intelligence and attachment style. Pers. Individ. Differ. 168, 109726. https://doi.org/10.1016/j.paid.2019.109726

Kessler, K., Rutherford, H., 2010. The Two Forms of Visuo-Spatial Perspective Taking are Differently Embodied and Subserve Different Spatial Prepositions. Front. Psychol. 1, 213. https://doi.org/10.3389/fphys.2010.00213

Kessler, K., Wang, H., 2012. Spatial perspective taking is an embodied process, but not for everyone in the same way: Differences predicted by sex and social skills score. Spatial Cognit. Comput. 12, 133–158. https://doi.org/10.1080/13875868.2011.634533

Khalsa, S. S., Craske, M. G., Li, W., Vangala, S., Strober, M., Feusner, J. D., 2015. Altered interoceptive awareness in anorexia nervosa: Effects of meal anticipation, consumption and bodily arousal. Int. J. Eat. Disord. 48, 889–897. https://doi.org/10.1002/eat.22387

Khalsa, S. S., Adolphs, R., Cameron, O. G., Critchley, H. D., Davenport, P. W., Feinstein, J. S., Feusner et al., 2018. Interoception and Mental Health: A Roadmap. Biol. Psychiatry Cogn. Neurosci. Neuroimaging. 3, 501–513. https://doi.org/10.1016/j.bpsc.2017.12.004

Krautwurst, S., Gerlach, A. L., Witthöft, M., 2016. Interoception in pathological health anxiety. J. Abnorm. Psychol. 125, 1179–1184. https://doi.org/10.1037/abn0000210

Kucyi A., Moayedi M., Weissman-Fogel I., Hodaie M., Davis, K. D., 2012, Hemispheric asymmetry in white matter connectivity of the temporoparietal junction with the insula and prefrontal cortex. PLoS One. 7, e35589. https://doi.org/10.1371/journal.pone.0035589

Lenggenhager, B., Lopez, C., 2015. Vestibular contributions to the sense of body, self, and others. Frankfurt am Main: MIND Group. London.

Lyyra, P., Parviainen, T., 2018. Behavioral Inhibition Underlies the Link Between Interoceptive Sensitivity and Anxiety-Related Temperamental Traits. Front. Psychol. 9, 1026. https://doi.org/10.3389/fpsyg.2018.01026

Menon, V., Uddin, L. Q., 2010. Saliency, switching, attention and control: a network model of insula function. Brain Struct. Funct. 214, 655–667. https://doi.org/10.1007/s00429-010-0262-0

Michelon, P., Zacks, J. M., 2006. Two kinds of visual perspective taking. Percept. Psychophys. 68(2), 327–337. https://doi.org/10.3758/bf03193680

Mul, C. L., Stagg, S. D., Herbelin, B., Aspell, J. E., 2018. The Feeling of Me Feeling for You: Interoception, Alexithymia and Empathy in Autism. J. Autism. Dev. Disord. 48, 2953–2967. https://doi.org/10.1007/s10803-018-3564-3

Nakul, E., Dabard, C., Toupet, M., Hautefort, C., van Nechel, C., Lenggenhager, B., Lopez, C., 2020. Interoception and embodiment in patients with bilateral vestibulopathy. J. Neurol. 267, 109–117. https://doi.org/10.1007/s00415-020-10221-x

Negd, M., Mallan, K. M., Lipp, O.V., 2011. The role of anxiety and perspective-taking strategy on affective empathic responses. Behav. Res. Ther. 49, 852–857. https://doi.org/10.1016/j.brat.2011.09.008

Nemiah, J. C., Freyberger, H., Sifneos, P. E., 1976. Alexithymia: a view of the psychosomatic process. In: Hill OW, editor. Modern Trends in Psychosomatic Medicine. 3rd vol. Butterworths, London.

Ondobaka, S., Kilner, J., Friston, K., 2017. The role of interoceptive inference in theory of mind. Brain Cogn. 112, 64–68. https://doi.org/10.1016/j.bandc.2015.08.002

Palmer, C. E., Tsakiris, M., 2018. Going at the heart of social cognition: is there a role for interoception in self-other distinction? Curr. Opin. Psychol. 24, 21–26. https://doi.org/10.1016/j.copsyc.2018.04.008

Palser, E. R., Palmer, C. E., Galvez-Pol, A., Hannah, R., Fotopoulou, A., Kilner, J. M., 2018a. Alexithymia mediates the relationship between interoceptive sensibility and anxiety. PLoS One 13, e0203212. https://doi.org/10.1371/journal.pone.0203212

Palser, E. R., Fotopoulou, A., Pellicano, E., Kilner, J. M., 2018b. The link between interoceptive processing and anxiety in children diagnosed with autism spectrum disorder:

Extending adult findings into a developmental sample. Biol. Psychol. 136, 13–21. https://doi.org/10.1016/j.biopsycho.2018.05.003

Palser, E. R., Fotopoulou, A., Pellicano, E., Kilner, J. M., 2020. Dissociation in How Core Autism Features Relate to Interoceptive Dimensions: Evidence from Cardiac Awareness in Children. J. Autism Dev. Disord. 50, 572–582. https://doi.org/s10803-019-04279-4

Papageorgiou, C., Wells, A., 1999. Process and meta-cognitive dimensions of depressive and anxious thoughts and relationships with emotional intensity. Clin. Psychol. Psychother. 6, 156-162. https://doi.org/10.1002/(SICI)1099-0879(199905)6:2<156::AID-CPP196>3.0.CO;2-A

Park, H. D., Tallon-Baudry, C., 2014. The neural subjective frame: from bodily signals to perceptual consciousness. Philos. Trans. R. Soc. Lond. B Biol. Sci. 369, 20130208. http://dx.doi.org/10.1098/rstb.2013.0208

Paulus, M. P., Stein, M. B., 2010. Interoception in anxiety and depression. Brain Struct. Funct. 214, 451–463. https://doi.org/10.1007/s00429-010-0258-9

Parsons, L. M., 1987. Imagined spatial transformation of one's body. J. Exp. Psychol. Gen. 116, 172–191. https://doi.org/10.1037/0096-3445.116.2.172

Petzschner, F. H., Garfinkel, S. N., Paulus, M. P., Koch, C., Khalsa, S. S., 2021. Computational Models of Interoception and Body Regulation. Trends Neurosci. 44, 63–76. https://doi.org/10.1016/j.tins.2020.09.012

Pile, V., Haller, S., Hiu, C. F., Lau, J., 2017. Young people with higher social anxiety are less likely to adopt the perspective of another: Data from the Director task. J. Behav. Ther. Exp. Psychiatry. 55, 41–48. https://doi.org/10.1016/j.jbtep.2016.11.002

Pollatos, O., Herbert, B. M., Matthias, E., Schandry, R., 2007. Heart rate response after emotional picture presentation is modulated by interoceptive awareness, Int. J. Psychophysiol. 63, 117 – 124, https://doi.org/10.1016/j.ijpsycho.2006.09.003.

Pollatos, O., Georgiou, E., 2016. Normal interoceptive accuracy in women with bulimia nervosa. Psychiatry Res. 240, 328–332. https://doi.org/10.1016/j.psychres.2016.04.072

Ponzo, S., Kirsch, L. P., Fotopoulou, A., Jenkinson, P. M., 2018. Balancing body ownership: Visual capture of proprioception and affectivity during vestibular stimulation. Neuropsychologia.117, 311 – 321. https://doi.org/10.1016/j.neuropsychologia.2018.06.020

Proulx, M. J., Todorov, O. S., Taylor Aiken, A., de Sousa, A. A., 2016. Where am I? Who am I? The Relation Between Spatial Cognition, Social Cognition and Individual Differences in the Built Environment. Front. Psychol. 7, 64. https://doi.org/10.3389/fpsyg.2016.00064

Ricciardi, L., Ferrazzano, G., Demartini, B., Morgante, F., Erro, R., Ganos, C., Bhatia, K. P., Berardelli, A., Edwards, M., 2016. Know thyself: Exploring interoceptive sensitivity in Parkinson's disease. J. Neurol. Sci. 364, 110–115. https://doi.org/10.1016/j.jns.2016.03.019

Rice, H. J., Rubin, D. C., 2009. I can see it both ways: First- and third-person visual perspectives at retrieval. Conscious. Cogn. 18(4), 877–890. https://doi.org/10.1016/j.concog.2009.07.004

Ring, C., Brener, J., 2018. Heartbeat counting is unrelated to heartbeat detection: A comparison of methods to quantify interoception. Psychophysiology. 55, e13084. https://doi.org/10.1111/psyp.13084

Robinson, J. A., Swanson, K. L., 1993. Field and observer modes of remembering. *Memory. 1*(3), 169–184. https://doi.org/10.1080/09658219308258230

Ruby, P., Decety, J., 2004. How would you feel versus how do you think she would feel? A neuroimaging study of perspective-taking with social emotions. J. Cogn. Neurosci. 16(6), 988–999. https://doi.org/10.1162/0898929041502661

Salgues, S., Plancher, G., Jacquot, L., Naveteur, J., Fanuel, L., Gálvez-García, G., Michael, G. A., 2021. To the self and beyond: Arousal and functional connectivity of the temporo-parietal junction contributes to spontaneous sensations perception. Behav. Brain Res. 396, 112880. https://doi.org/10.1016/j.bbr.2020.112880

Santangelo, G., Vitale, C., Baiano, C., D'Iorio, A., Longo, K., Barone, P., Amboni, M., Conson, M., 2018. Interoceptive processing deficit: A behavioral marker for subtyping Parkinson's disease. Parkinsonism Relat. Disord. 53, 64–69. https://doi.org/10.1016/j.parkreldis.2018.05.001

Santiesteban, I., White, S., Cook, J., Gilbert, S. J., Heyes, C., Bird, G., 2012. Training social cognition: From imitation to theory of mind. Cognition. 122, 228–235. https://doi.org/10.1016/j.cogni tion.2011.11.004.

Santiesteban, I., Banissy, M. J., Catmur, C., Bird, G., 2015. Functional lateralization of temporoparietal junction - imitation inhibition, visual perspective-taking and theory of mind. Eur. J. Neurosci. 42, 2527–2533. https://doi.org/10.1111/ejn.13036

Saxe, R., Wexler, A., 2005. Making sense of another mind: The role of the right temporo-parietal junction. Neuropsychologia. 43,1391–1399.https://doi.org/10.1016/j.neuropsychologia.2005.02.013

Schandry R., 1981. Heart beat perception and emotional experience. Psychophysiology. 18, 483–488. https://doi.org/10.1111/j.1469-8986.1981.tb02486.x

Schulz S. M., 2016. Neural correlates of heart-focused interoception: a functional magnetic resonance imaging meta-analysis. Philos. Trans. R. Soc. Lond. B Biol. Sci. 371, 20160018. https://doi.org/10.1098/rstb.2016.0018

Shah, P., Catmur, C., Bird, G., 2017. From heart to mind: Linking interoception, emotion, and theory of mind. Cortex. 93, 220–223. https://doi.org/10.1016/j.cortex.2017.02.010

Shaw, D. J., Czekóová, K., Pennington, C. R., Qureshi, A. W., Špiláková, B., Salazar, M., Brázdil, M., Urbánek, T., 2020. You ≠ me: individual differences in the structure of social cognition. Psychol. Res. 84, 1139–1156. https://doi.org/10.1007/s00426-018-1107-3

Stietz, J., Jauk, E., Krach, S., Kanske, P., 2019. Dissociating Empathy From Perspective-Taking: Evidence From Intra- and Inter-Individual Differences Research. Front. Psychiatry. 10, 126. https://doi.org/10.3389/fpsyt.2019.00126

Sperduti, M., Delaveau, P., Fossati, P., Nadel, J., 2011. Different brain structures related to self- and external-agency attribution: a brief review and meta-analysis. Brain Struct. Funct. 216, 151–157. https://doi.org/10.1007/s00429-010-0298-1

Steinbeis, N., 2016. The role of self-other distinction in understanding others' mental and emotional states: neurocognitive mechanisms in children and adults. Phil. Trans. R. Soc. Lond. B Biol. Sci. 371, 20150074. https://doi.org/10.1098/rstb.2015.0074

Stoica, T., Depue, B. E., 2020a. Interoceptive Awareness and Affective Empathy Share Intrinsic Spatial Connectivity and Temporal Variability. (pre-print). https://doi.org/10.1101/2020.04.30.070490.

Stoica, T., Depue, B. 2020b. Shared Characteristics of Intrinsic Connectivity Networks Underlying Interoceptive Awareness and Empathy. Front. Hum. Neurosci. 14, 571070. https://doi.org/10.3389/fnhum.2020.571070

Sugawara, A., Terasawa, Y., Katsunuma, R., Sekiguchi, A., 2020. Effects of interoceptive training on decision making, anxiety, and somatic symptoms. Biopsychosoc. Med. 17, 14–7. https://doi.org/10.1186/s13030-020-00179-7

Surtees, A., Apperly, I., Samson, D., 2013. Similarities and differences in visual and spatial perspective-taking processes. Cognition, 129, 426–438. https://doi.org/10.1016/j.cognition.2013.06.008

Suzuki, K., Garfinkel, S. N., Critchley, H. D., Seth, A. K., 2013. Multisensory integration across exteroceptive and interoceptive domains modulates self-experience in the rubber-hand illusion. Neuropsychologia. 51, 2909–2917. https://doi.org/10.1016/j. neuropsychologia.2013.08.014.

Terasawa, Y., Moriguchi, Y., Tochizawa, S., Umeda, S., 2014. Interoceptive senstivity predcits sensitivity to the emotions of others. Cogn. Emot. 28, 37–41. https://doi.org/10.1080/02699931.2014.888988

Terasawa, Y., Motomura, K., Natsume, A., Iijima, K., Chalise, L., Sugiura, J., Yamamoto, H., Koyama, K., Wakabayashi, T., Umeda, S., 2021. Effects of insular resection on interactions between cardiac interoception and emotion recognition. Cortex. https://doi.org/10.1016/j.cortex.2021.01.011

Todd, A. R., Simpson, A. J., 2016. Anxiety impairs spontaneous perspective calculation: Evidence from a level-1 visual perspective-taking task. Cognition. 156, 88–94. https://doi.org/10.1016/j. cognition.2016.08.004

Todd, A. R., Cameron, C. D., Simpson, A. J., 2017. Dissociating processes underlying level-1 visual perspective taking in adults. Cognition. 159, 97–101. https://doi.org/10.1016/j.cognition.2016.11.010

Tone, E. B., Tully, E. C., 2014. Empathy as a "risky strength": a multilevel examination of empathy and risk for internalizing disorders. Dev. Psychopathol. 26,1547–1565. https://doi.org/10.1017/S0954579414001199

Tsakiris, M., 2017. The multisensory basis of the self: from body to identity to others. Q. J. Exp. Psychol. 70, 597–609. https://doi.org/10.1080/17470218.2016.1181768.

Tsakiris, M., Tajadura-Jiménez, A., Costantini, M., 2011. Just a heartbeat away from one’s body: interoceptive sensitivity predicts malleability of body-representations. Proc. Biol. Sci. 278, 2470–2476. https://doi.org/10.1098/rspb.2010.2547

van Dyck Z., Vögele C., Blechert J., Lutz A. P. C., Schulz A., Herbert B. M., 2016. The Water Load Test as a measure of gastric interoception: Development of a two-stage protocol and application to a healthy female population. PLoS One. 11, e0163574 https://doi.org/10.1371/journal.pone.0163574

von Mohr, M., Finotti, G., Villani, V., Tsakiris, M., 2020. Taking the pulse of social cognition: cardiac afferent activity and interoceptive accuracy modulate emotional egocentricity bias. (pre-print)

Wang, H., Callaghan, E., Gooding-Williams, G., McAllister, C., Kessler, K., 2016. Rhythm makes the world go round: An MEG-TMS study on the role of right TPJ theta oscillations in embodied perspective taking. Cortex. 75, 68–81. https://doi.org/10.1016/j.cortex.2015.11.011

Whitehead, W. E., Drescher, V. M., Heiman, P., Blackwell, B., 1977. Relation of heart rate control to heartbeat perception. Biofeedback Self Regul. 2, 371–392.

Yoris, A., Esteves, S., Couto, B., Melloni, M., Kichic, R., Cetkovich, M., Favaloro, R., Moser, J., Manes, F., Ibanez, A., Sedeño, L., 2015. The roles of interoceptive sensitivity and metacognitive interoception in panic. Behav Brain Funct. 11, 14. https://doi.org/10.1186/s12993-015-0058-8

Zaki, J., Ochsner, K., 2012. The neuroscience of empathy: progress, pitfalls and promise. Nat. Neurosci. 15, 675–680. https://doi.org/10.1038/nn.3085