**Going at the heart of social cognition: is there a role for interoception in self-other distinction?**

Clare E Palmer1\* & Manos Tsakiris 1,2

1 Lab of Action & Body, Royal Holloway University of London, Egham TW20 0EX, UK

2 The Warburg Institute, School of Advanced Study, University of London, Woburn Square, WC1H 0AB, UK

\*Corresponding author: Clare E Palmer (clare.palmer@rhul.ac.uk)

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**Highlights**

* Interoception is the processing of the physiological state of the body.
* Integrating interoceptive and exteroceptive inputs modulates bodily self-awareness.
* Distinguishing between self and others is an essential aspect of social cognition.
* Interoceptive awareness may play a fundamental role in self-other distinction.
* Interoception may be important for social cognition.

**Abstract**

Interoception describes the processing and awareness of bodily signals arising from visceral organs, essential for the organism’s homeostatic needs. Beyond homeostasis, the integration of exteroceptive and interoceptive signals is required for the coherence of bodily self-awareness. Here we suggest that interoception also plays a critical role in social cognition. Relating to others as individuals who are distinct from one’s self requires the simultaneous yet distinct co-representation of self and others. We propose that interoceptive awareness appears to stabilise the mental representation of one’s self as distinct from others. A more nuanced understanding of the role of interoception in the representation of others in relation to ourselves is vital to determine its importance in social cognition.

**Introduction**

Interoception describes the afferent processing of internal bodily signals that arise from visceral organs, used to determine the physiological condition of the body and its homeostatic needs [1,2]. This definition has been broadened recently to include pleasant touch, pain and skin temperature, which are transmitted to the brain via the same spinothalamic tract and activate a similar cortical network [1,3]. There has been a long standing interest in the role of interoception in emotion processing motivated by the hypothesis that the physiological condition of the body acts as the basic substrate for feeling states and emotions [4,5]. Indeed, interoceptive signals have also been shown to modulate emotion processing; for example fearful faces are rated as more intense when presented at a particular point in the cardiac cycle [6]. In addition, functional neuroimaging studies have highlighted a substantial overlap between the neural substrates of emotion and interoception (for a review see [7]).

Beyond non-conscious interoceptive signalling, we are also capable of becoming aware of interoceptive states and changes thereof. Recent research has focused on individual differences in people’s ability to access interoceptive information and highlighted how this predicts individual emotionality for similar levels of autonomic reactivity [8–11]. However, the definition of this interoceptive awareness (IAw) is very diverse within the literature and includes multiple dissociable facets. A recent review by Khalsa et al (2017) elegantly summarises these different dimensions[12]. In this paper we define IAw as representing an individual’s ability to accurately and consciously perceive changes in their interoceptive state. This is dissociable from interoceptive metacognitive awareness as described by Garfinkel et al [13], which describes how good we think we are at detecting interoceptive signals; but, is comparable to previously described measures of interoceptive accuracy (IAcc), which is defined by behavioural performance on a task requiring explicit detection of interoceptive signals (e.g. the most commonly used heartbeat counting task). We therefore use the terms IAcc and IAw interchangeably throughout this paper.

**Beyond emotion: the embodied foundations of self-awareness**

The ubiquitous role of the insula cortex in a wide range of interoceptive, affective and social tasks [3,14,15] led to the hypothesis that the insula plays an essential functional role in body-ownership and self-awareness. Somatoparaphrenia (a loss of experienced ownership over ones limbs) is associated with right posterior insula function [16] and body ownership in the rubber hand illusion (RHI) has been associated with right mid-posterior insula cortex activity ([17], see also [18]). Interoceptive information is thought to be integrated with exteroceptive signals along the insula cortex from posterior to anterior generating a representation of self that may be integral for a wide range of socio-cognitive processes.

Recent work has sought to understand not simply *where* in the brain but *how* exteroceptive and interoceptive signals are integrated to produce a unified experience of the bodily self by determining the relationship between IAcc and body-ownership. The RHI and the Enfacement Illusion are used to modulate body-ownership in response to exteroceptive multisensory stimulation and reveal the malleability of an individual’s representation of self; this is driven by the brain’s integration of multisensory exteroceptive signals to update the mental [19] and physiological [20] representation of one’s body [21]. Tsakiris et al (2011) showed that a stronger RHI, measured behaviourally (i.e. increased proprioceptive drift) and homeostatically (i.e. a drop in skin temperature), was induced in those with lower compared to higher IAcc [22] (see also [23]). Similar negative correlations between the effects of multisensory stimulation and trait-like levels of IAcc were observed in the Enfacement Illusion: participants with lower IAcc experienced a stronger sense of identification with another person’s face [24]. These findings suggest that those with higher IAcc have a stronger sense of self, which is grounded in their interoceptive states, making them less susceptible to body illusions. If exteroceptive influences highlight the malleability of body-awareness, awareness of interoceptive signals seem to serve the stability of the self, reflecting a psychological consequence of the biologically necessary function of homeostasis.

Beyond these correlational observations, other studies used cardiac signals as inducers of changes in body-ownership. The substitution of exteroceptive visuo-tactile stimulation with cardio-visual stimulation (i.e., a combination of interoceptive and exteroceptive signals) led to the study of the potentially causal role of interoceptive signals for body-awareness. Suzuki et al. (2013) showed that looking at a virtual hand that pulsated in synchrony with one’s heartbeat led to changes in body-ownership similar to those reported in the classic RHI (see also [25] and [26]). Here enhancing the saliency of interoceptive signals modulated perceived body-ownership and self-identification [27,28], especially for people with higher levels of IAcc [26,29].

**Beyond selfhood: interoception for alteroception**

The question of how bodily self-awareness emerges in the brain is intrinsically linked to the question of how we relate to others. It is through intersubjective interactions in early life that the self emerges [30–32]. This ever-present social relatedness has a dual nature: on one hand the self is built and represented as distinct from others, but on the other hand the boundaries between self and other are not fixed. Predictive accounts of mentalising suggest that we generate hypotheses about other’s mental and bodily states based on our own archive of behaviours, which are used to predict other’s behaviour. Recently this has been extended to include interoceptive states [33,34]. At the ontogenetic level carer-infant bodily interactions enable infants to develop a predictive model of their own interoception [35]. Using this we can then integrate exteroceptive input and learned contextual knowledge to infer another person’s interoceptive state [33]. A fundamental question in social neuroscience is how it becomes possible to distinguish between self and other at the very time that we are trying to relate to each other? For example, how can I share another individual’s pain without forgetting it is not *my* pain?

Emotional contagion, mimicry, body resonance, perspective-taking, theory of mind (ToM) and egocentricity biases have been used to operationalize different facets of empathy. Although its exact meaning is still debated, empathy is considered one of the hallmarks of social cognition [36,37]. A critical but unresolved issue is this question of “self-other” overlap [38]. “Self-other” overlap is thought to arise when an observer engages in an isomorphic state (e.g. same emotion) to the person observed. However, what is or should be the extent of this overlap? Interoception may play a key role in enabling us to navigate the different degrees of social relatedness, by allowing us to correctly attribute the origin of bodily and mental states to oneself or to others.

Previous theories of self-other distinction focus on the central role of the sensorimotor system in generating a sense of agency and body-ownership through the integration of proprioceptive and exteroceptive inputs [39–41]. Our self-awareness comes from the understanding of how we interact with the environment from a first person perspective. Indeed, the default *modus operandi* of the social brain seems to be to represent one’s own self (e.g. one’s own perspective, emotion, beliefs), therefore switching from self to other, to achieve a partial co-representation of self and other, is an effortful process that to some extent requires the attenuation of self-representations [42]. Indeed, inhibitory control is deemed a necessary component of mentalising [41] and inhibition of imitative behaviour is used as a measure of online control of self-other representations[43,44]. We extend these ideas to incorporate interoception.

We propose that interoceptive processing acts to stabilise the model of our self, such that we can readily attribute emotional and mental states to the self or to others without blurring the distinction between “self” and “other”. In line with recent theoretical accounts of self-processing, we characterise the underlying mechanism for this within the Predictive Coding framework [21,27,45]. Probabilistic representations of the self are generated by the integration of top-down “predictions” about the bodily state and bottom-up “prediction errors” (PEs) across interoceptive and exteroceptive modalities. The importance or salience of these inputs and relative contribution to the resultant percept is determined by their “precision-weighting” or inverse variance. We hypothesise that stability in our model of the self comes from the level of precision attributed to interoceptive relative to exteroceptive PEs, which is optimised by attention [34,46]. When integrating a precise interoceptive PE with a relatively less precise exteroceptive PE, the interoceptive input will dominate the resultant percept and optimise higher level beliefs about the self. Precise interoception throughout development will therefore accommodate the experience of the self as stable and continuous.

The importance of this can be demonstrated with the RHI [47]. The experience of the illusion depends on how PEs across modalities are explained away. Reducing the precision of interoceptive PEs will increase the relative precision of exteroceptive PEs and update higher-order beliefs about the ownership of the rubber hand [26,48]. We hypothesise that individuals with lower IAw will be more readily able to attenuate relatively less precise interoceptive PE signals, therefore high level beliefs about the self are easily modified to explain away more precise exteroceptive PEs. Alternatively, those with higher IAw will have more precise interoceptive PEs, which are not as easily attenuated relative to conflicting exteroceptive PEs. In line with this theory, those with high IAcc are less susceptible to the RHI [22] and the Enfacement Illusion [24].

Based on these ideas we can generate alternative hypotheses regarding the impact of IAw on social-cognitive processes with a different magnitude of self-other overlap. Emotional contagion, the most basic level of empathy, is the process by which our own interoceptive state automatically mimics that of the observed person, and is associated with activity across the network of neural areas activated when the person experiences the emotion themselves [49]. We hypothesise that those with lower IAw may be more readily able to attenuate less precise interoceptive PEs in order to update higher order beliefs about another person’s emotional state. At a higher level of empathy, an individual may be required to represent another’s emotional state that may be incongruent with their own emotional state. Consider a couple arguing: the spouse is angry, her blood pressure and heart rate increase as she quarrels with her husband who suddenly starts crying eliciting conflicting interoceptive and emotional reactions in the wife. The co-presence of her own-generated interoceptive states and those generated by her husband’s reaction are now conflicting but co-represented both cognitively and physiologically. In this context, individual differences in the relative precision-weighting of interoceptive and expteroceptive states may be important for maintaining a self-other distinction, therefore higher IAw may be advantageous (see Figure 1). Understanding others may therefore require at least a ‘good enough’ representation of one’s own (interoceptive) state because the key element in representing other’s states is how ***their*** states affect ***us***.

The proposed interaction between levels of IAw and “self-other” overlap, which is integral to all social interactions, can be empirically tested by adopting a hierarchical approach: 1) emotion contagion where the self-other overlap is almost complete, and demands on self-other distinction are minimal; 2) empathy for pain where there is partial self-other sharing; and 3) a complete distinction between self and other where individuals must relate to each other in an empathetic way whilst maintaining a dissociable emotional and interoceptive state, which can be measured using an egocentricity bias task [50]. Individual differences in trait interoception measures can then be compared to social cognition measures at each level of self-other overlap to determine their inter-relationship.

**Evidence and future directions for the role of interoception in social cognition**

Empathy is a multidimensional construct that necessitates a more fine-grained, nuanced approach to understanding the influence of interoception on empathy. While the links between interoceptive processing and the nuanced examples of empathy remain largely unexplored, there is some supporting evidence for the hypothesis we put forward. Individuals with Autism Spectrum Disorder (ASD), characterised by deficits in social cognition, have impaired interoceptive processing [51,52]. However, their interoceptive deficits appear to be mainly linked to the co-morbid presence of alexithymia (a difficulty identifying emotions) rather than mentalising ability [53]. In neurotypical participants, IAcc has been shown to correlate with performance on emotional items in the Movie for the Assessment of Social Cognition (MASC), but not for non-emotional items [54], and with empathy for pain [55]. However, no association was found between IAcc and cognitive or self-report measures of empathy [56] but IAcc did predict altruistic behaviour [57]. Interoception may be more relevant for those emotional aspects of social cognition that influence our ability to empathise with others.

The field should also seek to go beyond correlational designs and trait measures of interoception. The validity of the current tasks used to measure trait IAcc and IAw has been questioned [58,59], therefore novel tasks to measure state and trait interoception are required. Presenting stimuli at specific points in the cardiac cycle allows control over the autonomic context with which stimuli are perceived. At systole, during a heartbeat, arterial baroreceptors signal to the brain, but at diastole, between heartbeats, this pathway is silent. Baroreceptor firing during systole amplifies threat processing to fearful faces [6], decreases memory for words [60] and increases the expression of threat-related racial stereotyping [61]. Arousal can also be modulated using masked stimuli to induce general increases in autonomic activity [62] and the effect of this on socio-cognitive processing can be explored. Modulations in interoceptive modalities outside of the cardiovascular system are harder to control, however other modalities, such as the gastrointestinal system [63] and respiratory system [64,65] are now being studied to determine the specificity and contribution of different interoceptive inputs to social cognition. Importantly, direct and controlled manipulations of interoceptive signalling, such as the use of CO2 inhalation, beta blockers or water load, will enable us to probe the causal impact of interoception on tasks requiring self-other processing. Moreover, the ontogenetic origins of interoception [66] must also be explored. Using these methods we can better elucidate the causal role of interoception and awareness thereof on the processing of self-related and socially relevant stimuli.

**Conclusion**

Interoception plays an important role in the mental representation of the self [35]. Those with lower interoceptive awareness are more susceptible to bodily illusions due to a greater malleability of their self-representation. This has important consequences for social cognition and in particular for our ability to empathise. One needs an accurate sense of her own interoceptive body in order to be able to correctly attribute mental and bodily states to oneself or another person and understand the causes of those states, whilst maintaining the distinction between self and other. Empirical evidence using paradigms that manipulate the interoceptive state are necessary to determine the nuanced relationship between interoceptive processing and the self-other overlap, which is integral to understanding the role of interoception in social cognition.

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**This paper provides a useful introduction to interoception and summarises the current methodological issues facing interoception research. The authors also highlight how interoception may be dysfunctional in particular psychopathologies which is of particular relevance for the framework put forward here as many of these disorders also include symptoms of abnormal self-other processing.**

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**This theoretical perspective describes how differences in IAcc can be explained by differences in the optimisation of precision between and within modalities. It is this idea which is extended in the current paper to explain self-other processing.**

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**This study found that IAcc only predicted performance on emotional items in a Theory of Mind task not non-emotional items. This suggests that good IAcc is only advantageous in social contexts when emotion understanding is required.**



**Figure 1** illustrates a nuanced perspective of how interoceptive awareness (IAw) may impact on social cognitive performance depending on the levels of self-other overlap in the task. For tasks with a low level of self-other distinction, for example emotional contagion, it may be advantageous to have lower level of IAw, and we predict that such individuals will display greater emotional contagion. In contrast, when a social task requires a high level of self-other distinction, individuals with higher IAw may be better able to understand the emotional state of others because these individuals have a more stable representation of their own bodily self, which prevents the blurring of self and other resulting in improved performance.