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Department of Brain and Behavioral Sciences (DBBS)
MSc in Psychology, Neuroscience and Human Sciences

Effects of Interoceptive Sensibility on Skin Temperature Response in Visual Capture of Ownership

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ABSTRACT

Interoception, alongside exteroception and proprioception, has been shown to give rise to bodily self-awareness. This complex interaction is at the basis of body ownership paradigms, which typically rely on multisensory integration to alter, disrupt or expand the brain's standard perception of the body. A recent study, however, demonstrated that the simple observation of an external hand can induce a sense of ownership over the hand and result in an increase in skin temperature within a virtual reality setting. In the present study, we aimed to (i) replicate the visual capture of ownership effect in a real-world setting and (ii) explore how interoceptive components affect the visual capture of ownership paradigm and the related modulation of skin temperature. In the experiment, participants were instructed to fix their gaze on a realistic rubber left hand while their real left hand was hidden from view. Feelings of ownership and feelings of agency were assessed through questionnaires, and thermographic measurements were recorded to monitor skin temperature changes. Additionally, interoception was evaluated by administering the Multidimensional Assessment of Interoceptive Awareness (MAIA) questionnaire. Results indicated that participants reported experiencing feelings of ownership and feelings of agency over the rubber hand after mere passive observation. However, no skin temperature changes were detected in response to the paradigm. Notably, an interplay emerged between interoceptive sensibility and skin temperature modulation, suggesting an interaction between these factors. These findings provide new insights into how aspects of body representation and body ownership might be shaped by different perceptual processes and individual differences.

Keywords: interoceptive sensibility, body ownership, visual capture of ownership, skin temperature

1. Introduction

1.1 The Concept of Interoception

Interoception, a complex and multifaceted concept, has seen its definition evolve as our understanding of how the brain perceives and interprets internal bodily signals has advanced. Today, interoception is widely defined as the awareness of the body's physiological state at any given moment (Craig, 2002). The growing interest in interoception is reflected by its fundamental functions in various physiological and psychological processes. It is crucial for homeostatic control, the self-regulating process of biological systems (Billman, 2020), and allostatic adaptation, which maintains stability by anticipating physiological demands (Sterling and Eyer, 1988). Additionally, interoception significantly influences cognitive functions, including decision-making, memory, and emotional processing (Tsakiris and Critchley, 2016). Notably, interoception also plays a pivotal role in the cognitive dimension of bodily self-awareness (BSA) (Toussaint et al., 2024). BSA describes the relationship between the body and the self, which is central to our work. Although it is now widely accepted that BSA arises from the integration of interoceptive, exteroceptive, and proprioceptive signals, the specific importance of interoception in this process has only recently been acknowledged (Salvato et al., 2020). This newly recognized significance of interoception requires a thorough examination. Following this discussion, we will provide an in-depth exploration of the essential aspects of BSA.

The first to introduce terms related to interoception was Sherrington in his landmark publication *The Integrative Action of the Nervous System* (1906). Sherrington (1906) introduced the concept of interoception by categorizing bodily sensations into three distinct types: exteroceptive, interoceptive, and proprioceptive. Toussaint and colleagues (2024) highlight how

Sherrington's classification was grounded in the anatomical knowledge of his time, leading him to consider interoception as strictly related to perceptions coming from the viscera (Toussaint et al., 2024). In contrast to interoception, exteroception was understood as the perception of external stimuli and proprioception was associated with the awareness of the body position (Enmalm, 2020). Notably, temperature perception was categorized as part of exteroception, viewing it as a response to external environmental changes rather than an internal bodily signal (Toussaint et al., 2024). Today, the understanding of interoception has advanced considerably beyond Sherrington's initial classification, encompassing a more nuanced view of internal bodily signals.

The tendency to conceptualize 'exteroception' and 'interoception' as strict opposites has led to the emergence of conflicting positions in literature. The conventional perspective emphasizes the stimulus origin—exogenous or endogenous—suggesting that exteroception pertains to the sensory perception of external stimuli, while interoception, by contrast, must be triggered by internal stimuli (Ceunen et al., 2016). A key issue arises from the fact that many bodily sensations, though typically categorized as interoceptive, are often triggered by external stimuli; for instance, the sensation of cold can stem from external temperature changes rather than internal factors like illness (Ceunen et al., 2016). Given that the body constantly interacts with its environment, it is crucial to distinguish between the stimulus origin (exogenous vs. endogenous) and the nature of sensory perception (interoception vs. exteroception) (Ceunen et al., 2016). In the inclusive definition of interoception, the focus is not on whether the stimulus is exogenous or endogenous, but rather on whether the sensation provides information about the body's internal state or the external environment (Ceunen et al., 2016).

Notably, Craig (2003) made a significant contribution to redefining interoception, suggesting that it should be understood as "the sense of the physiological condition of the entire body, not just the viscera" (Craig, 2003). Craig's (2003) model fundamentally altered the understanding of interoception by suggesting that it reflects all signals regarding the homeostatic needs of the body (Craig, 2003). In this framework, sensations such as pain, itch, sensual touch and temperature – previously classified as exteroceptive – are redefined as interoceptive. These sensory modalities are integral to the interoceptive system because they provide continuous feedback on the body's internal state and its interactions with the external environment. In essence, pain, temperature, and sensual touch are now understood to be part of the interoceptive system, which monitors and regulates physiological conditions. By providing critical information about both internal and external conditions, these sensations allow the body to make necessary adjustments to preserve homeostasis, thereby ensuring survival and optimal functioning.

Craig (2003) further explored the interoceptive system, emphasizing the crucial role of the insula. He proposed that the dorsal posterior insula hosts a primary interoceptive representation, where bodily sensations—such as pain, temperature, itch, sensual touch, muscle and visceral sensations, vasomotor activity, hunger, thirst, and air hunger—are processed. Craig's work emphasizes that bodily sensations are not merely registered passively but are actively represented in dorsal posterior insula, creating a map of the internal body state (Craig, 2003). Additionally, Craig identified the right anterior insula as a key region where these interoceptive signals are integrated with emotional awareness. This integration, he argued, is vital for creating the subjective experience of self—a "feeling sentient entity" that synthesizes interoceptive information into a coherent representation of all feelings at a given moment (Craig, 2010). This model sets apart primates from non-primates; in non-primates the interoceptive system has a basic function of maintaining homeostasis (Craig, 2003). For instance, this category has a simpler neural organization where interoceptive signals are processed in more rudimentary brain regions dedicated to survival purposes. On the other hand, primates have been found to have a more advanced and complex primary interoceptive system which involves affective and motivational components of the anterior cingulate cortex (ACC; Craig, 2003). In humans, the activation of both the interoceptive cortex and the ACC enables the simultaneous experience of sensation and motivation (Craig, 2003). This feeling sentient entity, referred by Craig as 'physical self' is characteristic of human consciousness and is rooted in the interoceptive sense of the homeostatic condition of the individual, termed the 'material me' (Craig, 2003). According to Craig, while both primates and non-primates elaborate interoceptive information, primates possess a more sophisticated system that not only supports basic interoceptive awareness but also contributes to a complex self-awareness and emotional experience (Craig, 2003).

1.1.1 Neural Basis of Interoception

Craig (2003) aimed to clarify the neural mechanisms underlying interoception, focusing on identifying the physiological processes at the basis of the conscious awareness of bodily states. His research sought to understand how the brain integrates various sensory inputs from the body to produce a cohesive sense of both physical and emotional self. Through his work, Craig (2003) uncovered a hierarchical organization within the interoceptive system, where signals - such as cutaneous, muscular, visceral, and vascular - are transmitted to the central nervous system via small-diameter primary afferent fibers (Ad and C fibers) that ascend through the spinothalamic tract. Before reaching the thalamus, these signals undergo preliminary processing in the parabrachial nucleus (PB), which plays a crucial role in regulating cardiovascular, respiratory, energy, and fluid balances (Craig, 2003) The integrated homeostatic information from PB reaches the posterior ventral medial nucleus (VMpo) of the thalamus, where it is filtered and modulated and later transmitted to the insular cortex and higher cortical regions, the anterior cingulate cortex (ACC; Craig, 2003). The VMpo further receives input from the PB and the nucleus of the solitary tract (NTS; Craig, 2003) Once in the insular cortex, the interoceptive information is organized in a topographical manner, with the dorsal insula primarily involved in homeostatic regulation and the anterior insula responsible for integrating interoceptive signals with emotional and cognitive contexts (Craig, 2003). This integration within the anterior insula is crucial for forming a unified representation of the self as both a physical and emotional entity. he processed information is subsequently conveyed to the ACC, which Craig refers to as the "behavioral agent." The ACC is integral to the interoceptive system's role in enriching the subjective sense of self by incorporating affective and motivational aspects into the experience of bodily states.

Salvato and colleagues (2020) corroborated Craig’s (2002) findings through a meta-analysis of interoception studies, reinforcing the neural basis of bodily sensations (Fig. 1). Their analysis confirmed the involvement of the bilateral insulae, which are central components in Craig’s (2003) model (Salvato et al., 2020). Additionally, they identified the participation of the middle and anterior cingulate cortex, as highlighted by Craig (2003) for its role in linking emotion with interoception (Salvato et al., 2020). Furthermore, their findings revealed connections between the anterior insula and the ACC, along with activation clusters associated with interoception within the lamina I spino-thalamo-cortical pathway (Salvato et al., 2020).

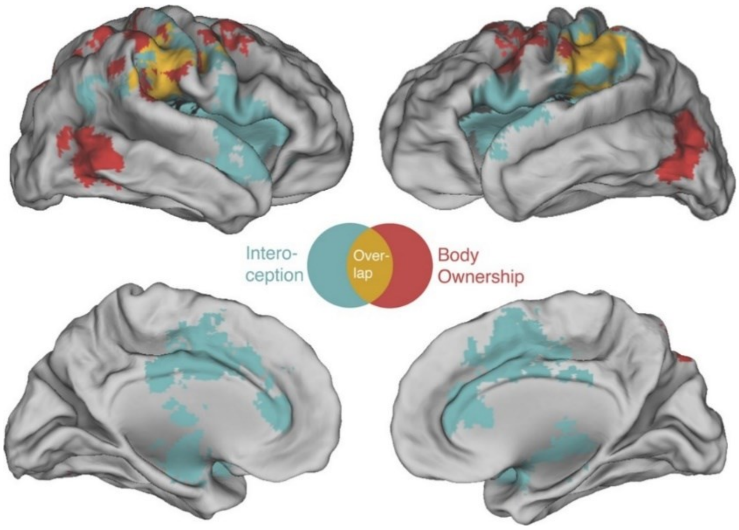

Figure 1. Overlapping activation of brain areas associated with interoception and body ownership (Salvato et al., 2020)

1.2 Bodily Self-Awareness

Experiencing the world through touch, sensing our body's presence, and being aware of our internal state and limb movements are fundamental aspects of human cognition. This awareness, known as Bodily Self-Awareness (BSA), is defined as “the feeling that conscious experiences are bound to the self as a unitary entity” (Salvato, 2020). BSA arises from the intricate and continuous perception and integration of a vast array of multisensory and motor signals (Aspell et al., 2012). Aspell and colleagues (2012) noted that one’s own body is possibly the most multisensory “object” in the world. These signals originate from various sensory modalities, such as vision, touch, and proprioception, which collectively contribute to the perception of the body as a unified whole (Salvato et al., 2020). Moreover, the significance of BSA extends beyond multisensory integration, including higher-order cognitive functions and emotional regulation (Tsakiris and Critchley, 2016). A pertinent model within this framework is the body matrix model proposed by Moseley and colleagues (2012). This model describes a dynamic representation of the body that maintains homeostatic control by integrating psychological and physiological parameters within a body-centred framework (Moseley et al., 2012).

Building on this, Riva (2018) proposed an extensive framework that offers insight into how we process and integrate perceptual information. According to this model, our perceptual experiences are not merely passive receptions of external stimuli; instead, they are actively shaped by the integration of sensory data with pre-existing information in our cognitive system (i.e., body memory) resulting in a predictive coding model (Riva, 2018; Fig.2). In this predictive coding framework, the brain continuously constructs and updates predictions about incoming sensory information based on prior knowledge and expectations, allowing us to make sense of the world in a coherent and contextually relevant manner.

Disruptions in bodily self-awareness are associated with neurological and psychiatric conditions, including Somatoparaphrenia (Salvato et al., 2015), Body Integrity Dysphoria (Salvato et al., 2022), and various manifestations of Disturbed sense of body ownership (in brief DSO; Gentsch et al., 2016). Understanding the mechanisms underlying bodily self-awareness can thus provide insights into these disorders and inform therapeutic interventions.

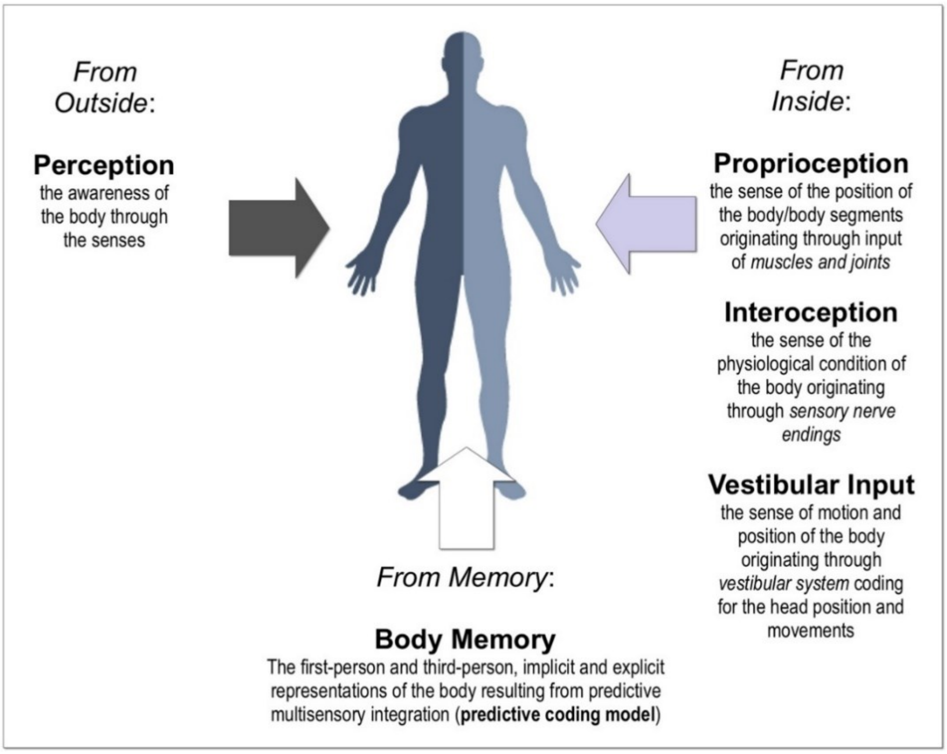

Figure 2. Body Memory Model (Riva, 2018)

Several components shape the experience of the self: the sense of ownership of one's body (body ownership), the feeling of control over one's actions and their outcomes (sense of agency), the perception of one's position in space (self-location), and the first-person perspective on the environment (perspective) (Salvato et al., 2020). Each of these dimensions plays a distinct role in shaping the self as an embodied entity, supported by the integration of this information into autobiographical knowledge (Balconi, 2010).

In theoretical discussions, the sense of agency and the sense of ownership are the two aspects of the self that constitute the minimal level of self-awareness (Balconi, 2010). Although typically referred to as two different concepts being part of the same structure (i.e., BSA), in everyday life situations we have a unified experience of ownership and agency. For instance, the deliberate act of writing with one's own hand is intricately linked with the sense of ownership over said hand. To study the interaction between the sense of agency and the sense of ownership, Kalckert and Ehrsson (2012) developed a variant of the rubber hand illusion designed to separate these two components. The paradigm required that the participant's real hand was hidden inside a box and on top of this box was placed a life-sized model hand. The index fingers of the model hand and the real hand were connected by a light stick attached to finger caps. By doing so, whenever the participant moved their index finger this caused the model finger to lift simultaneously. The authors found that both the sense of agency and the sense of ownership were triggered by the illusion and, crucially, they found that while these two concepts could be dissociated, they also had the potential to enhance each other (Kalckert and Ehrsson, 2012). Braun et al. (2014) confirmed these results and further demonstrated a double dissociation between the sense of ownership and the sense of agency. However, until now no neurocognitive model explains the interaction between the two components (Braun et al., 2018). On the other hand, self-location and first-person perspective coincide under normal circumstances and only in isolated cases the two concepts can dissociate (Blanke, 2012). For instance, Ehrsson (2007) reported an experimental induction of out-of-body experiences, where participants felt as though they were located outside their physical bodies and viewing themselves from this external perspective. This indicates that during the illusion, subjects experienced changes in both self-location and perspective, both of which were influenced by the illusion. Moreover, alterations in first-person perspective and self-location have been reported in neurological patients experiencing out-of-body experiences following focal brain damage (Blanke et al., 2002; De Ridder et al., 2007). Although these concepts require more in-depth investigation, they are undoubtedly essential for the awareness of the bodily self. These elements play a crucial role in shaping our understanding of how we perceive and experience our own bodies, influencing our sense of self-awareness and the way we relate to our physical presence.

1.2.1 Multisensory Integration

The above-mentioned integration of interoceptive, exteroceptive and proprioceptive information forms the foundation for the development of BSA (Salvato et al., 2020). Interoception has been toughly discussed above, however, for a complete understanding of BSA, it is essential to explore the roles of exteroceptive and proprioceptive information.

Proprioceptive signals, which convey information about the position of our body and its movements (de Vignemont, 2020), enable us to automatically assess our posture, and the tightness of our muscles without the need for visual information and, importantly, they play an essential role in motor control (Horváth et al., 2019). Proprioception, along with interoception and exteroception, constitutes the primary component utilized in experimental settings to alter the sense of agency and the sense of ownership (Serino et al., 2013).

Salvato and colleagues (2020) investigated how bodily self-awareness is constructed through the integration of internal and external sensory information. Specifically, for body ownership (Fig.1), the authors found that the signals converge in the bilateral supramarginal gyri (SMG), rolandic opercula, insula, right precentral, postcentral, and superior temporal gyri (Salvato et al., 2020). Importantly, Crivelli and colleagues (2021) demonstrated the critical role of coordinating exteroceptive, interoceptive, autonomic, and proprioceptive signals in sustaining a coherent sense of body ownership.

To develop a coherent sense of body awareness, proprioceptive, interoceptive, and exteroceptive signals must be integrated with visual, tactile, and vestibular information about the body's position and orientation in space (Ferrè and Haggard, 2016). The vestibular system, located in the inner ear, plays a crucial role by providing essential information for maintaining balance and coordination (Lopez and Blanke, 2011). The contribution of the vestibular system has been explored both in the healthy population (Lopez et al., 2010; Ferrè et al., 2015;

Lenggenhager and Lopez, 2015; Sedda et al., 2016) and in clinical populations by studying disorders such as somatoparaphrenia (Salvato et al., 2015; Spitoni et al., 2016; Salvato et al., 2018) and BIID (i.e., Body Identity Integrity Disorder; Lenggenhager et al., 2014). The application of Caloric Vestibular Stimulation (CVS), which involves irrigating the ear canal with warm or cold water to stimulate the vestibular nerve, temporarily restored body awareness deficits in patients with somatoparaphrenia (Salvato et al., 2018).

1.2.2 Neural Mechanisms of Bodily Self-Awareness

The intricate phenomenon of bodily self-awareness is supported by an extensive network of brain regions and neural mechanisms; however, there is currently no definitive evidence for a specific supramodal form of body awareness (Salvato et al., 2020). Instead, studies analyzing the neural networks of different components of BSA suggest that it arises from the dynamic interplay of multiple sensory and cognitive processes distributed across various brain areas.

One contribution to this complex phenomenon is proposed by Ionta and colleagues (2014), identifying a functional structural network involved in self-location and first-person perspective. This predominantly right-hemispheric network includes the bilateral temporoparietal junction (TPJ), right insula and right supplementary motor area (SMA). This network seems to be responsible for processing multisensory information associated with the two sub-components of BSA (Ionta et al., 2014). In relation to the sense of agency, Balconi (2010) noted that various brain regions are involved. Specifically, the premotor and prefrontal areas are implicated in encoding higher-level aspects of agency, while the parietal-cerebellar regions play a role in integrating sensory and motor information, predicting action outcomes, and correcting errors to ensure that actions align with intentions (Balconi, 2010). By utilizing positron emission tomography, Tsakiris and colleagues (2007) identified brain areas associated with body ownership, revealing activation in the right posterior insula and the right frontal operculum during the effective rubber hand illusion.

Serino and colleagues (2013) proposed a network supporting bodily-self processes focusing on body ownership and self-location (Fig.3). The authors highlight the role of the parietal and occipital cortices in separate processing of sensory signals, while the extrastriate body area (EBA) and the ventral premotor cortex (vMPc) are responsible for a unified body representation. The posterior parietal cortex (PPc) is proposed to be responsible for on-line mapping of different body parts, while body ownership is proposed to be modulated by off-line body representations. The insular cortices are highlighted for the importance in processing internal bodily states, allowing the internal experience of the body (Serino et al., 2013). Lastly, the authors highlighted the temporal parietal junction (TPJ) for the critical role in self-localization in a world-centered reference frame.

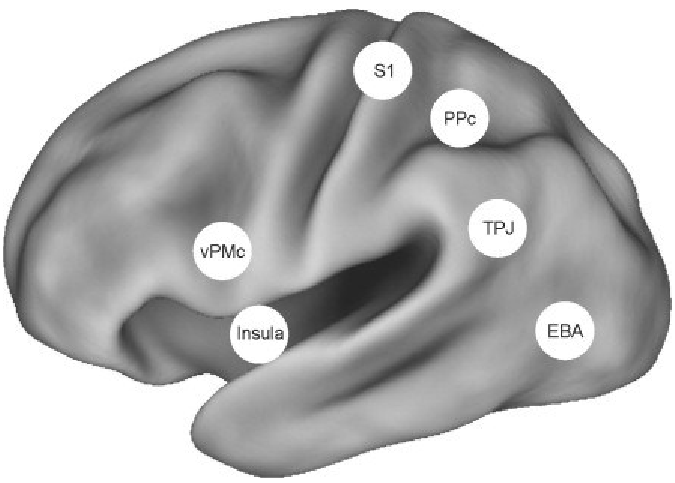

Figure 3. Neural mechanisms of bodily self (Serino et al., 2013)

1.3 Body Ownership

Among the notable contributions to this field are the studies by de Vignemont, which offer a comprehensive philosophical perspective on body ownership. Although body ownership can be succinctly defined as the "perceptual status of one's own body as belonging to oneself" (Tsakiris, 2007), the underlying concepts and theories are intricate and multifaceted.

de Vignemont (2011) anchors the concept of body ownership within the broader sense of embodiment, which Longo et al. (2008) define as the feeling of having a body. According to de Vignemont, body ownership is a critical subcomponent of embodiment. Essentially, body ownership is not an isolated phenomenon but rather an integral aspect of the comprehensive and multifaceted sense of embodiment, which encompasses all the sensory and cognitive processes that contribute to the experience of having and being in a body (de Vignemont, 2011) In the context of experimental studies on bodily awareness, the body model hypothesis (Preester and Tsakiris, 2009) posits that a realistic mental representation of the body must be maintained. Consequently, only anatomically shaped objects can be incorporated into the body schema. This hypothesis is supported by evidence indicating that objects resembling one's own hands can be integrated into the body schema, whereas non-anatomical objects cannot (Haans et al., 2008). However, this model does not account for situations where the body model is not strictly respected, such as the integration of a third fake limb, a phenomenon known as the supernumerary hand effect (Ehrsson, 2009; Newport et al., 2010). This flexibility highlights the brain's ability to dynamically adjust its body representation in response to novel or unexpected sensory experiences. Furthermore, de Vignemont (2011) suggests that body ownership is rooted in the assumption of ownership; the stronger the belief in this assumption, the more intense the feeling of ownership. In this framework, the degree of multimodal integration derived from the convergence of various sensory inputs strengthens the sense of ownership (de Vignemont, 2011).

Tsakiris (2010) proposed a neurocognitive model to explain how the brain generates the sense that one's body belongs to oneself. Central to this model is the integration of internal body maps with various sources of information. As illustrated in Figure 4, the model operates through a three-level mechanism. First, it involves comparing the internal body model with visual information. The second level assesses how the body's current posture (i.e., body schema, the body's current postural configuration) aligns with the posture observed through vision. The third level compares different sensory modalities, such as the visual perception of touch versus the actual tactile sensation. If all these comparisons align, the sense of ownership is established. The anatomical correlates for each of the three comparators are as follows: the first comparison involves the right temporoparietal junction (rTPJ); the second is supported by activity in the anterior parietal regions, including the primary and secondary somatosensory cortices; and the third comparison is underpinned by the posterior parietal cortex (PPC) (Tsakiris, 2010). Finally, the subjective experience of ownership is associated with activity in the right posterior insula, which is involved in the physiological regulation of the body (see Moseley, 2012).

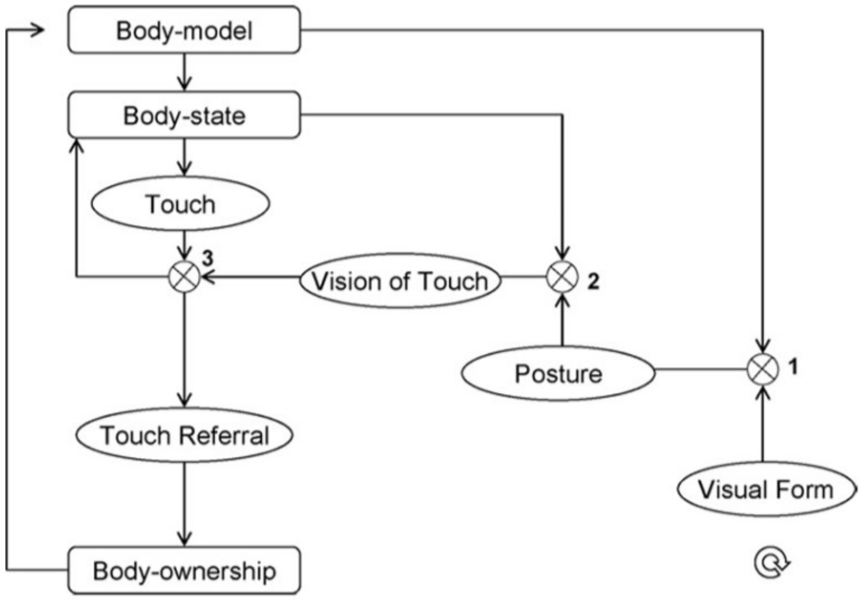

Figure 4. Neurocognitive model of the sense of body ownership (Tsakiris, 2010)

Salvato and colleagues (2020) further examined the neural correlates of the sense of body ownership. Through a meta-analysis, they identified a set of brain regions implicated in body ownership paradigms, including occipitotemporal, premotor, parietal, and insular areas; the temporal gyrus and the left inferior occipital lobe were found to be particularly involved, with their activation linked to the perception and identification of bodies (Salvato et al., 2020). An involvement of the insula has also been postulated (Craig, 2009; Moseley et al., 2012), given its role in self-awareness and interoceptive integration (Braun et al., 2018). However, Salvato and colleagues (2020) did not identify the insula as a site of activation when specifically analyzing brain activity during body ownership experimental paradigms.

1.3.1 Experimental Investigation of Body Ownership

Illusion paradigms play a key role in studies of bodily self-awareness. They offer a controlled scenario that enables researchers to induce alterations, disruptions, or expansions in the brain's standard perception of the body. The following sections outline the primary paradigms in recent research: the rubber hand illusion, mirror-box illusion and full-body illusion.

1.3.1.1 Rubber Hand Illusion (RHI)

Originally developed by Botvinick and Cohen (1998), the rubber hand illusion (RHI; Fig.5) integrates visual, tactile, and proprioceptive inputs to investigate how the sense of body ownership can be disrupted. In the original experiment, participants were seated at a table with one hand resting on its surface, while a standing panel obscured the hand from their sight. A realistic rubber hand was positioned directly in front of them. Participants were instructed to focus their gaze on the artificial hand while two paintbrushes were used to synchronously stroke both the hidden real hand and the rubber hand for 10 minutes. Participants were then asked to complete a questionnaire to assess perceptual effects experienced over the rubber hand. Analysis of the responses revealed that participants reported feeling the sensation of touch on the rubber hand, indicating the effectiveness of the illusion (Botvinick and Cohen, 1998). In a second experiment in the same study, Botvinick and Cohen (1998) extended the conditions' duration to investigate proprioceptive distortions. The results showed that participants felt their real hand had shifted toward the rubber hand, with the extent of this drift increasing as the illusion persisted (Botvinick and Cohen, 1998). This phenomenon, now recognized as proprioceptive drift, has become a crucial aspect of experimental research on the rubber hand illusion. Notably, when the brushing of the hidden real hand and the rubber hand was slightly asynchronous, the prevalence of the illusion was significantly reduced compared to the synchronous brushing condition (Botvinick and Cohen, 1998).

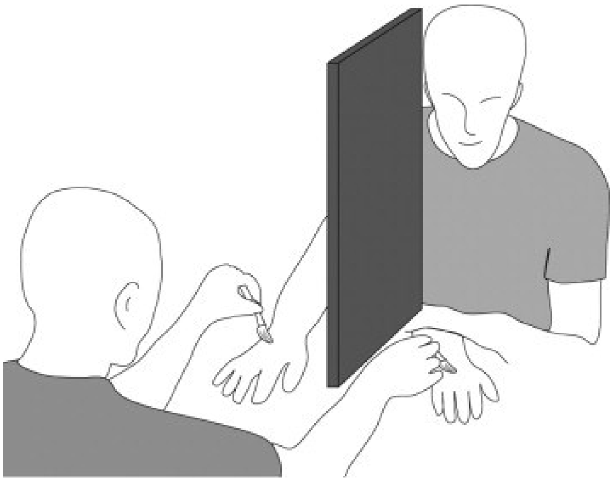

Figure 5. Rubber hand illusion set-up (Moseley et al., 2012)

Following the introduction of the RHI, researchers have adjusted the experiment in many ways to better understand its key elements. Nevertheless, three crucial factors have emerged as necessary for the illusion to work: temporal and spatial congruency, along with a realistic anatomical positioning and aspect of the hand (Valenzuela Moguillansky et al., 2013; Brundin, 2020). The strength of the illusion has been found to be significantly reduced when the artificial object is incongruent with the human body, for example when the rubber hand is replaced by a wooden stick (Tsakiris and Haggard, 2005), a balloon (Kalckert et al., 2019), a tabletop (Armel and Ramachandran, 2003) or a 2-dimensional projection of a hand (Ijsselsteijn et al., 2006). Research on spatial congruency has shown that rotating the rubber hand by 180° or 270° clockwise weakens the strength of the RHI (Ehrsson et al., 2004; Tsakiris and Haggard, 2005). These findings highlight that the effectiveness of the RHI is influenced by more than just the integration of multisensory inputs, such as visual, tactile, and proprioceptive signals (Haans et al., 2008). Top-down accounts, such as the neurocognitive model of ownership proposed by Tsakiris (2010), suggest that our brain maintains a detailed cognitive model of our body's structure, proportions, and positioning. This internal body map doesn't just passively receive sensory information but actively influences how we interpret and integrate these inputs (Tsakiris, 2010).

Research has also explored the neural mechanisms underlying the RHI. Golaszewski and colleagues' (2021) systematic review revealed a significant involvement of the primary motor cortex in the disembodiment of the real hand, a process that occurs when the artificial hand is perceived as part of one's own body. Specifically, the authors found a significantly reduced motor-evoked potentials amplitude from the real hand when subjects experienced the rubber hand as their own (Golaszewski et al., 2021). Additionally, the review of neuroimaging data pointed to the involvement of the posterior parietal cortex in the recalibration of the perceived position of the real hand following the illusion (Golaszewski et al., 2021). Furthermore, evoked potential studies revealed interactions within the occipital-premotor network during the RHI, suggesting a hierarchical process that integrates multisensory inputs.

1.3.1.2 Mirror-Box Illusion (MBI)

The mirror box illusion paradigm (MBI) offers insights into the brain's ability to reconcile conflicting sensory information and adapt its perception of the body (Holmes et al., 2004). In this setup, the participant positions one hand behind a vertical mirror and places the other hand in front of it (Fig.6). The mirror is aligned so that the reflection of the visible hand appears to align with the position of the hidden hand. Participants are then instructed to perform synchronous movements with both limbs while observing the mirror image. The visual feedback provided by the mirror creates the illusion that the hidden limb is moving synchronously with the visible limb.

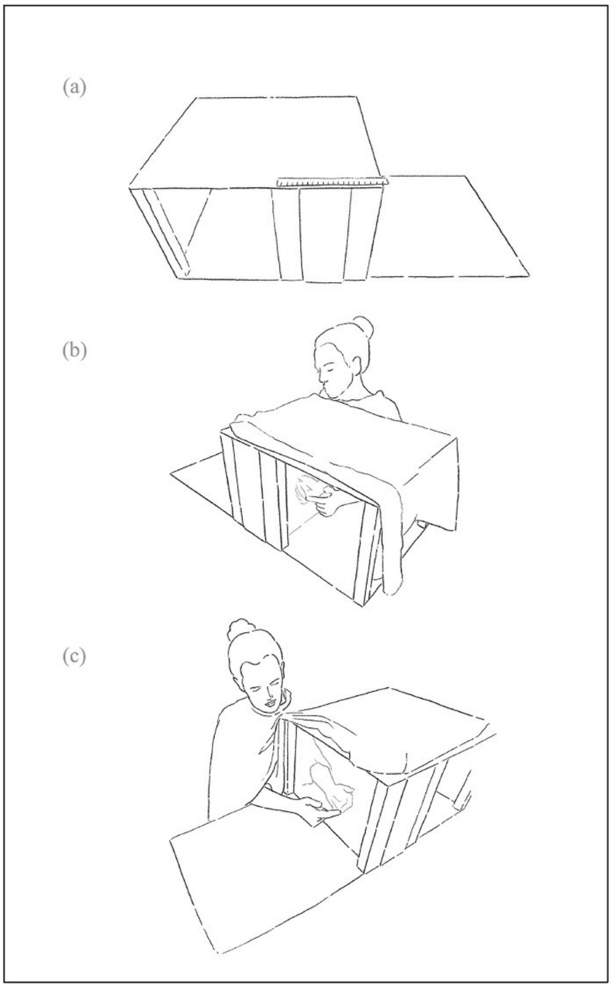

Figure 6. Mirror-box illusion set up (Crivelli et al., 2021)

Similarly to the RHI, the MBI can be explained as resulting from the integration of visual and somatosensory information (Metral et al., 2017). Nonetheless, the MBI offers distinct advantages over the RHI. Firstly, the reflected hand in the MBI appears realistic and avoids the incongruencies associated with the fake hand used in the RHI (Leach and Medina, 2022). Secondly, the MBI incorporates active movement, such as tapping on the mirror, which enables further exploration of the sense of agency (Leach and Medina, 2022). Thirdly, unlike the RHI, where the visuo-tactile procedure is applied unilaterally, both hands are actively engaged in touching the mirror's surfaces in both conditions in the MBI (Crivelli et al., 2021).

1.3.1.3 Full-Body Illusion (FBI)

Lenggenhager and colleagues (2007) first introduced the full-body illusion (FBI), during which participants experienced a virtual body as their own, experiencing an out-of-body sensation by mentally relocating their sense of self to a different spatial position. Similar to the previously mentioned illusions, the FBI is induced through the integration of visual, tactile, and vestibular information, resulting in a sense of embodiment within an external virtual body (Pyasik et al., 2020). In this experimental setup, participants either wear a head-mounted display (HMD) or view a screen that presents the back of a virtual body or mannequin from a third-person perspective, as though they were standing behind it (Fig.7). The participant's real body is hidden from view. To induce the illusion, the participant's back is stroked or touched in synchrony with the visual stimuli seen on the virtual body. The visual feedback provided by the HMD or screen allows the participant to see the virtual body being touched synchronously with the tactile sensations they are experiencing on their own body. This congruent multisensory stimulation leads the participant to perceive the virtual body as their own, leading to a shift in self-location towards the virtual body as if their "self" is now positioned within the virtual body (Lenggenhager et al., 2007).

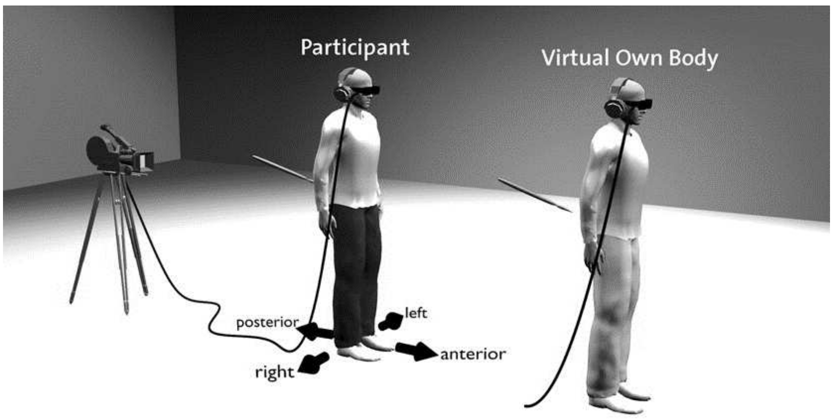

Figure 7. Full-body illusion set-up (Lenggenhager et al., 2007)

Maselli and Slater (2013) identified the building blocks of the FBI by examining three variations of the illusion. They determined that a first-person perspective is a requirement for the illusion to be provoked (Maselli and Slater, 2013). Additionally, their study showed that the realism of the virtual body, including factors like skin tone and clothing, significantly affects the illusion's intensity (Maselli and Slater, 2013). Interestingly, they found that when the virtual body closely resembled the physical body and shared the same posture, multisensory integration was not necessary to evoke the illusion (Maselli and Slater, 2013). However, visuo-tactile stimuli played a key role, enhancing the illusion when aligned and weakening it when misaligned (Maselli and Slater, 2013). Lastly, when the strength of the illusion was high, participants did not perceive incongruent visuo-tactile cues as incorrect (Maselli and Slater, 2013).

1.3.2 The Role of Skin Temperature in Body Ownership

The redefinition of temperature as a component of the interoceptive system has significantly influenced the trajectory of research in this field. As previously discussed, temperature plays a crucial role in conveying information regarding the body's physiological state and works alongside other interoceptive signals to maintain a coherent sense of self (Craig, 2003). This expanded understanding has prompted researchers to investigate how temperature, as an interoceptive signal, integrates with other sensory inputs to shape our perception of body ownership. From an evolutionary standpoint, thermoregulation is critical for survival, as it ensures the body’s core temperature remains within an optimal range (Crucianelli and Ehrsson, 2023). Incorporating thermoregulation into interoceptive research has highlighted its importance in the experience of body ownership. Moseley and colleagues (2008) made a significant contribution to understanding the relationship between body ownership and thermoregulation by identifying a connection between disturbances in body ownership and abnormal temperature regulation in certain pathological conditions, as anorexia nervosa and complex regional pain syndrome (CRPS). To investigate the relation between temperature and body ownership, the authors employed the traditional RHI (Moseley et al., 2008). They observed a decrease in temperature in the real hidden hand that correlated with the strength of the ownership illusion over the rubber hand (Moseley et al., 2008). However, these findings have not been consistently replicated, leading to varying interpretations and debates due to the conflicting results.

A first issue lies in the inconsistency of replicating the temperature change. An example of conflicting results is the study by Van Stralen and colleagues (2014), which reported a temperature drop associated with the RHI when slower stroking velocities were used, as these velocities evoke an affective touch sensation and enhance the RHI effect. However, in a subsequent experiment within the same study, although the increase in proprioceptive drift with slower stroking was replicated, the temperature change did not occur despite employing the same method (Van Stralen et al., 2014). Kammers and colleagues (2011) added a new interesting perspective on the relationship between skin temperature and ownership. First, they replicated previous studies by showing that the RHI did in fact lead to a temperature drop in the 'replaced' hand. Second, they applied temperature changes to the participants' hand, such as warming and cooling, affecting the participants' sense of ownership over a body part (Kammers et al., 2011). Specifically, cooling the participant's hand enhanced the strength of the RHI, whereas warming the hand externally reduced the illusion's intensity (Kammers et al., 2011). To further investigate the inconsistent results, de Haan and colleagues (2017) conducted five attempts using the RHI paradigm but were unable to replicate the temperature drop in the hidden hand. Despite employing the same methodological approaches and experimental conditions as those used by Moseley and colleagues (2008), de Haan and colleagues found no evidence of a temperature decrease in the hidden hand during the RHI (de Haan et al., 2017). The inconsistent replication of findings suggests that the relationship between body ownership and thermoregulation is complex and influenced by many factors such as experimental design, measurement methods, and variations in the administration of the RHI (de Haan et al., 2017).

Traditionally, research has emphasized a cooling effect in the hidden hand during the illusion, which was interpreted as a physiological correlate of disrupted body ownership (Moseley et al., 2008). However, emerging evidence has complicated this view, suggesting that the temperature response to the RHI may not be uniform and could vary under different conditions. In contrast to studies reporting a cooling effect, some researchers identified a warming response to the RHI. For instance, Llorens et al. (2017) found a slight increase in skin temperature in the hidden hand of healthy individuals who experienced a sense of ownership over the rubber hand. Palomo et al. (2018) reported similar findings, further suggesting that the RHI can lead to a temperature rise in the hidden hand rather than a decrease.

The sense of limb ownership has been also investigated in relation to the stimulated hand, finding differences between the perturbation of the right or left hand in right-handed individuals (Ocklenburg et al., 2011; Dempsey-Jones and Kritikos, 2019). For instance, Dempsey-Jones and Kritikos (2019) found that both right- and left-handed participants exhibited significantly less malleability to the RHI in their dominant hand compared to their non-dominant hand. These results suggest that the habitual use of the dominant hand leads to greater representational stability, making it more resistant to the illusion (Dempsey-Jones and Kritikos, 2019). This trend is further supported by findings in clinical populations, where patients with somatoparaphrenia often exhibit a pathological alteration in the sense of limb ownership specifically affecting the left non-dominant hand (Vallar and Ronchi, 2009).

Expanding on this, Crivelli and colleagues (2023) investigated the physiological response to body ownership perturbations in both hands of right-handed individuals, specifically by examining skin temperature changes. They applied a variant of MBI paradigm to both hands finding a bilateral decrease in hand skin temperature specific to the application of the illusion over the left hand, further indicating that the non-dominant hand is more susceptible to alterations in the sense of body ownership (Crivelli et al., 2023).

Recently, Tieri and colleagues (2017) investigated whether ownership in the context of virtual reality causes physiological changes in skin temperature following visual appearance of a virtual limb. The authors introduced a novel approach to the classical Visual Capture of Ownership (VCO) paradigm by incorporating Immersive Virtual Reality (IVR) along with continuous skin temperature recordings and subjective assessment of ownership (Tieri et al., 2017). Subjects were instructed to fixate on different stimuli: a realistic virtual hand, a wooden block as control condition that vaguely resembled a hand, and a 3D virtual ball as baseline condition (Tieri et al., 2017). A significant finding from this study was that the simple passive observation of the virtual hand in first person perspective elicited feelings of ownership, even in the absence of multisensory integration employed in traditional ownership paradigms (Tieri et al., 2017). The authors administered a subjective questionnaire to measure feelings of ownership and feelings of agency towards the virtual hand, both elicited by the illusion (Tieri et al, 2017). Of important note is the physiological change in skin temperature following the illusion. Specifically, the illusion provoked an increase in hand skin temperature in both hands (Tieri et al., 2017). However, the increase in skin temperature was less pronounced when participants viewed the realistic virtual limb compared to other non-realistic conditions, despite the subjective ratings indicating a stronger sense of ownership toward the realistic hand (Tieri et al., 2017). The next section provides an overview of our study, which expands on the research conducted by Tieri and colleagues (2017).

1.4 Current Study

This review provided an understanding of the intricate — and still not fully understood — concept of the 'body in the mind', which encompasses the different modalities in which we perceive and experience our own body and its parts. Despite progress in the field, the precise interactions between body ownership and body part temperature remain unclear, leaving significant uncertainties surrounding the role of interoception. This study aims to contribute to our evolving understanding of these complex interactions by building upon the work of Tieri and colleagues (2017).

Our first aim was to verify Tieri and colleagues' (2017) findings by applying the visual capture of ownership paradigm in a real-life setting. We focused on examining both behavioral and physiological responses to the paradigm. Specifically, we explored (i) the subjective experience of body ownership over an external hand using visual cues alone and (ii) the skin temperature-related outcomes associated with the paradigm's application. We expected that, unlike the virtual reality paradigm applied by Tieri and colleagues (2017), a real-life setting would lead to greater incorporation of the rubber hand, which would, in turn, significantly affect skin temperature modulation. Therefore, our primary hypothesis was that there would be a significant modulation of skin temperature in the experimental condition compared to the control condition.

Our second objective was to explore the impact of interoceptive sensitivity on body ownership and skin temperature modulation. As discussed earlier, prior research has identified a relationship between interoceptive sensitivity and skin temperature modulation (Craig, 2003; Tsakiris et al., 2011). Notably, Tsakiris et al. (2011) demonstrated that interoceptive awareness significantly contributes to modulating the sense of ownership in bodily illusion tasks. Building on these findings, we hypothesized that individual differences in interoceptive sensitivity would influence both behavioral and physiological responses to the illusion paradigm. Specifically, we expect a significant interaction between the different scales of the MAIA questionnaire and skin temperature modulation when comparing the experimental and control conditions.

2. Materials and Methods

2.1 Participants

25 healthy volunteers participated in the study (18 females and 7 males, mean age = 22.6, SD ± 2.36). Their education levels varied between 12 and 16 years (M = 14.4, SD ± 1.58). The Edinburgh Handedness Inventory (EHI) (Oldfield, 1971) was administered to ensure participants' right-handedness. Informed consent was obtained, and documentation regarding privacy and personal data handling was provided. The study was approved by the Ethics Committee of the University of Pavia and was conducted in respecting the ethical standards of the Declaration of Helsinki.

2.2 Experimental Procedure and Task

A modified version of the Visual Capture of Ownership (VCO) paradigm, adapted from Tieri et al., (2017) was employed. The experimental design was divided into two conditions: (i) experimental condition with the use of a rubber hand (RH); (ii) control condition with the use of a wooden block (WB) that resembled the general shape of a hand. The procedure for the two conditions was identical, differing only in the type of stimulus presented (RH or WB). Additionally, prior to both conditions, participants passively observed a fixation point, which served as control condition.

To maintain naivety, the experimental objectives were not disclosed to the participants. During the experiment participants were asked to position both their hands on a table; their left hand was occluded from the sight by a white, silk towel positioned on a vertical panel standing between the participants' hands (Fig.8). The hidden hand was placed by the experimenter in a slightly external position, while the experimental stimuli (RH, or WB) were placed in place of the left hidden hand, in an anatomical congruent position. In the experimental condition, the distance between the left real index finger and the left rubber index finger was standardized at 15 cm, a similar distance was adopted for the control condition. Firstly, participants were asked to indicate the perceived position of their hidden left index finger on a numbered line (i.e., pre-task pointing). They were instructed to fix the gaze on the rubber hand for 60 seconds. Thermographic measurements of both subjects' hands were recorded before and after the fixation period. Lastly, participants were asked to once again indicate the perceived position of their left index finger on the numbered line (i.e., post-task pointing) to assess an eventual proprioceptive drift.

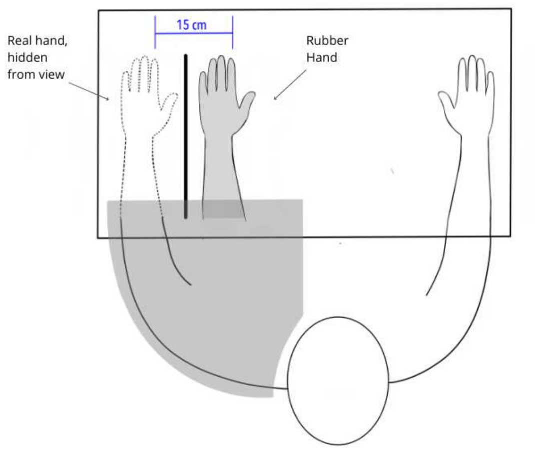

Figure 8. Experimental set-up

Other measurements adopted were a questionnaire to assess subjective feelings of ownership and agency, and the Multidimensional Assessment of Interoceptive Awareness (i.e., MAIA, Mehling et al., 2012) (Detailed descriptions of these measures are provided in the below sections). Finally, the State-Trait Anxiety Inventory (i.e., STAI, Spielberger et al., 1983) questionnaire (versions: STAI-1, STAI-2) was administered to evaluate possible states of anxiety that could influence the temperature measurements.

2.3 Measurements

2.3.1 Thermal Imaging

To avoid potential distortions in hand temperature measurement, a particular procedure was followed. First, the temperature of the room and of the table were controlled before starting the experiment and monitored during the temperature data analysis. An air conditioner kept the room temperature at 26 degrees Celsius. Before starting the experiment, all participants waited a 15-minute acclimatization period, during which they were asked to remain still and in a comfortable, relaxed position. During the acclimatization period, the experimenter verified that the temperature range of the participants' hands was between 26° and 36° C. The experiment only began if, at the end of the acclimatisation period, the temperature was relatively stable, i.e. it did not fluctuate more than 0.2 degrees centigrade for three consecutive measurements. Moreover, participants were required to position their hands on the table during the experiment, to avoid temperature fluctuations due to contact with external objects. Finally, participants were instructed to keep their eyes closed during temperature readings to avoid the eventual thermal response of the attention towards the limb (Crivelli et al., 2021).

Temperature measurements were taken using the advanced thermal imaging camera FLIR E76. A total of 24 measurements were taken during the experiment, organized in sets of 3 consequent recordings, following the procedure of previous studies (Crivelli et al., 2021; 2023; Salvato et al., 2018). The temperature data were analyzed before and after the fixation period in both the experimental and the control conditions. Both conditions were preceded by the passive observation of a fixation point in which temperature measurements were taken as a control.

Each measurement was analyzed employing the software FLIR Research Studio Version 3.1.0. The Regions Of Interest (ROIs) analyses included the skin temperature of the dorsal side of the hand and forearm of both the right and left arms (Fig.9).

Figure 9. ROIs for skin temperature analysis

2.3.2 Interoceptive Awareness

To assess the interplay between skin temperature modulation and interoception awareness we asked participants to fill the Multidimensional Assessment of Interoceptive Awareness (i.e., MAIA, Mehling et al., 2012), a self-report measure. In Table1 we report the eight scales of the self-report measure with a brief description.

Scale	Description
Noticing	Awareness of uncomfortable, comfortable, and neutral body sensations.
Not Distracting	Tendency to ignore or distract oneself from sensations of pain and discomfort.
Not Worrying	Emotional distress or worry with sensations of pain or discomfort.
Attention Regulation	Ability to sustain and control attention to body sensation.
Emotional Awareness	Awareness of connection between body sensations and emotional states.
Self-Regulation	Ability to regulate psychological distress by attention of body sensations.
Body-Listening	Actively listens to the body for insight.
Trusting	Experiences one's body as safe and trustworthy.

Table 1. Description of the eight MAIA scales (Mehling et al., 2012)

2.3.3 Subjective Reports

To evaluate the degree of feeling of ownership and vicarious agency, participants completed a questionnaire adapted by Tieri et al., (2017) for both conditions. The questionnaire (Table2) consisted of 15 items, including 12 from the original questionnaire and 3 additional items rated on a 7-point rating scale (-3 = strongly disagree to +3 = strongly agree). The questionnaire included six items concerning the feeling of ownership (3 experimental questions, 3 control questions) and six items related to vicarious agency (3 experimental questions, 3 control questions). Additionally, 3 questions were added to assess the perceived change in skin temperature (warmer, colder) of the left hidden hand and the perceived realism of the rubber hand.

		Item
Experimental – Ownership	1)	I felt as if I were looking at my own hand
	2)	I felt as if the rubber hand/wooden block were part of my body
	3)	I felt as if the rubber hand/wooden block were my hand
Control- Ownership	4)	It felt as if I had more than one left hand
	5)	It felt as if I had no longer a left hand
	6)	I felt as if my real hand were turning rubbery
Experimental – Agency	7)	It felt as if I could control the rubber hand/wooden block
	8)	I felt as if I could have caused the movement of the rubber hand/wooden block
	9)	It felt as if the rubber hand/wooden block were obeying or could obey my will
Control- Agency	10)	I felt as if the rubber hand/wooden block were controlling me
	11)	It felt as if the rubber hand/wooden block caused a movement of my hand
	12)	I felt as if the rubber hand/wooden block were controlling my will
Extra	13)	I felt as if my left hand were becoming colder
	14)	I felt as if my left hand were becoming warmer
	15)	How realistic did the rubber hand seem to you?

Table 2. Questionnaire to evaluate feelings of ownership and agency (adapted from Tieri et al., 2017)

2.3.4 Proprioceptive Drift

To evaluate the strength of the illusion, we measured proprioceptive drift. Participants were instructed to indicate the perceived position of their left index finger on a numbered line. The assessment was conducted before and after the two conditions, indicating baseline measurement and subsequent proprioceptive drift. This measurement was performed for both the experimental and the control condition. The proprioceptive drift value was calculated using the formula: proprioceptive drift = post-task proprioception – pre-task proprioception, indicating the shifting of the perceived position before and after the task.

3. Results

Data were analyzed using JAMOVI (version 2.3.28) (Jamovi, 2024).

3.1 Skin Temperature and Interoceptive Awareness

To assess the skin temperature response, we performed a 2-levels repeated measure ANOVA with the variables Condition (rubber hand, wooden block) and Side (right, left). We found no significant modulation of skin temperature following the task.

Considering that previous findings has demonstrated a link between interoceptive sensitivity and the malleability of body ownership (Tsakiris et al., 2011), we investigated whether interoception influenced ownership feelings and the subsequent effect on temperature. To analyze the impact of different variables of the experiment on skin temperature we conducted a repeated measures ANOVA with 2-levels (Condition x Side), adding each of the MAIA scales as a covariate. Specifically, our analysis focus on the ΔTemperature pre- and post-Conditions (Rubber hand, Wooden Block) for the right side (i.e., right hand) and left side (i.e., left hand). Significant results were found on one of the eight scales, the Trusting scale.

We found a main effect of Condition with a large effect size ($F=7.561$, $p = .012$, $\eta^2p = 0.256$). Additionally, we found an interaction effect Condition by Trusting with a large effect size ($F=5.939$, $p = .023$, $\eta^2p = 0.213$), indicating that the bilateral skin temperature effect is mediated by the Trusting subcomponent of interoception awareness as defined by the MAIA test.

The variable Side showed no main effect and its interaction with the other variables was not significant, meaning that there was no significant difference in skin temperature between the right and left hand.

3.2 Subjective Reports

To analyze the subjective feelings of ownership, agency, and temperature perception reported by the participants we chose to compare reports across conditions (Rubber hand, Wooden block). First, the Shapiro-Wilk test was conducted to examine the distribution of the collected data, which did not follow a normal distribution. Consequently, we employed a Wilcoxon signed-rank test for paired samples.

The analysis of the questionnaire resulted in a significant difference between means for experimental ownership ($W=231.0$, $p < .001$) and agency measurements ($W=177.5$, $p<0.001$) among conditions. In figure 9 and figure 10 we report the descriptive plots of ownership and agency.

The same analysis was computed on the values of the questionnaire assessing subjective feelings of temperature (warm, cold) for both conditions, resulting in a non-significant difference between means. Participants did not report a feeling of temperature changes neither during the experimental conditions nor during the control conditions, differing from the results obtained by Tieri et al. (2017). Importantly, this result highlights a discrepancy between the actual skin temperature change reported above (i.e., skin temperature measurements) and the subjective feeling of the change in temperature.

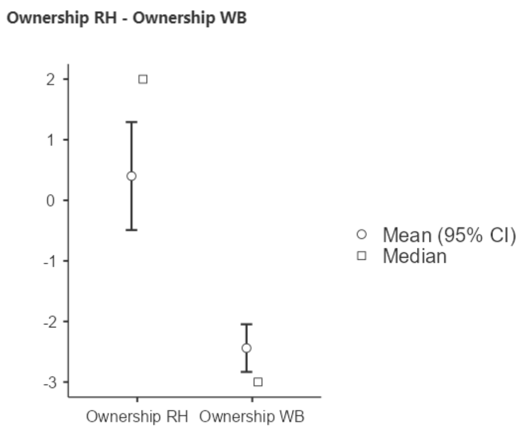

Figure 10. Ownership Rubber Hand - Ownership Wooden Block

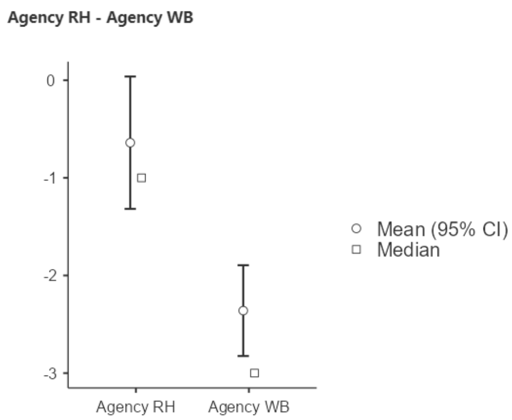

Figure 11. Agency Rubber Hand - Agency Wooden Block

3.3 Proprioceptive Drift

We performed a Shapiro-Wilk test to assess the normality of the data, which revealed a non-normal distribution. As a result, we computed a Wilcoxon signed-rank test for paired samples to analyze the data. ΔProprioceptive drift was significant in the experimental condition ($W=0.753$, $p<.001$), whereas it was not significant in the control condition. However, there was only a marginal difference between the means ($p = .057$), which was not sufficient to declare a significant result.

4. Discussion

Bodily self-awareness arises from the complex interplay of different perceptive channels. Considering the role of multisensory integration in the formation of bodily self-awareness (Salvato et al., 2020), it is important to investigate the reciprocal relationship between these components. However, although interoception has been proven to have a role in the formation of the self (Craig, 2002), its definition and its measurement remain a challenge. One major difficulty in measuring interoception arises from its variability depending on the measure adopted. Objective, subjective and metacognitive aspects of interoception lead to inconsistent results (Garfinkel and Critchley, 2013). To address this issue, Garfinkel and colleagues (2015) developed a three-dimensional model which dissociates three components of interoception: interoceptive-accuracy, sensibility and awareness. Interoceptive accuracy refers to the behavioral examination of objective performance. Interoceptive sensibility is evaluated through self-reports concerning sensitivity to bodily signals. Lastly, interoceptive awareness concerns the metacognitive aspects of interoception, and reflects individual awareness.

This current study was built upon the work of Tieri and colleagues (2017). Our primary objectives were the verify Tieri and colleagues' (2017) temperature-related results in response to the application of the VCO paradigm, without incorporating Virtual Reality (VR). Secondly, this study aimed to explore the role of interoception in relation to body ownership and skin temperature.

To further investigate the relationship between the manipulation of body ownership and skin temperature response, we applied the paradigm designed by their research group, the Visual Capture of Ownership (VCO), adapting it to our research aims. The main difference was the shift from VR setting to a real-life setting with the use of a real rubber hand. Additionally, our interest in achieving a deeper understanding of the interoceptive mechanism, lead us to integrate specific implicit and explicit measures. To this aim, we collected a self-report measure of interoception through the use of the Multidimensional Assessment of Interoceptive Awareness (MAIA; Mehling et al., 2012). A further difference, linked to our interest in assessing the change in skin temperature before and after conditions, consisted in recording temperature readings pre- and post-conditions, rather than using continuous recording as in Tieri and colleagues (2017). Lastly, we chose to add three questions to the subjective assessment of interoception, two questions related to the perceived sensation of skin temperature change (colder, warmer) and one additional question investigating the perceived realism of the rubber hand to explore also subjective sensation of the eventual skin thermal response.

To summarize, we analyzed four dimensions: (1) skin temperature measurements, (2) interoceptive sensibility by administering the MAIA questionnaire, (3) subjective measures of ownership and agency by adapting the questionnaire used by Tieri to our study and, (4) behavioral measure through proprioceptive drift to assess the strength of illusion.

4.1 Skin Temperature Response

In their study, Tieri and colleagues (2017) found a significant modulation of temperature depending on the virtual limb's visual appearance. Specifically, they found a large temperature increase during the observation of non-realistic virtual limbs (about 0.14 °C) and a slight increase during the observation of the realistic limb (about 0.02 °C). However, our results did not replicate these findings. Our thermal imaging analysis between pre- and post-condition did not result in any significant skin temperature modulation. Therefore, our results suggest that mere observation of a rubber hand is not sufficient to provoke a change in temperature as in the original rubber hand illusion per sè, where visuo-tactile integration has been proven to be an essential element for temperature effects to be evoked (Tsakiris et al., 2010). Nevertheless, it is important to remember the differences in methodologies between the two studies; especially the replacement of Immersive Virtual Reality (IVR) with a real-life rubber hand, which could have resulted in different skin temperature modulation. This alteration results not only in a methodological difference, but also in a perspective difference: the use of IVR allowed subjects to have a different first-person perspective compared to the perspective evoked by a real-life scenario (Tieri et al., 2017). As Tieri and colleagues (2017) explained, this specific perspective could have led to a unification of the overall body representation, giving rise to a 'replacement' of the real hand rather than disownership feelings towards the hidden hand. The match between proprioceptive information and visual information of the virtual hand could result in different temperature outcomes compared to the classical rubber hand illusion paradigm, where there is a mismatch between the proprioceptive information coming from the real hand and the vision of the rubber hand. As reported by Haghzare (2024), realistic virtual reality can provoke a stronger sense of embodiment, affecting the experience of body ownership. Moreover, the author reports that physiological parameters used in IVR have a significant effect on perceived body ownership (Haghzare, 2024). Additionally, Tsakiris and colleagues (2011) claim that the congruency of visual form, anatomy, and volume modulates the experience of body ownership. In fact, in the original VCO paradigm, the avatar's size and the point-of-view of each participant were adjusted accordingly. This variation is limited when using a rubber hand. Therefore, the different outcomes in temperature can be attributed to variations in methodologies. It would be interesting to further analyze embodiment comparing real-life and virtual scenarios. This approach could provide valuable insights into the similarities and differences in body ownership and multisensory integration across different contexts.

4.2 Skin Temperature Response in Relation to Interoceptive Awareness

Previous research on the relation between interoception and susceptibility of the body representation led us to further explore this topic. Specifically, Tsakiris and colleagues (2011) found that subjects with low interoceptive sensitivity were more susceptible to the illusion of ownership toward an external hand in the context of the RHI paradigm. Our analysis resulted in an interplay between skin temperature modulation and interoception awareness. This second analysis provided context and explanation for the unexpected null result of our first hypothesis. Specifically, we found a thermal modulation based on the condition and a significant interaction between the condition and one of the scales of the MAIA test, the Trusting scale. For a deeper understanding of this result, a specific description of the Trusting component of the MAIA scale is needed. Mehling and colleagues (2012), the authors of the MAIA, developed the Trusting scale as a measure of attitude of interoceptive awareness and it refers to how individuals relate to bodily signals. As the authors stated, trusting or viewing bodily sensations as valuable for decision-making is a crucial aspect of the sense of self (Mehling et al., 2012). This dimension of the scale was developed as a measurement of factors influencing the perceived sensations; trusting body sensation reflects the extent to which one believes that body awareness is relevant for decision making or health (Mehling et al., 2012). The specific Trusting items are: (i) 'I am at home in my body', (ii) 'I feel my body is a safe place', (iii) 'I trust my body sensations' (Mehling et al., 2012).

Of important note is that the broad concept of interoception interacts both with cognition and emotion (Garfinkel et al., 2015). Interoception includes the metacognitive component of one's own perception of awareness; this additional component underlies individual differences in conscious processing of internal bodily cues and beliefs related to our own perception (Garfinkel et al., 2015). Specifically, individuals prone to anxiety seem to exhibit an altered interoception prediction between observed and expected bodily states and an enhanced interoceptive processing (Garfinkel et al., 2015). Therefore, we can read our results as an important signal in considering not only different dimensions of interoception but also individual variabilities, especially when measuring interoceptive awareness.

In support of these findings, we should consider that interoception is not only a bottom-up process (Enmalm, 2020). As Enmalm (2020) reported, interoception has been classically studied as an only afferent process; however, Seth (2013) defined it as both a bottom-up and top-down process, able to cause behavioral changes. While interoception is classically thought of as only afferent, meaning one way from the body to the brain, Seth (2013) argues interoception to be involved in both bottom-up and top-down processes, as the afferent stimulus directly causes not only an emotional shift, but also a behavioural change. As highlighted before, Tsakiris and colleagues (2011) addressed this question by investigating how interoceptive awareness may influence bodily representations. The authors found that interoceptive sensitivity predicts the degree to which body ownership can be altered during the RHI manipulation; specifically, low interoceptive sensitivity resulted in a stronger illusion compared to high interoceptive sensitivity (Tsakiris et al., 2011). To this matter, our decision to include a measure of interoceptive awareness aimed at exploring the relationship between interoceptive accuracy and awareness, indicating an influence of the latter. Tsakiris and colleagues (2011) report two possible explanations to this matter. First, this modulation could be attributed to a different allocation of attentional resources; individuals with low interoceptive awareness could allocate greater attentional resources to the illusion because they are less aware of their internal states, intensifying the illusion (Tsakiris et al., 2011). Another explanation is that individuals with high interoception awareness prioritize both interoceptive and exteroceptive information, leading to a more integrated processing of perceptual cues (Tsakiris et al., 2011). In contrast, individuals with low interoceptive awareness, who may primarily focus on exteroceptive information, resulting in different outcomes (Tsakiris et al., 2011).

To conclude, we strongly highlight the importance of studying the weight of interoceptive signals in body ownership illusions and, generally, in forming a body representation.

4.3 Subjective Experience of Ownership and Agency

Moreover, we obtained interesting results by analysing the subjective experience reported by the participants. Specifically, we are referring to the reports of the questionnaire adapted from Tieri et al. (2017), above described in detail. We performed an analysis of the questionnaires comparing conditions, analysing experienced ownership and agency. We replicated the results obtained in the original VCO experiment: simple passive observation of the fake hand was sufficient to elicit both ownership feelings and agency feelings. Traditionally, extensive literature highlights the importance of multisensory integration to evoke feelings of embodiment (Moseley et al., 2012; Makin et al., 2008); as shown by studies with the Rubber Hand Illusion (Ehrsson et al., 2004; Kammers et al., 2009), Mirror Box Illusion (Crivelli et al., 2021; Leach and Medina, 2022), Full Body Illusion (Maselli and Slater, 2013; Salomon et al., 2013), Virtual Rubber Hand Illusion (Yuan et al., 2010; Slater et al., 2008). However, recent literature has demonstrated that embodiment can be evoked even in the absence of multisensory integration. For example, Sadibolova and Longo (2014) demonstrated that participants who looked at their own hand, without any additional stimulation, had increased skin temperature in the observed hand, but not in the contralateral hand. Taken together, these findings highlight the importance of investigating subjective feelings of ownership and subsequent temperature modulation following visual stimulation paradigms of ownership compared to paradigms employing multisensory integration.

Additionally, to investigate the reported sensations of temperature changes, we analysed the two extra items added to Tieri’s and colleagues' (2017) subjective questionnaire (i.e., warmer or colder feeling after the illusion). By comparing the reported questions between the experimental and control conditions, we found no significant results, meaning that participants did not report a sensation of their left hand becoming colder or warmer after the experiment. However, the reported feelings did not match with the skin temperature changes detected. Further studies are needed to investigate the relationship between skin temperature and the sensation of temperature changes. However, one possible reason behind those results could be found in individual degree of awareness of bodily sensations.

4.4 Behavioral Measure of Proprioceptive Drift

Lastly, the proprioceptive drift was also studied, a measurement used as an implicit value for the embodiment of the rubber hand. Participants were asked to indicate the position of their hidden left index finger before and after the illusion, based on the knowledge that participants’ judgment is biased toward the position of the artificial hand when the illusion has an effect (Fuchs et al., 2016). However, we report non-significant results in terms of shift of the felt position of the hand. One reason behind the absence of the expected displacement might be the missing multisensory integration. However, dissociations between feelings of ownership and the behavioral measurement of proprioceptive drift have been reported before: Rohde and colleagues (2011) report this dissociation in their study, leading the authors to suggest that different processes are involved in the two phenomena. Moreover, Critchley and colleagues (2021) found only a partial correlation between proprioceptive drift and subjective ratings, suggesting that the two measures are independent. According to the authors, these measures might reflect different measures of body ownership (Critchley et al., 2021). Specifically, body location could be linked to proprioceptive drift while the subjective experiences reported are linked to the actual body ownership (Critchley et al., 2021). Further studies might analyze the dissociation between feelings of ownership and agency and proprioceptive drift when studying ownership through visual capture.

4.5 Remarks on Inconsistency Among Measurements

Of important notice for this study is the inconsistency between measurements results. Specifically, we observed (i) an increase in temperature that did not correspond with the participants' reported sensation of temperature change, (ii) the increase in temperature that was not accompanied by a proprioceptive drift following the illusion, and (iii) a reported feeling of ownership and feeling of agency towards the rubber hand that did not align with measurements of proprioceptive drift. The inconsistency between temperature perception and reported sensation suggests a disconnection between objective temperature measurements and reported sensation of temperature change, highlighting the complexity of accurately capturing sensory perception through quantitative means. While the absence of proprioceptive drift when compared to the temperature increase and the reported ownership and agency, indicates a potential decoupling between the measurements.

Such inconsistences in measurements within bodily illusions paradigms are not uncommon. In their study, Critchley and colleagues (2021) highlight a relevant challenge in the field of body ownership, bodily illusions and interoception: the difficulty in identifying objective measures of physiological signals not influenced by individual variables. Their study, similarly, to the present study, revealed an independence between proprioceptive drift and subjective ratings (Critchley et al., 2021). The authors suggested a that the two measures might relate to different dimensions of bodily ownership, respectively body location and body ownership (Critchley et al., 2021). Moreover, the authors focus on the impact of social factors and individual factors (e.g., suggestibility, implicit task requirements, response bias) which have been reported to explain around 10% of the variability in subjective measures of the rubber hand illusion (Critchley et al., 2021). Romano and colleagues (2021) further explored the influence of individual differences on the rubber hand illusion. The authors focused specifically on empathy and self-esteem, finding a relation between the two constructs and the sense of body ownership (Romano et al., 2021).

Furthermore, research has indicated that the proprioceptive drift measure is distinct from the reported sense of ownership (Rohde et al., 2011). This indicates that although participants may experience a sense of ownership over the rubber hand, their proprioceptive sense of where their actual limb is located may not shift correspondingly. Other studies found no correlation between temperature and proprioceptive drift in the rubber hand illusion (Kocur et al., 2022; de Haan et al., 2017). On the same line, other studies found no significant correlation between subjective measures of ownership and temperature (Crivelli et al., 2021; Lang et al., 2021; Kammers and Haggard, 2011).

In conclusion, such findings highlight the complexity of body ownership studies and the interplay between various factors in body perception. Moreover, these findings underscore the need to consider how different aspects of body representation and ownership might be influenced by distinct perceptual processes and individual differences. They reveal that illusions as the rubber hand illusion and, in our case, the visual capture of ownership, involve complex mechanisms influenced also by subjective experiences. This highlights once again the nuanced nature of how our brain constructs and maintains a coherent sense of self. Therefore, future studies in this field would benefit from considering how this complexity contributes to the overall experience of the self.

5. Conclusion

The present study investigated the relationship between body ownership manipulation and skin temperature response by applying the VCO paradigm in a real-life setting. A central aspect of the current research was to explore the concept of interoception, particularly how individual sensibility to internal bodily signals might interact with or influence the VCO paradigm. The findings indicated that visual information alone was not sufficient to induce changes in skin temperature. However, a deeper examination of the data revealed that this lack of temperature effects could be explained by our second hypothesis, which posited that interoceptive sensibility plays a critical role in body ownership paradigms. Our findings demonstrated an interplay between skin temperature modulation and interoception awareness, highlighting the impact of individual differences in processing interoceptive information. By applying the VCO paradigm in a real-life context and focusing on the role of interoception, this study aimed to contribute to the current understanding of the literature. The results underscore the importance of considering a range of factors when applying body ownership paradigms, particularly the influence of individual differences in interoceptive components, such as interoceptive sensibility.

6. References

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