Biofeedback differentially modulates interoceptive awareness

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1 Introduction

Human beings are conscious not only of the world around them but also of themselves: their bodies, their emotions, and their thoughts and desires; they are, that is, self-conscious. Self-consciousness can be understood as an awareness of oneself, a unified non-conceptual representation of being at a specific place and time (Lenggenhager, Tadi, Metzinger, & Blanke, 2007). One of the ongoing mysteries in cognitive science is how the experience of selfhood is constituted.

Definitions about the nature of the self has dominated philosophical and psychological research, from Descartes to Dennet, from James to Freud. Providing a conceptual and explanatory framework for “the self” is surely an endeavor that will be met with skepticism. However, there is a key, intuitive understanding of self, as this unique, personal boundary that separates us from others(Shoemaker, 1968). Starting from this point, and assuming an embodied cognition approach, self has been conceptualized emerging from two distinct parts: the minimal self and the narrative self (Gallagher, 2000). The narrative self is the emerging image of one’s self, after integrating past experiences The minimal self is the consciousness of oneself emerging as an immediate subject of experience, unextended in time and is heavily tied with the idea of sense of agency, the idea of possessing my body and being the effector of all its actions. This space-time, minimal – narrative dipole gives us a framework for probing and examining one’s sense of self, its emergence, its development and possible pathologies associated with it (e.g. schizophrenia).

There is good reason to believe that brain-body interactions support this profound subjective experience, and not the brain alone. This ”embodied stance” holds that cognition emerges not just as a result of biochemical brain processes, but by a holistic account of bodily functions, where the peripheral body and central nervous system contribute to emergence of mental phenomena (Newen, 2018; Varela, Thompson, Rosch, & Kabat-Zinn, 2016).

Bodily Self-Consciousness , the feeling of body ownership, is considered one of the main experimental windows into the sense of self in cognitive neuroscience (Blanke, Slater, & Serino, 2015; Blefari et al., 2017; Tsakiris, 2017) and the complex brain-body interactions that underpin it (Porciello, Bufalari, Minio-Paluello, Di Pace, & Aglioti, 2018; Suzuki, Garfinkel, Critchley, & Seth, 2013). Recently, studies on Exteroception, the external, sensory input of an organism (Bufalari, Porciello, Sperduti, & Minio-Paluello, 2015; Porciello et al., 2018) have drawn attention to the role of sensory inputs in creating self/other distinction illusions. Indeed, one of the most known experimental paradigms, the Rubber Hand Illusion (Tsakiris, Carpenter, James, & Fotopoulou, 2010), has shown the synchronous multisensory integration underpins the emergence of body ownership. Neurological findings have shown that electrical interference or damage to these multisensory integration areas leads to illusory bodily percepts, such as the feeling that an artificial body is one's own (Blanke, Landis, Spinelli, & Seeck, 2004; Blanke & Mohr, 2005).

More recents accounts of the "self " have attempted to ground self in the multimodal integration of exteroceptive signals with interoceptive afferents about bodily states(Apps & Tsakiris, 2014; Craig, 2009; Suzuki et al., 2013). These theories suggest that the emergence and awareness of self follows a dynamic central representations of physiological state, driven by interoceptive signals from the peripheral body, with the mental representation of self ultimately grounded in the representation of the body.

However, experimental evidence for interoceptive illusions, cause by the misattribution of bodily signals akin to exteroceptive ones (e.g Rubber Hand Illusion) are scarce in the literature (Iodice, Porciello, Bufalari, Barca, & Pezzulo, 2019). We here aimed at probing aspects of selfhood by manipulating the attribution of interoceptive signals, such as one's own heartbeats. The goal of this study is to strengthen the previous experimental links in the literature about interoception on the bidirectional links between bodily states and self-consciousness, and provide evidence for misattribution of bodily signals to the self , due to biofeedback manipulation.

1.1 Interoception

Human bodies are in a constant process of maintaining Homeostasis, a state of optimal internal functioning, characterized by a steady internal environment (Craig, 2002, 2003). This unconscious regulation is supported by a complex network of brain-body interactions, aiming at reaching homeostatic equilibrium (body temperature, glucose levels, blood pressure (Cannon, 1932). Interoception constitutes the encoding and representation of the visceral afferent signals from the peripheral body (heart and gastrointestinal tract, primarily, but also respiratory and genitourinary systems, and sometimes including other systems such as the endocrine, as well as chemical, osmotic, and volume changes) that contribute to the physiological optimization (Critchley & Harrison, 2013). Interoception has been conceptualized also as the conscious perception of the incoming signal from the peripheral body necessary for homeostatic balance (Barrett, Bliss-Moreau, Quigley, & Aronson, 2004; Craig, 2003, 2013). Whether interoception constitutes a conscious or unconscious process is still debated.Interoception should be dissociated from exteroception, namely the perception of stimuli external to an organism, as well as from proprioception, namely the awareness of the position of the body and its movement (Sherrington, 1906).

Earlier accounts of interoception attempted to understand brain-body interactions by examining the brain structures implicated in the processing of afferent visceral projections to the central nervous system. Projections from visceral receptors have been identified in the brainstem, the posterolateral thalamus, the hypothalamus, the insular cortex, the anterior cingulate cortex and somatosensory regions and orbitofrontal regions (Cameron, 2001; Craig, 2002, 2003; Critchley, Wiens, Rotshtein, Öhman, & Dolan, 2004) .

However, extensive feedback loops and divergent projections between these regions make identifying hierarchical organization and the examination of multimodal convergence and integration of these visceral signals difficult (Cameron, 2001).

Peripheral theories of emotions have been one of the first to establish a connection between bodily signals and cognitive-affective states, proposing a basis for emotional states in the central representation and perception of changes in bodily physiology (Barrett et al., 2004; Cannon, 1987; Critchley & Garfinkel, 2017). The James-Lange theory maintains that visceral feedback about bodily states contributes to our perception of emotional states. Therefore, the role of bodily states is not to be viewed as a response to perceived emotions, but as effectors that modulate the expression of emotion, with external stimuli eliciting distinct interoceptive responses that contribute to unique emotional states. Although this idea has been extensively discussed (Cannon, 1987), theoretical approaches have emerged, contextualizing emotion within interoceptive feedback. Damasio's (2010) somatic marker hypothesis suggested that distinct patterns of somatovisceral afferents weigh in to the perception of unique affective states. In other words, somatic markers are bodily sensations which are associated with emotions, for example rapid heartbeat is associated with anxiety or disgust. Recent studies have provided evidence for this "embodied" view of emotion, with subjective feelings of the body modulating emotion expression (Barrett et al., 2004; Garfinkel et al., 2014; Pollatos, Gramann, & Schandry, 2007)) and emotion regulation (Füstös, Gramann, Herbert, & Pollatos, 2013).

The study of interception aims at pinpointing the multivariate interactions between autonomic and cerebral functions. A wide array of such somatovisceral systems have been proposed, contributing the interoceptive afferent pathways, as windows to these interactions, namely the respiratory, the urogenital, the gastrointestinal and the cardiovascular (Vignemont & Alsmith, 2017) and vestibular (Ponzo, Kirsch, Fotopoulou, & Jenkinson, 2018). However, cardiovascular signals have been examined most prominently (Critchley & Harrison, 2013; Tsakiris, 2017) as foci between the visceral body and the brain, because they are informationally reach, bidirectional in their effects, quantifiable, measureable and can be subjected to non-invasive perturbation easily(Ring & Brener, 2018; Ring, Brener, Knapp, & Mailloux, 2015; Vignemont & Alsmith, 2017) . Therefore, research of interception has moved gradually towards investigating the role of heart signals in brain-body communication.

Two main experimental protocols have emerged, focusing on the measurement of a person's interoceptive sensitivity (i.e., a person's ability to identify his interoceptive signals) based on heartbeat tasks: a) heartbeat counting tasks (Dale & Anderson, 1978; Schandry, 1981) and b) heartbeat detection tasks(BRENER, LIU, & RING, 1993). Heartbeat counting tasks require from the subject to count their own heartbeat during distinct, small time periods. In this context, interoceptive sensitivity is quantified by a perception score based on the difference between actual and perceived heartbeats. Individual differences in this task are attributed on the real-time processing of heartbeat sensations and not on individual beliefs about one's own heartbeat. Recent research has questioned this principle, showing that there is not a clear dissociation between heartbeat perception and heartbeat beliefs during the heartbeat counting task (Ring & Brener, 1996; Ring et al., 2015), questioning the usefulness of such tasks in probing interoceptive processes (Ring & Brener, 2018). A proposed alternative to the heartbeat counting has been heartbeat detection tasks. During a detection task, participants have to assess whether external stimuli (usually visual or auditory) are presented synchronously or asynchronously to their own heartbeat. Brener Ring (2016) supported that heartbeat detection provides more accurate estimates of the temporal aspects of heartbeat tracking and precision measurements of a person's interoceptive sensitivity(Brener & Ring, 2016), as it is not affected by a person's subjective beliefs about their heartbeat(Brener & Ring, 2016).

Interoceptive awareness – that is often operationalized as Interoceptive Accuracy (IAcc) – is the ability to perceive internal bodily signals such as cardiac activity, hunger, and distension of bladder and other visceral organs (Craig, 2002; Herbert & Pollatos, 2012). We define IAw - Interoceptive Awareness- as representing an individual's sensitivity toward one's visceral signals, a trait-like ability to accurately and consciously perceive interoceptive afferent signals from the peripheral body. Recently, literature has examined IAcc, evaluating participants as 'good or poor heartbeat perceivers, based on measurements from the heartbeat tasks described above. At this point, it is important to make the distinction between different dimensions of interoceptive measurements: (1) interoceptive accuracy (performance on objective behavioural tests of heartbeat detection), (2) interoceptive sensibility (self-evaluated assessment of subjective interoception, measured using interviews/questionnaires) and (3) interoceptive awareness (metacognitive awareness of interoceptive accuracy, e.g. confidence-accuracy correspondence)(Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015). Interoceptive awareness represents only accuracy in behavioural tasks, excluding a person's beliefs about his interoceptive abilities.

1.2 Heartbeat Perception

Electrophysiological studies have suggested that the perception of visceroceptive signals lead to cortical electrical potentials, strengthening the link between the peripheral body and the cortex. Heartbeat Evoked Potentials (HEP) refer to electrical potentials evoked during the processing of signals from the cardiovascular system(Jones, 1994; Schandry, 1981; Schandry, Sparrer, & Weitkunat, 1986). Time averaging EEG recordings at the R peak gives rise to frontal – prefrontal – central negative shift, roughly 200-300 ms after the R peak (Montoya, Schandry, & Müller, 1993; Pollatos & Schandry, 2004) , providing a valid reflection of brain processes related to cardiac perception. Pollatos Schandry (2004) found that HEP amplitude is correlated with performance in heartbeat counting tasks, with participants categorized as good heartbeat perceivers showing significantly more negative shifts than bad heartbeat perceivers. The interaction between accuracy in a heartbeat counting task and attention showed significant modulation of the HEP (Montoya et al., 1993). Although good heartbeat perceivers showed higher HEP amplitude, in the attentive condition, poor perceivers showed an enhancement in their HEP amplitude not found in the other group. This was attributed to a novelty effect, with good heartbeat perceivers habitually paying attention to their heartbeat signals, not modulated by external effects. The role of feedback information in heartbeat perception was recently examined by Canales-Johnson et al. (2015). The authors provided participants with auditory feedback of their heartbeat during a task, where they had to tap synchronously to their heartbeat. Participants who received auditory feedback through a stethoscope showed increased interoceptive sensitivity, by tapping more synchronously to their heartbeats(Canales-Johnson et al., 2015). In addition, HEP amplitude was increased in the group that showed increased performance due to feedback. These results confirm previous research, confirming the modulation of heartbeat perception due to external feedback (Schaefer, Egloff, Gerlach, & Witthöft, 2014; Schandry & Weitkunat, 1990).

1.3 Predictive Coding

Predictive Coding (PC) has emerged as a unifying theory of cortical processes aiming at providing an explanatory framework for brain functions, such as perception, action, and interoception (Friston, 2009; Seth, 2013). The predictive coding account is based on the free-energy principle, according to which any organism that has to adapt to its environment must minimize its free energy and resist a natural tendency toward disorder (Friston, 2010). Advancements in Bayesian predictive coding theory(Friston, 2009, 2010; Friston, Kilner, & Harrison, 2006) have emphasized the role of different neuronal hierarchies in minimizing “free energy”. The Free Energy Principle states that biological systems will always move towards minimizing “free energy” or surprise / prediction error from the environment (See Figure 1). The common underlying feature of these systems is the procedural generation of predictions about the environment based on an organism’s past learning history and contrasting these predictions with external stimuli feedback. Different levels of this hierarchy aim to explain that specific level and all below it. The mismatch between top-down predictions generated by the brain and sensory signals from the periphery constitute a “prediction error”. Therefore, the free energy principle considers the brain as an Active Inference machine that creates models about its environment. In this context, action aims at verifying the organism’s explanatory models by sampling sensory data that conform to its model and perception aims to verify or update these models.

Adopting this predictive model in interoception (Pezzulo, Rigoli, & Friston, 2015; Seth, 2013; Seth, Suzuki, & Critchley, 2012), interoceptive theories have suggested that the brain implements a process of interoceptive inference for physiological sensing and adaptive regulation. The brain generates models that attempt to explain incoming signals on different levels. If a certain level of this hierarchy of predictions cannot explain the signal, the prediction mismatch is forwarded to a higher level of the hierarchical models for explanation. Just as in perception hierarchical models generate causes of sensory inputs, different interoceptive hierarchical models predict how interoceptive signals are generated, suggesting the brain actively makes inferences about the source of bodily signals. The goal of the active inference process is to minimize the prediction errors between top-down predictions and bottom-up autonomic responses to sensory inputs and internally generated signals about the physiological state of the body(Ondobaka, Kilner, & Friston, 2017; Seth & Friston, 2016). Suppression of error prediction in interoceptive inferences is achieved either by modifying the organism’s internal model about its bodily states or by autonomically mediating reflexes that bring the organism

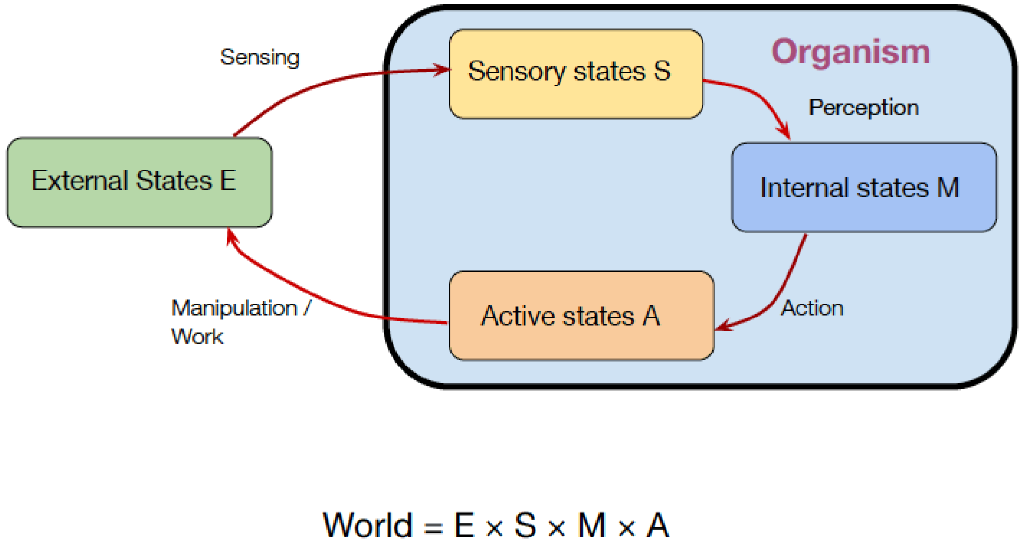


Figure 1: Free Energy Principle.The free energy principle states that the world is hidden from us(hidden states). We can only perceive the complex results (sensations) of hidden environmental interactions and make a priori assumptions(generative models - internal states) about the sources of our sensations. The models are continuously updated via sensation(selective sampling of sensory information) or action(movement towards environments that produce the expected sensory inputs) with the goal of minimizing the discrepancy between our internal models and our sensory inputs(free energy).For example, a fish has a high probability of being in water (low levels of surprise) and low probability of being in land (high levels of surprise). This high surprise state (i.e. being in land) is highly unlikely, both mathematically and emotionally, and the organism (in our example, the fish) moves towards minimizing the surprising state, or “free energy”. Adapted from Friston,2009

closer to homeostatic equilibrium(Ondobaka et al., 2017; Owens, Friston, Low, Mathias, & Critchley, 2018). Therefore, a response is elicited only if the interoceptive prediction error is not attenuated by somatovisceral afferent inputs.

1.4 Self-Awareness Coding Framework

Recent accounts of Self-Awareness and bodily self-consciousness have conceptualized the role of interoception (Craig, 2009) Damasio, 2010) within the greater framework of a predictive coding account of self-awareness(Aspell, Lenggenhager, & Blanke, 2009; Seth, 2013)(See figure2. Original accounts of bodily self-consciousness have considered the role of multisensory integration of exteroceptive signals in the emergence of selfhood, specifically due to the experimental plasticity of the sense of self due to multisensory illusions(Porciello et al., 2018; Tsakiris, 2017). Multisensory information has provided evidence for the update of the representation of self, due to changes about self-perception induced by multisensory illusions. The most common example of misperception of bodily parts due to multisensory information is the Rubber Hand Illusion, where synchronous multisensory, visuotactile stimulation of a rubber hand and a person's occluded hand, leads to the misattribution of the rubber hand as one's own(Botvinick & Cohen, 1998) . Interoceptive information has been suggested to compliment this model, by providing a framework for the emergence of a stable representation of self. In this framework, the multimodal integration of exteroceptive, proprioceptive and interoceptive information is essential to the emergence of a discrete and accurate representation of bodily self-consciousness(Seth et al., 2012). While studies generally agree that interoceptive information plays a role in bodily self-representation, questions remain as to whether awareness of interoceptive signals makes people more or less prone to body-related illusions. Tsakiris, Tajadura-Jimenez, Costantini (2011) showed that low scores in interoceptive heartbeat detection tasks predict higher levels of body-ownership malleability(Tsakiris, Tajadura-Jiménez, & Costantini, 2011). "Bad" heartbeat detectors were more susceptible to the Rubber Hand Illusion, as measured by physiological (proprioceptive drift) factors and self-reports. A series of experiments (Ainley, Maister, Brokfeld, Farmer, & Tsakiris, 2013; Ainley, Tajadura-Jiménez, Fotopoulou, & Tsakiris, 2012) examined the role of

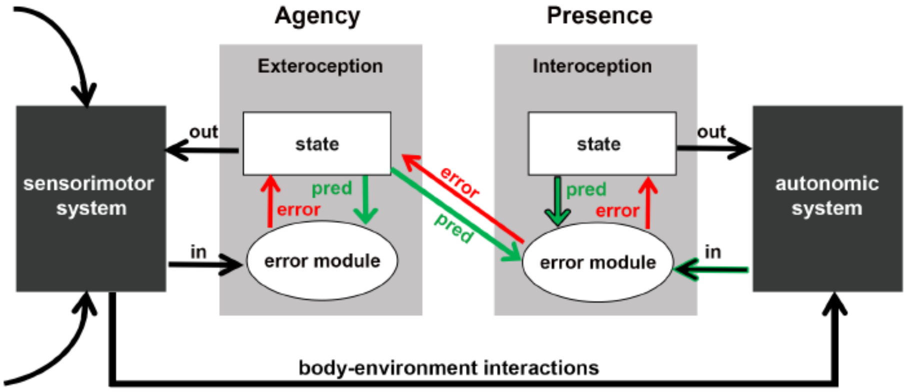


Figure 2: The interoceptive model of bodily self-consciousness, adapted from Seth, et al., 2012.The concept of self emerges as a product of the multimodel integration of various unimodal predictive hierarchies processing interoceptive and exteroceptive information. Interoceptive and exteroceptive selfhood hierarchies aim to minimize the discepancy between external and internal incoming signals relative to our selfhood. Minimal free energy is associated with selfhood, and high predictive errors are attributed to external sources to self.

attention to the bodily self in interoceptive sensitivity. By providing feedback about the self via a mirror(Ainley et al., 2012) and a picture of the participants(Ainley et al., 2013), researchers found that they could increase the performance in heartbeat perception tasks in "bad" detectors, hinting towards the effects of increased attention to self in interoceptive awareness. The above studies provide preliminary evidence for the bidirectional relationship of bodily self-consciousness and interoception.

Since the model predicts that interoception and exteroception constitute different levels of selfhood representation, a question arises whether there is interaction between these two hierarchies. In an alternative to the RHI, presentation of a virtual hand in augmented reality in synchrony to feedback about a participant's hand increases the illusory misattribution of the virtual hand to self (Suzuki et al., 2013). Synchronous multisensory integration resulting in self-other boundary diffusion has since then been replicated, showing that a representation of self is based on multimodal signal integration(Sel, Azevedo, & Tsakiris, 2017; Tajadura-Jiménez & Tsakiris, 2014). The reverse interaction has also been explored. Fillipeti, Tsakiris (2017) found that establishing a stronger sense of bodily self-consciousness through exteroceptive signals increased bad detectors' ability to perceive their heartbeats, increasing interoceptive sensitivity(Filippetti & Tsakiris, 2017). The above studies have indicated the significance of the interactions between exteroceptive and interoceptive signals in establishing a constant and secure sense of self. However, literature remains still poor in the effects of feedback on interoceptive signals and the perception of heartbeats. How does congruent and incongruent feedback modulate interoceptive awareness, and will different levels of congruency result in interoceptive illusions about one's own bodily signals?

Earlier accounts of incongruent interoceptive feedback has shown that false information about one's heartbeats modulate emotional evaluation of pictures (Valins, 1966; VALINS, 1967) and the perception of heartbeats (Ludwick-Rosenthal & Neufeld, 1985). However, the effect of fake interoceptive feedback in probing representations of self under a predictive coding paradigm has only recently been explored. Iodice, Porciello, Bufalari, Barca, Pezzulo (2019) manipulated the feedback participants received after a physical exertion task. Participants who received elevated heartbeat feedback tended to report higher levels of physical exertion. The reverse effect was not present(Iodice et al., 2019). Levels of biofeedback congruency have been shown to differentially modulate heartbeat detection (Schandry & Weitkunat, 1990) and cortical excitation(Pfeiffer & De Lucia, 2017), with mismatches driving cortical responses to incongruent feedback. Recently, Hodossy and Tsakiris (2020) reported that high frequency heart rate variability (HRV was higher when biofeedback was congruent with participants' prior beliefs about their interoceptive signals(Hodossy & Tsakiris, 2020). As such, providing false heartbeat information causes a mismatch between higher level beliefs (or internal representations in the context of predictive coding) and afferent inputs, causing the organism to update its internal models.

1.5 Insula

A growing body of research has suggested that the insula cortex is involved in the integration and processing of various stimulus types, especially interoceptive signals from the peripheral body (Craig, 2009). Neurophysiologically, the insula receives afferent projections from the autonomic brainstem nuclei and has rich, bidirectional connections with somatoparietal and frontal regions, as well as limbic structures, supporting the processing and integration of somatovisceral inputs, and establishing an interoceptive hub for homeostatic processes (Flynn, 1999)(For a simplified model, see figure3. In addition, the insular cortex has gained experimental evidence for its role in interoceptive signal processing, and the emergence of a coherent self representation can be attributed to recent neuroimaging and neuropsychological studies, hinting at the role of the insula in cognitive and emotional processes(Tsakiris, 2017). The right anterior insula (Allen et al., 2016) specifically has been suggested as the main integratory hub for information relating to the self(Craig, 2003, 2013; Klein et al., 2007) . Neuroimaging studies have suggested ties between activation of the insula heartbeat perception tasks (Critchley et al., 2004; Ronchi et al., 2015). Chitchley et al. (2004) found that fMRI activity in the insula cortex predicted performance in a heartbeat performance task, whereas Ronchi et al. (2015) reported lower IAcc (interoceptive accuracy) scores after insula resection.

Insula activity has also been reported during multimodal tasks probing body ownership (Baier & Karnath, 2008; Ehrsson, Spence, & Passingham, 2004; Grivaz, Blanke, & Serino, 2017), showing that stimulus processing extends to exteroceptive inputs contributing to updating a coherent sense of bodily self-consciousness and self of agency. The insular cortex has been suggested as a causal agent to the suppression of visual inputs from visual awareness due to presentation in synchrony with afferent cardiac interoceptive signals(Salomon et al., 2018, 2016), indicating the role of this structure in cardio-visual integration. Tsakiris et al (2007) used positron emission tomography to measure the proprioceptive drift during the Rubber Hand illusion. They found that the phenomenon of illusory incorporation of the hand was accompanied by activity in the right posterior insula(Tsakiris, Hesse, Boy, Haggard, & Fink, 2007). These studies extend the role of insula, from a homeostatic center to a central node in the emergence of a conscious representation of self. A recent meta-analysis on studies focusing on the structures activated in bodily self-consciousness related tasks confirmed the role of the insula in integrating interoceptive signals, but also emphasized the role of temporoparietal regions in integrating interoceptive and exteroceptive sig-

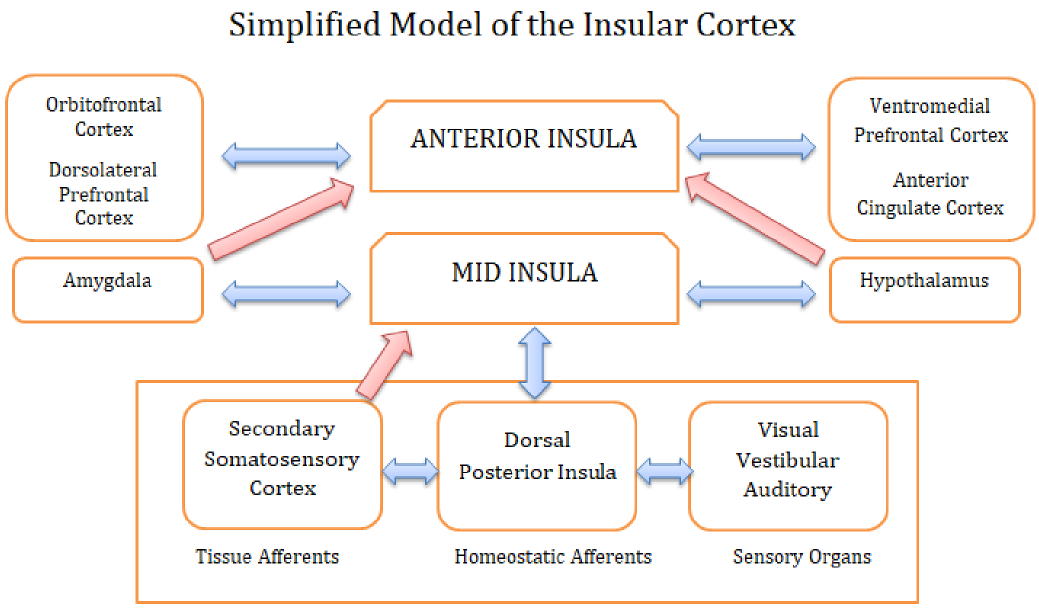


Figure 3: Feedforward and feedback convergence of interoceptive and exteroceptive information in the insular cortex. Blue arrows indicate reciprocal connections. Red arrows indicate feedforward connections. Adapted from Craig, 2003

nals in a coherent sense of self(Salvato, Richter, Sedeño, Bottini, & Paulesu, 2020). However, the role of this structure under a predictive coding account of self remains unclear.

Recent accounts of feedback mismatch tasks (Godefroid, Pourtois, & Wiersema, 2016; Gray, Harrison, Wiens, & Critchley, 2007) have suggested the insular cortex as the structure of comparison between bottom up sensory information about self (exteroceptive and interoceptive stimuli) and top down predictions about the causal agents of these signals(Ondobaka et al., 2017; Owens et al., 2018; Seth & Friston, 2016; Ullsperger, Harsay, Wessel, & Ridderinkhof, 2010). Gray et al. (2007) found that activity in the anterior insular cortex was higher due to false cardiac feedback during emotional appraisal of images(Gray et al., 2007), suggesting that one the main functions of the insula is error awareness(Klein et al., 2007) . A pattern of frontocentral negativity during error processing has been repeatedly replicated during EEG studies, probing error awareness(Godefroid et al., 2016; Ullsperger et al., 2010). Taken together, the mind holds coherent hierarchical representations of self and aims at explaining away prediction errors due to sensory stimuli by minimizing free energy. The insula is thought to play a key role in establishing a prediction error between bottom-up and top-down processes. However, the exact nature of signal propagation during interoceptive tasks is not clear. Although, experimental accounts of self indicate towards an embodied predictive coding account framework, the precise nature of interoceptive signal processes is not clear. Therefore, my thesis project aims to investigate the neural and behavioral substrate of the self-attribution of auditory heartbeat feedback

Hypothesis: Based on the above mentioned studies, we expect that a multisensory integration task will reveal how visceral signals contribute to our perception of bodily self-consciousness. We asked subjects to perform a heartbeat perception task, where they had to identify whether provided heartbeat feedback was synchronous or asynchronous to their own heart (For a full description of the experimental task, see the Experimental Procedure subsection in Methods). Behaviorally, we expect that the subjects presented with heartbeat feedback synchronously to their own will tend to attribute it to themselves. Additionally, we expect that better perceivers will access their body representation easier than bad perceivers, translating to fast response times. On the contrary, auditory heartbeat feedback asynchronous to their heartbeat will tend to be attributed to an external source. At the brain level, we expect synchronous feedback to increase BOLD activation within regions associated with auditory-interoceptive integration and emergence of bodily self-consciousness, namely the insular cortex and parietal regions

2 Materials and Methods

2.1 Participants

Twenty-three volunteers (13 female, 10 male; mean age, 25.1 6.7; range, 19-42 y) were recruited through posters and flyers displayed at the campus of the University of Paris, for participation in this study. All were naive with respect to the purpose of the experiment and the measurements. The study was approved by .... All participants provided signed informed consent before enrolling in the study. Participants were financially compensated for their participation time (50). One participant was excluded due to MRI compatibility issues. Five subjects were excluded from the analysis because the ECG signal was not strong enough to isolate individual heartbeats. The final sample used for the analysis consisted of 17 subjects (10 female, 7 male; mean age, 24.17; range, 19-38 y)

2.2 Experimental Procedure

The experimental task had a blocked design with one conditions of interest: Biofeedback Congruency (referring to the presence or lack of congruency between participants cardiac activity and visual feedback i.e. Synchronous or Asynchronous). On arrival, participants were introduced to the ECG recorder. A preliminary screening session, as specified in the ECG Acquisition section, aimed at creating a valid heartbeat detector algorithm for each individual, with which to predict each subjects heartbeat timing. After a valid model was constructed for each subject, the subjects were introduced to the fmri scanner. The subject was placed in the scanner with eyes open looking at a screen. A recording plate (MRI compatible button box) with two buttons was placed under the subject's dominant hand. The following instructions appeared on the screen: "For the next few minutes you will hear a series of sounds from heartbeats which can be either your own heartbeat or the experimenter's heartbeat located in the control room. At the end of each small block of sounds, please indicate if you think it is your heartbeat by pressing the left key on the keyboard or that of the experimenter by pressing the right key on the keyboard."

The "Mine – Other" condition was performed 25 times (blocks) for each participant. The trial order was randomly selected, and in each block, half trials corresponded to the "Sync" condition and half to the "Async". Among subjects, extra trials in either condition were counterbalanced. Each block consisted of 30 to 50 sounds (number randomly selected) and a final sound of higher pitch which worked as a prompt for the behavioral response. Each blocked lasted on average 40 seconds, accounting for the variance in the reaction time between the final auditory stimulus and the high pitch cue probing for response. The sounds were square waves generated by Arduino, an open-source electronic prototyping platform for creating electronical objects. For each block, the stimulus could either be delivered in synchrony with the ECG R peak, or out of synchrony (dephased), but maintaining the heart rate. The timing of the R peak was predicted by the individual's model established in the ECG Acquisition phase (See figure 4).

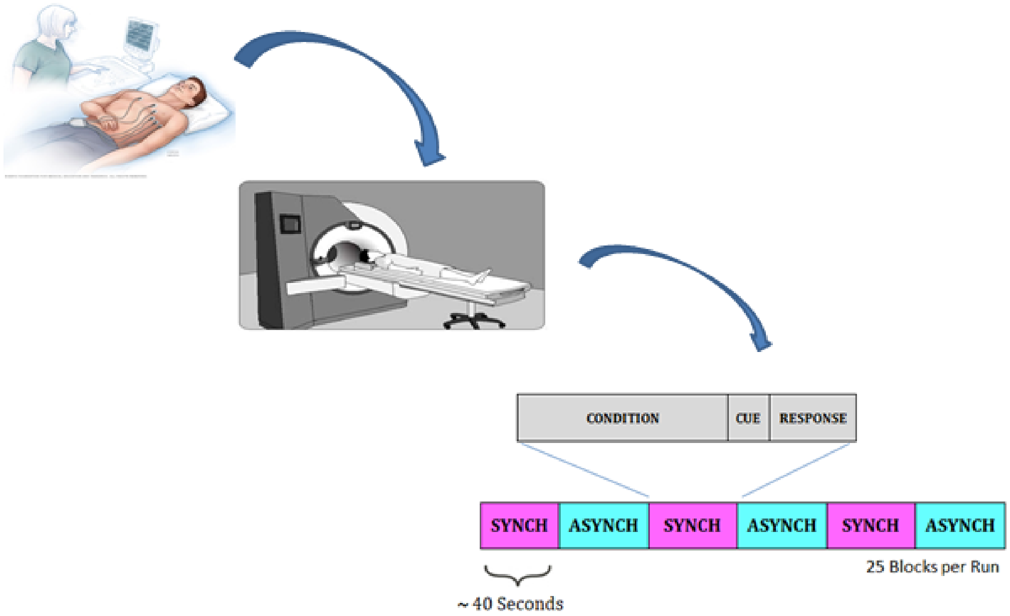


Figure 4: Interoceptive Awareness Task. During the first step of the task, we used an electrocardiograph to monitor a person's heartbeat. The ECG was attached to the person throughout the study. After locating the timing of the individual heartbeats, the person was introduced to the fmri scanner where he performed the following task. In a blocked design, as specified by the pink and blue colours, he heard a heart beating, either in sync or out of sync with his actual heart. At this end of the block, another higher pitch cue probed the person to state whether the feedback we gave him was his own or someone else's'.

2.3 ECG Acquisition Protocol

The chest skin was cleaned with alcohol to prepare it for the electrode placement. ECG disposable adhesive skin electrodes followed a bipolar arrangement of two electrodes and a ground. All electrodes were placed on the left chest of the participant. The positive electrode was placed on the top left side and the negative on low right side of the chest. The ground electrode was placed on the sternum. The lead cables (BIOPAC SS2LB lead set) were connected to the electrodes and then to the ECG amplifier (BIOPAC ECG100C-MRI Smart Amplifier). Surgical tape was used to hold the electrode leads in place and prevent them from tugging on electrodes.The sampling rate was 5000 Hz. A value of 1V for the Q wave was an acceptable threshold to continue with the electrode lead setup.

When the subjects were placed the MRI, a test for the detection of the heartbeat was performed,so as to create an acceptable predictor of the heartbeat, with which to properly synchronize the presentation of the auditory heartbeat feedback. We used a knowledge-based, numerically efficient, and robust that utilized prior knowledge about ECG features (ie average QRS duration,average heartbeat duration) to estimate an individual heartbeat predictor for each subject, as specified by (Elgendi, 2013) A beta parameter of the detector needed to be set correctly. A value around 0.9 was acceptable. Until the parameter reached the acceptable threshold, we decided to tune the beta, to increase its predictive properties. To tune up the beta parameter, an MRI test sequence was initiated by the experimenter with the subject within the scanner, and a manual control in the visualizer was performed, so that the heartbeat peaks were detected and predicted correctly. If peaks were missing, the individual beta value for detecting was lowered, so as to ease the detection of the threshold. If the peaks were detected incorrectly, the beta value were tuned higher. If the detector was inaccurate due to subject motion or it predicted too many peaks, a reset was done. Once the prediction was satisfactory (beta parameter reached threshold), the MRI test sequence stopped.

2.4 Behavioural Data

Data was analysed with mixed-model regressions using custom Python scripts and the lme4 v1.1 -17 package (Bates et al., 2014) available for R software (R Core Team, 2013) with participant's ID as a priori random factor, i.e. the model allowed subject-specific intercepts. Initially, the data were manually inspected for outliers. . A test of normality was conducted for the dependent variable using the Shapiro-Wilks test and revealed that the assumption of normality was significantly violated ($p < 0.001$). Rows of data containing responses during the 'TIMEOUT' of the recoding were excluded from the analysis ($< 1\%$). Cases were the reaction time of the subject was 0 were also discarded ($< 1\%$).

Reaction time – Reaction times were defined as the difference between the auditory probe and the key press by the subjects

Correct Responses - A correct response was registered when the subject attributed a synchronous block ('SYNC') as his own ('MINE') and an asynchronous block ('ASYNCH') as the researcher's ('OTHER'). Adopting Signal Theory Detection terminology, a 'Mine' response during the synchronous condition could be characterized as a "Hit", a 'Mine' response during the asynchronous condition could be characterized as a False Positive, an 'Other' response during the synchronous condition could be characterized as a "Miss", and an 'Other' response during the asynchronous condition could be characterized as a "Correct Rejection" (See Table 1).

Response	**Condition**	
	Synchronous	Asynchronous
Mine	Hit	False Alarm
Other	Miss	Correct Rejection

Table 1: Correct and Incorrect Responses at the Auditory Feedback Task. A participant scored a correct response when he correctly identified his own heartbeat or correctly rejected the foreign one.

Finally, we decided to separate subjects into good and bad interoceptive perceivers, to investigate possible interaction in reaction times between response modality, condition modality and ability to perceive our own heartbeat. An extended literature has shown differential behavioural performance in interoceptive tasks(Pollatos & Schandry, 2004; Schandry et al., 1986; Ludwick-Rosenthal & Neufeld, 1985). For each subject, we calculated an accuracy measure based on the following formula:

$$accuracy = \frac{HITs + CorrectRejections}{TotalResponses} \tag{1}$$

2.5 fMRI acquisition

Data were acquired on a 3T Siemens Prisma Fit MRI scanner (Siemens Medical Solutions, Erlangen, Germany): T2*-weighted images were acquired with a gradient-echo echo-planar imaging (EPI) sequence using transverse slice orientation and covering the whole brain (44 slices; slice thickness, 3 mm; repetition time, 2140 ms; echo time, 25 ms; voxel size, 3 3 3mm; flip angle, 78; field of view, 192 mm by 192 mm). A structural T1 magnetization-prepared rapid gradient echo (MPRAGE) sequence with sagittal slice orientation was used to collect a high resolution 3D anatomical volume (256 slices; repetition time, 2400 ms; inversion time, 1000 ms; echo time, 2.22 ms; voxel size, 0.8 0.8 1.2 mm; flip angle, 9) in order to allow for precise segmentation, corregistration.

2.6 fmri Preprocessing

The fMRI data from 20 subjects were pre-processed and statistically analysed using the general linear model approach in SPM12 (www.fil.ion.ucl.ac.uk) and MATLAB 7.11 (The Mathworks Inc., Natick, MA, USA).

The first five volumes were dropped to allow the blood-oxygen-level-dependent (BOLD) signal to reach a steady state, to avoid T1 saturation effects. Functional T2* weighted volumes were corrected for head motion. We used 4th degree B spline interpolation to rigid-body motion correction with least squares alignment of each volume to the first image. The realignment parameters were also saved to a file so that these variables can be used as regressors when fitting GLMs.The realligned and resliced data were slice-scan time corrected to account for the accumulation of offset delays between the first slice and all remaining slices. The mean EPI image created by the registration process was auto coregistered to the structural image. Then, the high resolution structural data were segmented into three tissues: white matter (WM), grey matter (GM), and cerebro spinal fluid (CRS). The segmentation process also yielded deformation fields, which were used to normalize the anatomical and the functional data into the MNI (Montreal Neurological Institute) space. The final process was spatially smoothing each fMRI volume (Gaussian kernel full width half maximum [FWHM] = 6 mm).

2.7 fmri Data Analysis

Univariate GLM analysis. To dissociate the neural activity associated with the feedback condition (synchronous/asynchronous) and the the attribution the self or others, a univariate GLM composed of four separate regressors of interest (see below) was modeled and convolved with the canonical hemodynamic response function (HRF) for each subject in the first-level analysis. The four regressors were defined as standard interaction of the factors of a 2x2 factorial design based on the the experimental conditions: a) Feedback-Synchronous - Response-Mine (Sync-Mine), b) Feedback-Synchronous - Response-Other (Sync-Other), c) Feedback-Asynchronous - Response-Mine (Async-Mine), d) Feedback-Asynchronous - Response-Other (Async-Other). Additionally, each subject's six motion parameters (three rigid body translations and three rotations from the realignment procedure) were included to regress out effects related to head movement-related variability. Regionally specific condition effects were tested using linear contrasts for each key event relative to the baseline and each subject. We used a high-pass filter cutoff of 1/128 Hz to remove the slow signal drifts with a longer period, and a first-order autoregressive model (AR (1)) was used for serial correlations with the classical restricted maximum likelihood (REML) parameter. The first level analysis yielded 4 contrasts of interest : . Self¿Other [1 -1 1 -1], Other¿ Self [-1 1 -1 1], (Synchronous Self – Synchronous Other)¿

(Asynchronous Self -Asynchronous Other) [1 -1 -1 1], and (Asynchronous Self -Asynchronous Other) ¿ (Synchronous Self – Synchronous Other) [-1 1 1 -1]. The resulting contrast parameter estimates from the individual subject level were entered into a random effects model for a second level analysis. The subject-specific accuracy scores were introduced to the second level as covariates (To see how the covariates were calculated, see the Behavioural Analysis subsection). First, we used a one-way within-subjects ANOVA with T contrast of “Positive Effect of Response” to examine BOLD activity when subjects responded mine over other. The opposite contrast was used to examine areas in regions associated with ”other” attribution of bodily signals. Second, to investigate the neural activity associated with both synchronicity and response, we used an one-way within-subjects ANOVA with T contrast of “Positive Effect of Interaction”. Significant clusters were determined from the group analysis using a well-accepted statistical criterion including a threshold of $p < 0.05$ with family-wise error (FWE) corrections. Additionally, for exploratory purposes, the threshold of uncorrected $p < 0.001$ was also used to detect activation, where no suprathreshold activation was found after FWE correction.

Small Volume Correction . Based on a priori hypothesis about the nature of the regions involved in interoceptive inference, we decided to perform small volume correction in 4 regions, based on previous metanalysis (Salvato et al., 2020), indicating robust activity, when a subject engages in interoceptive awareness tasks. We defined 4 mm spheres :1.Insular cortex (IC,x= 40, y= 8, z= 4), 2. Middle Cingulate Cortex (MCC,x= 2, y= 8, z= 42), 3.Righter Superior Parietal Lobule (SPL,x= 34, y= -52, z= 52), 4. Left Inferior Parietal Lobule (IPL, x= -60, y= -30, z= 28).

3 Results

3.1 Behavioural Analysis

Our initial analysis had one dependent variable : Reaction Time. The independent variables consisted off: a) Condition (categorical), b) Response (categorical). Accuracy (continuous) were included as covariate only when significantly ($p < 0.05$) improving the fit of the model (also testing for potential interaction between a certain covariate and our main predictors). We selected the optimal model by using buildmer (Version 1.0; Voeten, 2019) which can perform backward stepwise elimination based on the change in the set criterion. We defined the maximal model as:

```
Reaction Time ~ Condition + Response + Accuracy + (1|Subject)
```

The model that was providing the best fit with our data was the following linear regression:

```
Reaction Time ~ Accuracy + (1|Subject)
```

This model suggests a significant difference subject's accuracy and the time needed to make an interoceptive judgement (See figure 5). We ran a generalized linear regression for our main statistical analysis – using lme4 (Version 1.1-23; https://www.rdocumentation.org/packages/lme4) to predict reaction time based on accuracy. The model was statistically significant (b = -1.31, [CI]= -2.41 to -0.22 , p= .03, R2 = 0.14). Contrary to our assumptions, there was no modulation of the response time of the participants due to the experimental effect. Examining the boxplot and the descriptive tables of the two conditions, we do not notice any significant difference in the mean reaction times for the 4 groups (Condition x Response), possibly due to the great variance inherent in them (See figure 6).

To analyze the effects of Condition and Response on giving a Correct Response we used a mixed effects regression model with the participants ID as a random effects factor, i.e. the model allowed subject-specific intercepts. The

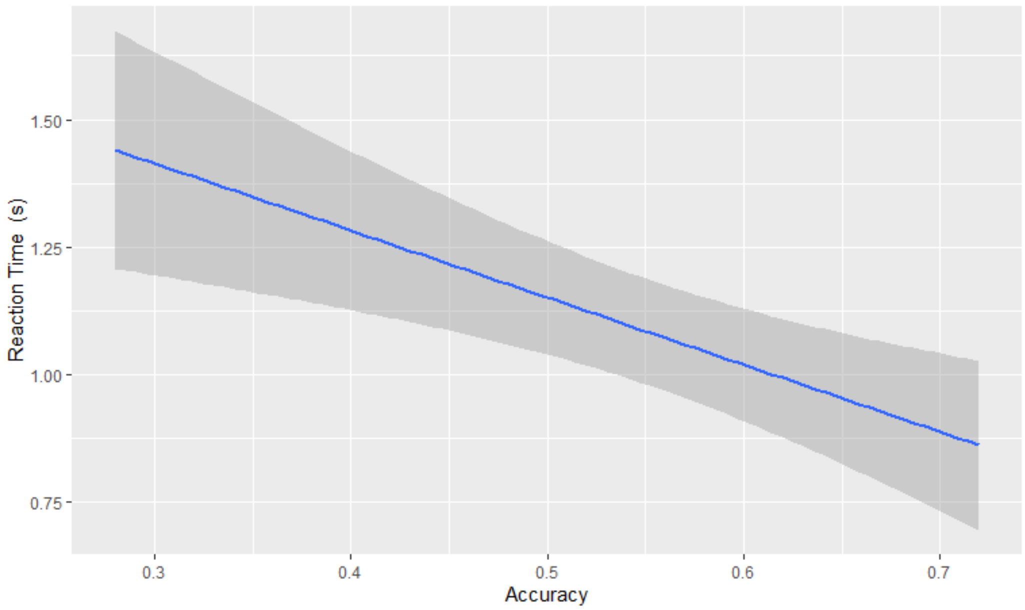
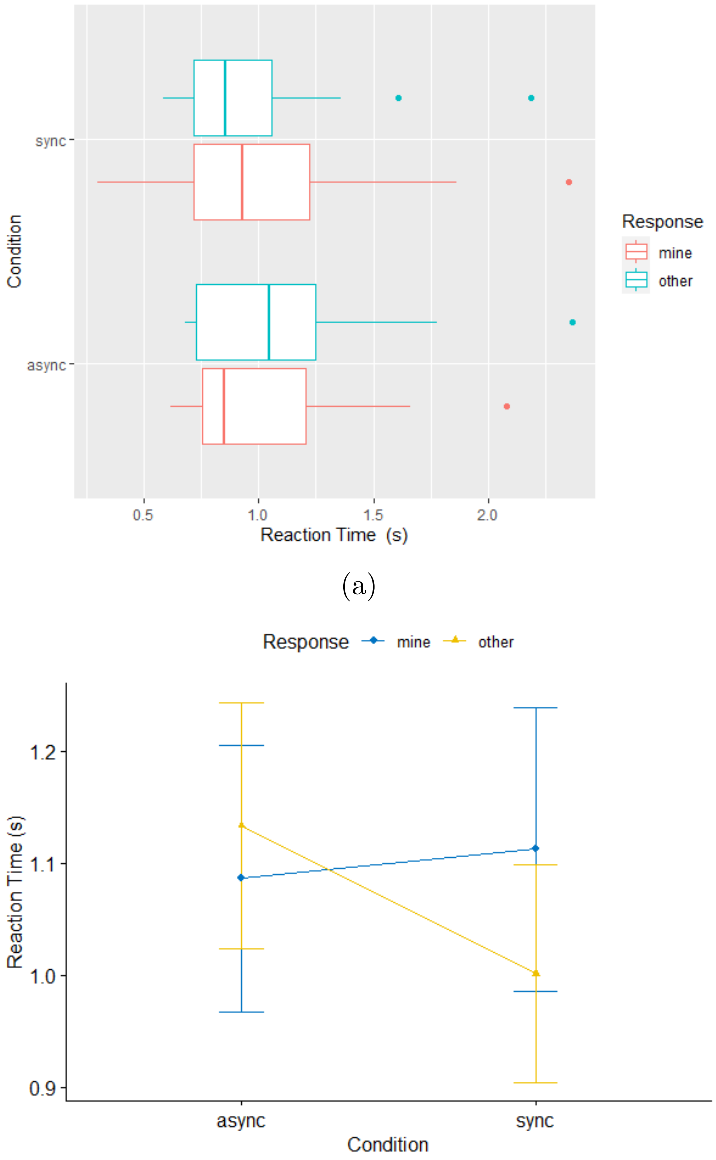


Figure 5: Median reaction Time as a function of accuracy scores. Shaded area shows standard error. Accuracy was calculated as the ratio between correct responses (Hits and Correct Rejection) over the overall responses. The lineplot shows a clear trend towards faster responses for participants with higher accuracy scores.

predictors were entered in the model as fixed factors and retained whenever improving model fit ($p < 0.05$). Model comparisons and statistical significance of each predictor of the final model were carried out through loglike lihood ratio statistics asymptotically approximated to a 2 distribution (Barr, 2013), using the anova functions of the lme4 package. The model that was providing the best fit with our data was:

```
Corrects ~  Condition
```

Our results revealed that participants tended to respond more correctly in Condition 1 (Synchronous Feedback) than in condition 2 (Asynchronous Feedback), = 0.63, S.E. = .19, [CI]=0.99 to -0.26 , p=. 001, R2 =0.03. The inclusion of the random effects intercept did not increase the significance



(a)

(b)

Figure 6: Effects of Condition and Response modality on Reaction Time. a)Boxplot.Lower and upper box boundaries 25th and 75th percentiles, respectively, line inside box median, lower and upper error lines 10th and 90th percentiles, respectively, filled circles data falling outside 10th and 90th percentiles. b) Lineplot of the mean per person reaction time differences. Errorbar indicate one standard mean error.

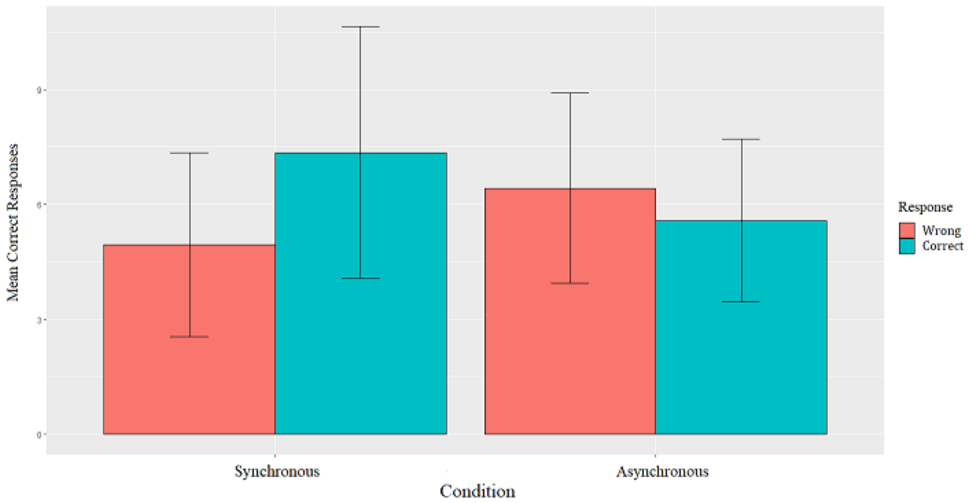


Figure 7: Barplot of Mean Correct Responses as a function of feedback modality.Error plots indicate standard deviation. Participants were more successfull in identifying heartbeat synchronous to their own than identifying fake asynchronous feedback.

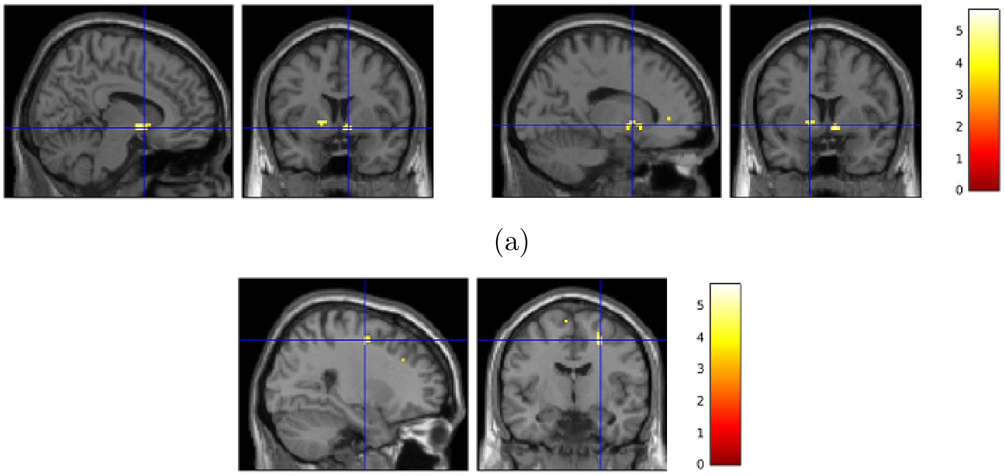
of the model.Mean performance in giving correct response declined moving from the synchronous to the asynchronous condition. In the Sync condition, subject gave on average M= 7.1 correct (SD = 3.28) responses in comparison to the ASync condition (M = 5.47, SD= 2.17). This indicates that subjects were much more successfull in scoring a HIT than scoring a correct rejection (See figure 7).

3.2 Neuroimaging Results

3.2.1 2nd Level Model

Results are expressed at the group level. Given the size of our subject pool and the variance in the areas displaying activity, we have decided to present the results at the $p < 0.001$ uncorrected.

The ”Mine¿Other” condition (trials when subjects responded to the con-



(a)

(b)

Figure 8: BOLD activit during interoceptive judgements. a)"Mine¿Other" - Interoceptive processing areas with activation peaks, during self-attribution of heartbeat (i.left pallidum (T =4.9415, p*uncorrected* =.000; MNI: -14,6,-1),ii. the right caudate nucleus (T = 3.8798, p*uncorrected*=.001; MNI: 9,11,-4)). Colorbars show T statics. b)"Other¿Mine" - Interoceptive processing areas with activation peaks, during external-attribution of heartbeat(i.right precentral gyrus (T = 5.63, p*uncorrected*=.000; MNI: 27,-7,50)). Colorbars show T statics.

dition as Mine) led to larger BOLD activation to subcortical, striatal, structures, mainly the left pallidum (T =4.9415, p*uncorrected*=.000; MNI: -14,6,-1), the right caudate nucleus (T = 3.8798, p*uncorrected* =.001; MNI: 9,11,-4) and the right accumbens area (T = 3.6861, p*uncorrected* = .000; MNI: 9,9,-6)(See figure 8).

The "Other¿Mine" condition(trials when subjects responded to the condition as other) led to BOLD activation to the right precentral gyrus (T = 5.63, p*uncorrected* =.000; MNI: 27,-7,50)(See figure 8).

To examine possible interactions between condition (Sync-Async) and response, we decided to examine the positive and negative interactions of our first level factorial design. No voxels survived in the second level model, suggesting no interactions between our two factors.

3.2.2 Covariate Analysis

To examine possible interactions between our experimental design and the partipants' interoceptive accuracy, we performed a linear regression analysis over all participants using their accuracy as a predictor variable.

When examining the correlation of the accuracy covariate with mine-other judgements (participants attributing a visceral signal to themselvers or others), no voxels survived in the second level model, suggesting no interactions between accuracy and judgement.

A linear regression analysis over all participants revealed that a high cardiac interoceptive accuracy was positively related to enhanced neuronal engagement during the positive interaction between condition and response, highlighting a diverse pattern of activity, specifically, bilateral superior parietal regions (right: T =5.50, p*uncorrected* =.0001; k*cluster* = 20; MNI:27,-61,38; left: T =3.70, p*uncorrected* =.001; k*cluster* = 20; MNI: 33,49,62), the bilateral supramarginal gyri (right: T = 3.55, p*uncorrected* =.0001; k*cluster* = 20; MNI:45,-25,41; left: T =6.71, p*uncorrected* =.001; k*cluster* = 20; MNI: 54,-25,38), the left parietal operculum (T = 3.68, p*uncorrected* =.0001; k*cluster* = 20; MNI:-51,-25,20), the right precentral gyrus (T =5.26, p*uncorrected* =.0001; k*cluster* = 20; MNI:42,-16,62), the right postcental gyrus (T = 4.95, p*uncorrected* =.0001; k*cluster* = 20; MNI:54,-19,41) and the left calcerine cortex (T = 4.79, p*uncorrected* =.0001; k*cluster* = 20; MNI:-51,-25,20) (See figure 9).

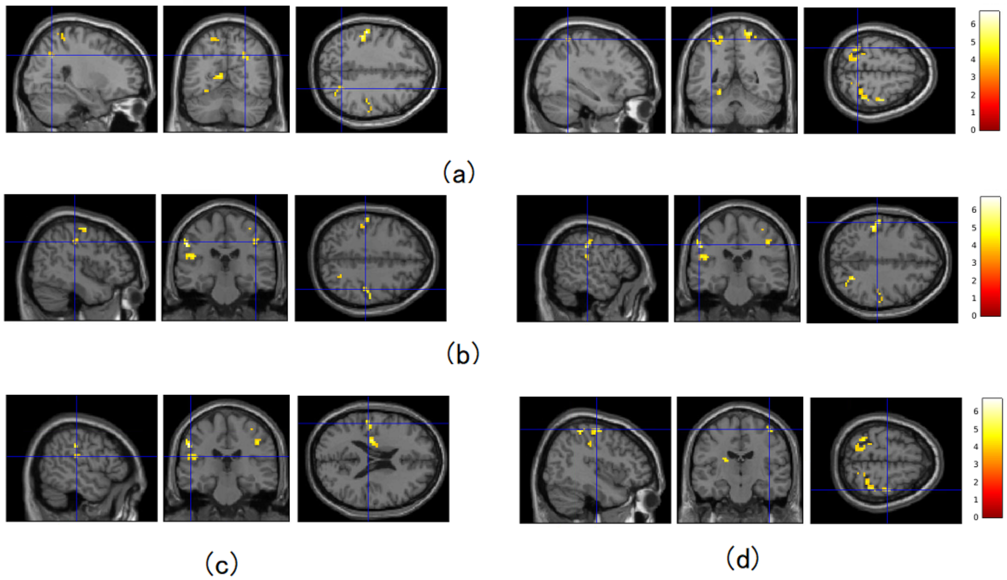


Figure 9: BOLD activity positively correlated with accuracy in heartbeat feedback task.a) Bilateral Superior Parietal Lobules (right: T =5.50, p*uncorrected* =.0001; k*cluster* = 20; MNI:27,-61,38; left: T =3.70, p*uncorrected* =.001; k*cluster* = 20; MNI: 33,49,62),b) Bilateral Supramarginal Gyri (right: T = 3.55, p*uncorrected* =.0001; k*cluster* = 20; MNI:45,-25,41; left: T =6.71, p*uncorrected* =.001; k*cluster* = 20; MNI: 54,-25,38),c) Left Parietal Operculum (T = 3.68, p*uncorrected* =.0001; k*cluster* = 20; MNI:-51,-25,20),d) Right Precentral Gyrus (T =5.26, p*uncorrected* =.0001; k*cluster* = 20; MNI:42,-16,62),

4 Discussion

4.1 Results Overview

The present study investigated the neural and behavioral correlates of interoceptive awareness, during synchronous and asynchronous feedback. We probed visceral aspects of bodily self-consciousness, by manipulating the multisensory intergretion of auditory-interoceptive signals, specifically one's own heartbeats. Based on previous research on bodily self-consiousness, we reasoned that biofeedback of interoceptive signals will elucidate the neural and behavioural substrate of selfhood. Overall, our results provide further support for the role of the basal ganglia and high order - association regions in bodily self-consiousness, while highlighting some key behavioural differences between good and bad interoceptive perceivers.

Our main results indicate that interoceptive awareness seems to engage a hierarchical, neural model, based on a two step process, where initial interoceptive judgements are performed at the thalamical - basal ganglia network level, and then, this judgement is incorporated with exteroceptive signals at, hierarchically, high level association regions. More specifically, Mine responses, irrespective of whether the subject was correct or incorrect, elicited activity in basal ganglia, specifically the putamen, the pallidum and the nucleus accumbens. To my knowledge, this is the first study reporting striatal activity in interoceptive tasks. Recent biological accounts of the self has attempted to elaborate on the brain structures involved in interoceptive processing(Seth & Friston, 2016; Barrett & Simmons, 2015).The authors highlight that visceromotor cortices(regions highly associated with interoceptive judgements) receive projections from basal ganglia structures via the thalamus, indicating that basal ganglia-thalamic networks are involved in the processing of visceral sensations. Our finding extend this idea, by suggesting that a preliminary abstract concept of self is already formed, as visceral sensations arrive and are encoded at the subcortical level. This suggestion is supported by the fact that Mine responses (judging biofeedback as mine, irrespective of whether it is actually in synchrony or not with the actual heartbeat) elicited the same activity in accurate and non accurate perceivers. Therefore, a minimal representation (akin to Gallagher's (Gallagher, 2000) idea of the minimal self that contributes to interoceptive judgements) exists at the subcortical level. "Other" responses elicited activity from the precentral gyrus. Research supporting the role of premotor areas in bodily self-consciousness processes has recently gained support, due to experimental finding highlighting the role of these regions in multisensory integration and neuronal contributions in altered bodily self-consciousness states(Ehrsson et al., 2004; Brozzoli, Gentile, & Henrik Ehrsson, 2012). These findings contribute to the idea that the precentral gyrus supports the perception of the self in space, where the body is placed in reference and opposition with other spatial objects (Grivaz et al., 2017; Serino et al., 2013).However, we did not observe any modulation of response reaction time due to response type (Mine/Other).Given methodological caveats in establishing temporal sequence of neural events in fmri, it is difficult to make assumptions about whether mine-other attribution is a sequential, bottom-up, processess where we first judge something as "Mine" and, then non-mine objects are classified as "Other". However, the distinct neural substrate identified in the study supports the idea that "Mine-Other" classification is supported by distinct networks, "Mine" from a subcortical thalomo-basal ganglial, recruting an abstract concept of self, and "Other" from premotor regions, associated with the experience of the self, as in space.

The introduction of the accuracy covariate highlighted the higher level association regions associated with interoceptive processing. During correct attribution of synchronous feedback to the self (Hits), accuracy was highly correlated with bilateral superior parietal regions,bilateral SMG regions, the left parietal operculum, the right postcental gyrus, and the left calcarine cortex. A recent meta-analysis on regions associated interoceptive processing and body ownership confirms our findings (Salvato et al., 2020). All the regions reported in the current study have previously been implicated in multisensory integration of interoceptive and exteroceptive signals and the parietal lobules mentioned above in self location and multisensory integration (Ionta et al., 2011; Brozzoli et al., 2012).These studies highlight the role of converging interoceptive and exteroceptive information in the creation of a coherent represenation of self.These parietal structures seem to be supported by information conveyed by premotor areas, similar to the precentral gyrus(Ehrsson et al., 2004; Gentile, Björnsdotter, Petkova, Abdulkarim, & Ehrsson, 2015; Brozzoli et al., 2012). These premotor and parietal regions seem to be a part of two larger, overlapping insular-intraparietal-premotor-temporoparietal networks, responsible for signal processing of self-location and self-identification(Park & Blanke, 2019). Finally, the operculum has recently gained research interest due to its involvement in the processing of cardiac signals and interoceptive awareness(Craig, 2002, 2003; Critchley et al., 2004; Garfinkel et al., 2015).Blefari and her coworkers highlighted the role of the bilateral rolandic operculum in heartbeat awareness and bodily-self consciousness (Blefari et al., 2017). Although the present behavioral data does not fully replicate previous behavioral bodily-self consciousness findings, we note that the activity observed in bodily-self consciousness induced during fMRI acquisitions were comparable (yet weaker and excluding the insula) with respect to those reported in previous behavioral investigations carried out in the standing position using ECG recordings (Aspell et al., 2009, 2013; Ronchi et al., 2015; Salomon et al., 2016; Salvato et al., 2020).

An interesting finding was that interoceptive accuracy, as measured by the ration of correct responses over the overall trials performed by the subjects, was a statistically significant predictor of reaction time. Subjects who were better at the interoceptive task performed, where also significantly faster. To my knowledge, this is the first study that has observed this effect of interoceptive accuracy on reaction times during interoceptive judgements. IAcc is thought to reflect a trait-like sensitivity to one's visceral signals, resulting in differential response patterns between good and bad interoceptive perceivers, in intuitive decision-making (Dunn et al., 2010),emotional experience and emotion regulation(Wiens, 2005)and ability to report reportability(Herbert & Pollatos, 2012). Recent literature on bodily self-consciousness illusions and multi-sensory integration has focused on the role on interoceptive accuracy(Tajadura-Jiménez & Tsakiris, 2014; Aspell et al., 2013; Suzuki et al., 2013). Suzuki et al. (2013) demonstrated that watching a virtual depiction of their own hand appearing in synchrony with the participant's heartbeats induced the subjective experience of ownership over the projected hand.Interestingly, higher IAcc was correlated with higher experienced a stronger illusory sense of ownership over the virtual hand. Tsakiris (2017) suggested that IAcc is a subjective trait, responsible for the flexibility of self-other boundaries, such that higher interoceptive accuracy translates to higher accessibility to interoceptive experience and bodily representation and ability to update our sense of self based on contextual evidence. We believe that our findings provide evidence for this idea, such that participants with higher interoceptive performance had easier accessibility to their bodily image. This more readily available image facilitated much faster response to the task performed.

4.2 Interoceptive Predictive Coding

We suggest that predicting coding under active inference assumptions provides an adequate explanatory framework for our findings. Predicitive coding views brain as a prediction machine, functioning based on Bayesian principles. On the most fundamental level, the brain creates predictions constantly about the world based on previous experiences (Bayesian updating), with the goal of minimizing the difference between the predicition and the actual sensory percept (Friston et al., 2006; Friston, 2009, 2010).One key assumption of this model is that these predicitions are hierarchically organized, such that a large prediction error from a predicitve model in the lower hierarchical levels (explaining immediate percepts) , will be propagated to higher level predictive model (explaining abstract supramodel concepts) (Ondobaka et al., 2017; Seth, 2013; Friston, 2010). This model has been extended to account for interoceptive processing, with the mind constantly trying to generate model about the body's internal states(Apps & Tsakiris, 2014; Seth & Friston, 2016; Barrett & Simmons, 2015). During Mine-Other judgements, a person contrasts ascending bodily signals about the self with generative models about bodily inputs, eliciting activity from a thalamical-basal ganglial network.However, this cannot explain the individual variancies in interoceptive accuracy and the engagement of multimodal regions in interoceptive processing. We suggest that interoceptive accuracy modulates the weighing of the interoceptive (internal cues) and exteroceptive (biofeedback) in a coherent multimodal construct. However, as per recent accounts of our sense of self, both interoceptive and exteroceptive signals are necessary for a coherent sense of bodily self-consciousness, in order to attentively create a sensory-visceral percept that minimizes prediction errors. Higher parietal association regions are responsible for the selection of relevant interoceptive and exteroceptive information ("weighing" of stimuli), evaluating the relevance of the information. Therefore, increased BOLD activation in parietal lobules, the operculum and precentral and postcentral areas reflects the subject's ability to precisely ''weigh" internal and external signals. This is why greater BOLD activity was found in higher IAcc performance relative to low IAcc. These subjects were able to more successfully identify the relevance of auditory feedback and their own actual heartbeats.Therefore, trait-like differences in IAcc accuracy can be explained in terms of variations in the "precision" with which interoceptive visceral, signals and exteroceptive stimuli are represented.

4.3 Limitations

At this point, some limitations about the study should be pointed.The first limitations refers to the use of the ratio of correct responses over all responses as the measure of the participant's interoceptive accuracy. Traditionally, heartbeat perception or discrimation tasks have been used as the tools of identifying the individual'cardiac interoceptive sensitivity. In the absence of such available data, we utilized the accuracy ratio, as defined in Signal Detection Theory, as we estimated that it most closely mirrors these tasks, while not recruiting the participants' meta-represenation of their interoceptive models. A second limitation is the imprecise nature of the ECG predictor used. Although the predicitive properties of the algorithm are well established, given the great variance inherent in the ECG signal, R-peak predicition still was still not perfectly administered in synchrony on certain trials. Finally, it should be noted that all neuroimaging results are presented at $p < 0.001$ uncorrected threshold. Given the size of our subject pool, we were not able to reach significance in multiple-comparison corrected activition maps. However, given that the region reported in this study, excluding the basal ganglia, are well established region in the literature of the nature of self and predictive coding, we estimate that replication studies with larger subject pools will identify the same regions.

4.4 Conclusions and Future Directions

The active inference account of interoceptive processing presented here provides a plausible explanation of the often striking effects that have been reported in relation to interoception and bodily self-consciousness over the last 20 years, as it explains how exteroceptive evidence can be used to minimize prediction errors during the construction of our self-awareness. This study focused on interoception and its interrelation with self. Specifically, it aimed to identify the behavioural and neural substates of our own subjective, experience of our body. On the basis of recent empirical work, we build upon a well established embodied predictive framework, by highlight the role of subcortical structures in creating a representation of self and examing the role of interoceptive awareness in our subjective experience. Overall, it appears that our sense of self is a multimodal concept that builds upon the integration of exteroceptive and interoceptive signals, relating to the body. We suggest that future research should be driven to tackle issues pertaining the supramodal, abstract construct of the self. Only recently has theoretical and experimental work attempted to bridge low level, unimodal, prediction loops and high level multisensory integration processes. Biological accounts of predictive coding map prediction model and error construction in agranular and granular cortical structures respectively. However, there is sparse experimental work, building upon these frameworks. These studies need not draw information only for cognitive neuroscience.Under predictive coding assumptions, clinical, psychological and psychosomatic conditions might differentially modulate interoceptive awareness. Additionally, since precision weighing mechanisms, guided by interoceptive accuracy, as assumed to underpin multisensory integration, developmental neuroscience could benefit us by inverstigating the trait-level interoceptive accuracy development trajectory. Overall , an multidiscplinary, account of the neurobiological and behavioural interactions of the neural substrates of the self will help construct a comprehensive understanding of the contributions of bodily representations to emotion, cognition, and consciousness.

Glossary

Active Inference An extension of predictive coding theory, where organisms attempt to minimize the surprise (prediction error) between internal models of the world and incoming signals, by performing actions that will bring about the states and incoming stimuli, most closely resembling those of their internal models. 10

Bodily Self-Consciousness The feeling of body ownership, our body as our own, a unitary experience in space and time. 4

Exteroception The ensitivity to stimuli originating outside the body (i.e. visual, auditory, tactile). 4

Free Energy Principle An extension of predictive coding theory, where organisms attempt to minimize the surprise (prediction error) between internal models of the world and incoming signals. 10

Homeostasis The tendency of organisms to maintain a state of optimal internal functioning. 5

Interoception The encoding and representation of the visceral afferent signals from the peripheral body. 5

Interoceptive Accuracy An individual's ability to shift attention internally and accurately track visceral signals– operationalized measure of Interoceptive Awareness. 8

Interoceptive Awareness The conscious encoding and representation of inner body sensations. 8

Predictive Coding The conscious encoding and representation of inner body sensations. 9

Self-Awareness The awareness of ones as a distinct individual. 12

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