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Interoception as independent cardiac, thermosensory, nociceptive, and affective touch perceptual submodalities

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Abstract

Interoception includes signals from inner organs and thin afferents in the skin, providing information about the body's physiological state. However, the functional relationships between interoceptive submodalities are unclear, and thermosensation as skin-based interoception has rarely been considered. We used five tasks to examine the relationships among cardiac awareness, thermosensation, affective touch, and nociception. Thermosensation was probed with a classic temperature detection task and the new *dynamic thermal matching task,* where participants matched perceived moving thermal stimuli in a range of colder/warmer stimuli around thermoneutrality. We also examined differences between hairy and non-hairy skin and found superior perception of dynamic temperature and static cooling on hairy skin. Notably, no significant correlations were observed across interoceptive submodality accuracies (except for cold and pain perception in the palm), which indicates that interoception at perceptual levels should be conceptualised as a set of relatively independent processes and abilities rather than a single construct.

Introduction

Interoception has been defined as the body-to-brain axis of sensations concerning the state of the visceral body (Cameron, 2001; Sherrington, 1948), thus involving signals originating from within the body (e.g., cardiac, respiratory, and digestive functions). However, physiological and anatomical observations led to a redefined and extended concept of interoception that encompasses information about the physiological condition of the entire body (Craig, 2002; Khalsa, Rudrauf, Feinstein, & Tranel, 2009), including signals originating from the body surface carrying thermal, noxious, and pleasant tactile signals (Crucianelli & Ehrsson, 2022). Such signals are conveyed by specialised afferent pathways from the spinal cord through the ventral medial posterior nucleus of the thalamus to the insular cortex (Björnsdotter, Löken, Olausson, Vallbo, & Wessberg, 2009; Craig et al., 2000; Kastrati et al., 2022), a cortical area involved in the processing of interoceptive information, including visceral signals. The posterior insula has strong anatomical connections to the anterior insula, where further processing and integration of various types of interoceptive signals occur; overall, the insular cortex has been proposed to be a critical region for interoceptive awareness and the experience of emotions (Critchley et al., 2004). Importantly, interoception is related to the generation of bodily (affective) feelings, informing the organism about its bodily needs and maintenance of homeostasis, and ultimately survival (Craig, 2003, 2008, 2009; Seth, 2013; von Mohr & Fotopoulou, 2018).

Traditionally, interoception has been quantified using heartbeat detection tasks (Schandry, 1981), in which participants are asked to focus on their own heartbeats by just feeling the sensation of their heart beating in the chest. This task has been widely used and studied, is easy to implement, and captures an important aspect of visceral bodily awareness. Moreover, heartbeat-evoked potentials have been related to activity in interoceptive brain networks, such as the anterior insular cortex (see Coll et al., 2021 for a review and meta-analysis). However, the heartbeat counting approach has several problems and limitations (please see Zamariola et al., 2018; Ainley et al., 2020; Zimprich et al., 2019; Corneille et al., 2020 for a full account of the recent debate). Performance in heartbeat detection tasks can be influenced by factors other than awareness of the heartbeats themselves, such as prior knowledge of typical baseline heart rates, differences in actual heart rates (that influence the difficulty of the task), practice, and variations in precise experimental instructions (Ring & Brener, 1996; Ring et al., 2015; Zamariola et al., 2018; Corneille et al., 2020; Desmedt et al., 2020). In addition, some participants use alternative bodily strategies to solve the task, such as feeling pulsations in the extremities (e.g., fingers and feet, Murphy et al., 2019), tensing their muscles, holding their breath or otherwise changing their respiration, and such strategies can bias the outcome measures (Ross & Brener, 1981; Whitehead & Drescher, 1980). From a physiological point of view, heartbeats produce a multitude of bodily signals that are not restricted to sensory information about the mechanical and chemical state of the heart but also include sensory inputs from secondary effects such as vascular reactivity, muscle contractions, and pulsations in other body parts. Moreover, an obvious limitation of the heartbeat counting task is that the sensory signal is not under experimental control, making it difficult to use classic perception science approaches to characterise the relationship between the sensory signal strength and subjective perception. In contrast, it is easy to deliver stimuli on the skin, making skin-based interoception an attractive complement to cardiac interoception from an experimental perspective.

Over the last two decades, there has been increasing interest in skin-mediated interoceptive modalities, such as pain and affective touch (Craig, 2002; 2003; Werner et al., 2009; Björnsdotter, Morrison & Olausson, 2010; Weiss et al., 2014; von Mohr & Fotopoulou, 2018). To a large extent, this interest has been driven by studies on affective touch, which are motivated by the discovery of a specialised group of skin afferents in humans called C-tactile afferents (CT; Vallbo, Olausson & Wessberg, 1999). CT afferents are ‘low-threshold mechanoreceptors’ in mammalian hairy skin that are sensitive to light touch, and microneurography studies in humans have shown that they discharge optimally to gentle moving stimuli such as moving finger or light brush over the skin. CT afferents have a significantly higher density in human hairy skin (Nordin, 1990; Vallbo et al., 1993, 1999) and are only sparsely present in glabrous skin (Watkins, Dione, Ackerley, Backlund Wasling, Wessberg, & Löken, 2020). CT afferents have been proposed as a key sensory system for the detection of affective touch (Löken et al., 2009; Morrison, Löken & Olausson, 2010), and CT signals reach the posterior insular cortex (Björnsdotter et al., 2009 but see Gazzola et al., 2012). As mentioned above, nociceptive and thermosensory information also reach the insular cortex (Craig et al., 2000; Kastrati et al., 2022).

Although pain, thermosensation, and affective touch are often mediated by external causes and events occurring on the skin, nociceptive and thermosensory signals can also originate from within the body, and these modalities are homeostatically relevant since they provide information about physiological safety or threats (Craig, 2003; von Mohr & Fotopoulou, 2018;

Crucianelli & Ehrsson, 2022). However, compared to affective touch, relatively little attention has been given to the perception of temperature as a skin-mediated interoceptive modality (Craig et al., 2000; Craig, 2014).

The perception of temperature is mediated by thermoreceptors, which are free nerve endings that signal sensations of warmth and coolness (Sinclair, 1981; Abraira & Ginty, 2013; Filingeri, 2011; Jänig, 2018 for reviews). The skin is innervated by different types of afferent fibres encoding temperatures that can range from noxious cold to noxious heat, with innocuous cold and innocuous warm perception between the two extremes (Jänig, 2018 for a review). In particular, the perception of cold is mainly mediated via Aδ fibres (range ≈ 5–40°C; maximally discharging at approximately 30°C) and C fibres (e.g., Hensel et al., 1960; Iriuchijima & Zotterman, 1960; Iggo, 1969; Hensel & Wurster, 1969; Hensel & Iggo,1971; Darian-Smith et al., 1973; Dubner et al., 1975; Kenshalo & Duclaux, 1977; Jänig, 2018 for a review). Cooling (but not warming) of the skin also activates unmyelinated, low-threshold mechanoreceptors (CTs; Nordin, 1990). In contrast, warmth perception is mainly mediated by C fibres (range ≈ 29–45°C; maximally discharging at approximately 45°C, e.g., Iriuchijima & Zotterman, 1960, Hensel & Huopaniemi, 1969, Konietzny & Hensel, 1975; 1977; La Motte & Campbell, 1978; Hallin et al.; 1982). C fibres also contribute to pain. Temperatures ≈ < 15 and > 45°C activate cold and hot nociceptors, respectively (Kandel et al., 2000, Jänig, 2018; Table 1). Many C-fibre afferents are polymodal, i.e., they respond to various combinations of thermal, mechanical, and chemical stimuli. C afferents are the most common receptor type in the body and are believed to represent an important source of information about the body's physiological state.

Table 1. Activation of the different skin receptors in response to thermal stimuli. Adapted from Jänig, 2018

<table>
<tr><th>SKIN TEMPERATURE</th><th>< 15°C
(Noxious cold)</th><th colspan="2">15–30°C
(Innocuous cold)</th><th colspan="2">30–45°C
(Innocuous warm)</th><th>> 45°C
(Noxious heat)</th></tr>
<tr><td rowspan="2">SKIN SENSATIONS</td><td rowspan="2">Cold pain–burning</td><td rowspan="2">Cold</td><td>Cool</td><td>Warm</td><td rowspan="2">Hot</td><td rowspan="2">Heat pain–burning</td></tr>
<tr><td colspan="2">THERMAL COMFORT ZONE</td></tr>
<tr><td rowspan="2">MOTOR REACTIONS</td><td rowspan="2">Protective body reactions</td><td colspan="2"></td><td>Thermoneutrality 30–34°C</td><td></td><td rowspan="2">Protective body reactions</td></tr>
<tr><td colspan="4">THERMOREGULATION</td></tr>
<tr><td>AFFERENTS NEURONS</td><td>Cold nociceptive neurons</td><td colspan="2">Cool-sensitive neurons</td><td colspan="2">Warm-sensitive neurons</td><td>Heat nociceptive neurons</td></tr>
<tr><td>RECEPTORS</td><td>Aδ</td><td colspan="2">Aδ, C</td><td colspan="2">Aδ, C</td><td>C</td></tr>
</table>

We recently proposed that temperature perception could represent a good model system to investigate interoception because it offers numerous advantages from experimental, theoretical, and ethical perspectives compared to other interoceptive submodalities (Crucianelli & Ehrsson, 2022). First, stimulation can be experimentally controlled in the sense that we can systematically manipulate the temperature we deliver to the skin with precision, which is difficult in visceral paradigms. Second, in contrast to pain or affective touch in which the affective facet can be very prominent (e.g., strong emotional distress with pain), thermal stimuli do not necessarily have a strong affective component when manipulated within the innocuous range (cool to warm perception) but can be associated with mild experiences of thermal comfort and discomfort. This is an advantage in experimental studies, as it is easier to match conditions and raises fewer ethical issues than when administering pain. Third, thermoreception is a non-invasive way to investigate interoception compared to other modalities, such as gastric and bladder functions and pain, and therefore raises fewer ethical issues. Fourth, unlike CT and nociceptors that are largely silent until stimulated, our brain receives continuous signals about the temperature of the external environment from the receptors in the skin and the body's core. This constant inflow in thermosensory signals to the brain is similar to the constant signals from the beating heart that traditionally have been emphasised as one of the advantages of focusing on cardiac interoception as "a constant signal in our life" (Azzalini, Rebollo & Tallon-Baudry, 2019). Similarly, as in the case of an increasing heart rate, we are prompted to pay attention to what is happening inside or outside our body as soon as there is a notable deviation from thermoneutrality. Thus, the body and the brain work in concert to maintain thermoneutrality, which is a task that involves our whole body (Proffitt, 2006; Davies et al., 2012).

The first aim of the present study was to investigate the relationships of cardiac interoception and three skin-based interoceptive submodalities, namely, affective touch, nociception, and thermosensation. By comparing performance on these tasks targeting both visceral and skin-mediated signals, we wanted to address the question of whether interoceptive abilities generalise and can be seen as a single ability or whether interoception is better described as a set of independent separate submodalities and abilities. This is important because several accounts of interoception point towards the importance of the insular cortex in processing interoceptive signals, and this has contributed to a rather widespread assumption in the psychological literature that interoception might be a unified construct (e.g., Pollatos et al., 2007; Zaki, Davis, & Ochsner, 2012). However, in line with the general principle of parallel and hierarchical processing of sensory information in the brain (Ungerleider & Mishkin, 1982), one can also hypothesise that the various interoceptive signals are initially processed relatively independently only to be gradually and increasingly integrated higher up in the cortical hierarchy. Moreover, in the psychological literature, cardiac interoception assessed by heartbeat detection tasks is often used as a proxy for interoception more generally. However, this could be misleading if the assumption of interoception as a generalised construct and ability is incorrect. Thus, we reasoned that more studies investigating interoception using a “battery of tests” are needed to clarify the above questions and obtain a more comprehensive understanding of interoception.

Accordingly, we tested a group of healthy participants on a battery of tests; in addition to the classic heartbeat counting task and the often-used affective touch paradigm, we added two validated change detection tasks to probe thermosensation and (thermal) nociception. We also added a new thermal task (see below) that was specifically designed with skin-based interoception in mind. Since affective touch is typically studied on both hairy and non-hairy skin due to the greater density of CT fibres in the former and thermosensation has been reported to differ between these two skin types (Filingeri et al., 2018), we conducted all skin-based interoceptive tasks on both hairy and non-hairy skin. This gave us the opportunity to directly test whether the generalisation or separation of interoceptive submodalities would hold true for both skin types.

The second aim of this study was to introduce a novel thermosensory task to probe thermosensation as skin-based interoception. Given that thermosensation has traditionally been seen as part of somatosensation and exteroception, existing tasks are often designed as somatosensory detection or discrimination tasks, which is not a problem in itself of course, but as we have argued elsewhere (Crucianelli & Ehrsson 2022), new thermosensory tasks designed from the perspective of interoception can make valuable contributions to future research. Thus, we designed the dynamic thermal matching task inspired by aspects of the heartbeat counting task, concept of deviations from thermoneutrality, and theoretical consideration from the affective touch literature. Therefore, we targeted temperatures around the thermoneutrality range (30–34°C, see Table 1) to probe relatively subtle thermosensory deviations from normal skin temperature. This is similar to the heartbeat counting task that captures small variations around resting baseline heart rates. Furthermore, the thermal stimuli were moving at an optimal speed for CT fibres, and the range of temperatures tested should lead to variations in CT activity, in addition to activating cold and warm receptors. Recent studies have shown optimal activation of CT afferents in response to light moving stimuli delivered at a typical skin temperature (i.e., 32°C) compared to cooler (18°C) or warmer (40°C) stimuli, and at such neutral temperatures, stimulation is perceived as most pleasant (Ackerley et al., 2014). As described above, we further compared hairy and non-hairy skin.

Finally, in line with recent theoretical and experimental developments arguing that interoception should be quantified as a multidimensional construct(s) taking into account both sensation–perception and metacognition (Garfinkel et al., 2015), for each interoceptive submodality, we distinguished between *interoceptive accuracy*, that is, the objective performance on an interoceptive task, i.e., perceptual detection or discrimination; *interoceptive sensibility*, which refers to subjective beliefs about the perception of bodily signals and task performance and is measured by means of self-report questionnaires or ratings *prior* to conducting the perceptual tasks; and *interoceptive awareness*, or metacognitive awareness of interoceptive accuracy, which is one's subjective confidence about the objective interoceptive performance that can be measured with confidence ratings directly after the tasks (Garfinkel et al., 2015). This multidimensional manner of describing interoception allows us to capture both perceptual and metacognitive levels of interoception and compare the relationships across the different submodalities at both levels, which has potentially higher translational relevance, as clinical studies often probe interoception at the metacognitive level using questionnaires where participants have to describe their degree of awareness of various interoceptive sensations in everyday life (see Khalsa et al., 2018 for clinical implications of interoceptive research).

Methods

Participants

A total of sixty-four healthy participants (31 males and 33 females) were recruited using social media and advertising on the Karolinska Institutet campus. Two participants (one male and one female) were excluded because they did not meet the inclusion criteria; thus, a total of 62 participants were considered for data analysis. A priori power analysis based on previous studies in the field of interoception (Garfinkel et al., 2016; Crucianelli et al., 2018) suggested that a minimum sample of N = 62 provided enough power (92%) to detect our effects of interests in the thermal matching task ($\alpha = 0.05$, effect size d = 0.4, two-tailed). Inclusion criteria were being 18-39 years old (mean age = 26.5 years, standard deviation = 5.4 years) and being right-handed. Exclusion criteria were having a history of any psychiatric or neurological conditions, taking any medications, having sensory or health conditions that might result in skin conditions (e.g., psoriasis), and having any scars or tattoos on the left forearm or hand. All participants were requested to wear short sleeves to make stimulation of the forearm easier. The study was approved by the Swedish Ethical Review Authority. All participants provided signed written consent, and they received a cinema ticket as compensation for their time. The study was conducted in accordance with the provisions of the Declaration of Helsinki 1975, as revised in 2008.

Self-report measures and interoceptive sensibility

Participants were asked to provide demographic information, such as age, weight and height (to calculate the body mass index, BMI), handedness and, for female subjects, the phase of the menstrual cycle at the time of testing (i.e., this is known to influence body temperature and consequently affect thermoregulatory processes; Kurz, 2008 for a review). Next, participants were asked to complete the following self-report questionnaires: the *Body Awareness Questionnaire* (BAQ), an 18-item questionnaire assessing body awareness (Shields, Mallory & Simon, 1989), and the *Body Perception Questionnaire* (very short form, BPQ), a 12-item questionnaire regarding perception of one’s body (Porges, 1993; Cabrera et al., 2017). The BAQ and BPQ were included as measures of interoceptive sensibility, that is, how aware participants reported being of their bodily sensations; the former questionnaire addresses more general body awareness, whereas the latter questionnaire targets bodily sensations more specifically, such as stomach and gut activity. Participants also completed the *Eating Disorder Examination Questionnaire* (EDE-Q 6.0, Fairburn & Beglin, 1994, 2008; Peterson et al., 2007) and the *Depression, Anxiety and Stress Scale – 21 Item* (DASS, Lovibond & Lovibond, 1995; Henry & Crawford, 2005). However, the BMI, EDE-Q and DASS were not considered in any of the following analyses because their inclusion lies beyond the scope of this manuscript.

Interoceptive accuracy tasks

Heartbeat counting task (HCT)

The experimenter recorded the heartbeat frequency by means of a Biopac MP150 Heart Rate oximeter attached to the participant's non-dominant index finger and connected to a Windows laptop with AcqKnowledge software (version 5.0), which enabled extraction of the actual number of heartbeats using the ‘count peak’ function. Care was taken to place the soft oximeter around the finger firmly but without being too tight to reduce the possibility that participants could perceive their pulse in their finger (Crucianelli et al., 2018; Murphy et al., 2019). As part of the task, a 5-minute heartbeat baseline was recorded to check for the presence of autonomic neuropathy. During this time, we presented the instructions for the heartbeat counting task (Schandry, 1981). Participants were instructed to breathe normally and to not cross their legs. Participants were asked to silently count their heartbeats between two verbal signals of 'go' and 'stop', without manually taking their or feeling their chest. They were encouraged to only count those heartbeats they were sure about, but also instructed to take into account weak sensations, rather than making their best guess (as in Ferentzi et al., 2018). Both of the participants' hands were placed on the table to ensure that no body part was touched. Participants completed a practice trial of 15 seconds before proceeding to the three experimental trials (interval lengths of 25 s, 45 s, and 65 s, as in Crucianelli et al., 2018), which were presented in a randomised order. Short breaks of 30 seconds were taken between each trial.

Temperature perception

(Dynamic) thermal matching task

Before proceeding with the task, the skin temperature of each participant's palm and forearm was measured with a contactless thermometer (Microlife NC150) at three different locations at each site. These values are reported in Table 1 of the Supplementary Materials. This was done to control for any significant individual differences in skin temperature that could influence task performance. Then, participants were stroked with a 25x50 mm thermode attached to a thermal stimulator (Somedic MSA, SenseLab, Sweden) at reference temperatures of 30°, 32° or 34°C; these temperatures were within the range of neutral/innocuous temperatures so to mirror the performance at the heartbeat counting task, which is usually performed at rest. Participants were instructed to pay close attention to this reference temperature because their task would be to match it by verbally indicating whenever they felt the same temperature again. That is, participants were asked to tell the experimenter which temperature felt the same as the reference temperature among a range of warmer or cooler stimuli. Next, in each experimental trial, the experimenter touched the participant with the thermode set at different temperatures starting from ± 8°C (which is 25% of the neutral temperature of 32°C; whether the starting temperature was +8°C or -8°C from the reference temperature was counterbalanced across participants) of the reference temperature (range 22-38°C for the reference temperature of 30°C; range 24-40°C for the reference temperature of 32°C; range 26-42°C for the reference temperature of 34°C). The task followed a staircase procedure, that is, the temperature was either increased (i.e., from cool to warm) or decreased (i.e., from warm to cool) towards the reference temperature in discrete steps of 2°C. Temperature was increased or decreased until participants verbally indicated they felt the reference temperature or until the maximum or minimum temperature was reached (± 8°C from the reference temperature, opposing the starting temperature) for a total of 9 potential strokes per trial, with a break of 3 seconds between trials. Participants were instructed to try to match the reference temperature that they previously experienced. The correct answer was always the reference temperature, and the order in which the reference temperatures were presented as well as the order of increasing and decreasing trials varied across trials to avoid anchor effects of the initial values (e.g., if one participant started with increasing trials based on one reference temperature, then they would start with decreasing trials for the following reference temperature, see Tajadura-Jiménez et al., 2015 for a similar approach in an embodiment paradigm). Two trials per reference temperature were repeated, one increasing and one decreasing, for a total of 6 trials presented in randomised order. The duration of each stroke was kept constant at 3 seconds; the velocity of tactile stimulation was CT-optimal (3 cm/s) and the direction of movement was always proximal to distal with respect to the participant. No additional pressure was applied aside from the weight of the thermode. The same procedure was repeated on the outer forearm (hairy skin) and on the palm (non-hairy skin) in areas of 9x4 cm.

(Static) temperature detection task

As in the dynamic thermal matching task, the tactile stimulus was delivered using the Somedic MSA Thermal Stimulator. The detection of cold and warm static thermal stimuli was measured by means of the well-established Marstock methods of the limits (Fruhstorfer et al., 1976), and we used the same protocol adopted by Heldestad et al., 2010. The experimenter held the thermode on the area of interest (left forearm or palm) without applying any additional pressure. The thermode was not secured on the forearm or hand to avoid any additional tactile signals that could interfere with the detection of temperature. Participants were asked to hold a response button using their right hand and to press it as soon as they perceived a change in temperature of any kind (i.e., warmer or colder than the previous perceived temperature, Heldestad et al., 2010). The starting temperature was always neutral (32°C); the maximum probe temperature was set to 50°C, and the minimum was set to 10°C for safety reasons. As soon as the button was pressed, the temperature automatically changed in the opposite direction and returned to the baseline temperature of 32°C; the temperature stayed at 32°C for 5 seconds before moving to the next trial. The temperature changed at a rate of 1°C/s and returned to baseline at a speed of 4°C/s. This method has been widely used to detect neuropathy in clinical settings, and it includes a total of five warm and five cold trials, presented in two blocks (warm and cold blocks). The procedure was repeated twice: once on the left forearm and once on the left palm, in a randomised order.

Affective touch task

This task takes advantage of the discovery that affective, hedonic touch on the skin can be reliably elicited by soft, light stroking at specific velocities within the range of 1-10 cm/s that activate a specialised peripheral system of C-tactile afferents (Löken, Wessberg, Morrison, McGlone & Olausson, 2009; McGlone, Valbo, Olausson, Löken, & Wessberg, 2007). Touches were delivered using a soft brush (i.e., precision cheek brush No 032, Åhléns, Sweden**)** on the left forearm (hairy skin that contains CT afferents) and left palm (non-hairy skin, where CT afferent activity has only partially been reported), and the task of the participants was always to verbally rate the pleasantness of the touch using the rating scale. Touches were delivered at seven velocities (0.3, 1, 3, 6, 9, 18 and 27 cm/s). Two slow velocities of 3 and 6 cm/s are typically perceived as more pleasant (i.e., CT optimal velocities) compared to the borderline optimal velocities (1 and 9 cm/s) and the CT non-optimal speeds (0.3, 18 and 27 cm/s, Löken et al., 2009). Each velocity was presented three times, for a total of 21 stroking trials per location (palm and forearm, in randomised order) and the direction of movement was always proximal to distal with respect to the participant.

(Static) pain detection task

The procedure of this task followed the same protocol to detect thermal pain thresholds used by Heldestad et al., 2010, and it was similar to the one described for static temperature detection. However, here, participants were instructed to press the button as soon as they perceived that the thermal stimulation was becoming uncomfortable or painful (Heldestad et al., 2010). When providing the instructions, the experimenter clarified that the task was to press the button as soon as the sensation of discomfort or pain was beginning (i.e., detection) rather than when the pain was unbearable (i.e., threshold). We performed the procedure in the left palm (non-hairy) and forearm (hairy), and we tested pain detection following warm stimuli only for a total of five trials per location. The baseline starting temperature was 32°C, and the maximum temperature was 50°C for safety reasons. If the participant did not press the button when reaching 50°C, the trial was considered invalid. The temperature changed at a rate of 2°C/s, whereas the return to baseline in all tests occurred at a speed of 4°C/s.

Interoceptive metacognitive awareness: Confidence and prior beliefs

In line with recent models of interoception (Garfinkel et al., 2015; 2016), we also measured metacognitive awareness in relation to interoception. We collected information about this measure as confidence after each answer (i.e., online) and as prior belief before participants completed each task (i.e., offline); these data have been analysed separately (Fleming et al., 2016). After receiving the instructions about each task and having been given the opportunity to ask any questions they might have, participants were asked to provide a prospective estimation of their ability to successfully complete the task by means of a rating scale ranging from 0 (not at all accurate/total guess) to 100 (very accurate) (Beck et al., 2019). Furthermore, participants were also asked after each individual trial within the tasks to rate their confidence with their answers (as in Garfinkel et al., 2015; Beck et al., 2019). This confidence rating was chosen on an 11-point scale ranging from 0 (not at all) to 10 (extremely). This was done for each trial of the tasks except for the static temperature detection task and static pain detection task, as these followed a standardised method-of-limits procedure, whereby temperature changes in a continuous manner; providing individual confidence ratings after each trial during the task would have disrupted the actual performance.

Experimental procedure

Participants were welcomed into the experimental room, and they were asked to sit on a table opposite the experimenter. Upon arrival, they were asked to sign a consent form and to complete the following questionnaires presented in an online format: the demographic questionnaire, BAQ, BPQ, EDE-Q and DASS. The questionnaires were always presented at the beginning of the experimental procedure to ensure that participants were given some time to stay at rest before completing the *heartbeat counting task*, which was the first interoceptive task that all participants completed. Previous studies showed that the heartbeat counting task might be influenced by other activities (e.g., Ring et al., 2015; Brener & Ring, 2016), therefore we decided to conduct this task first (for an overview of procedures and tasks, see Figure 1 and Table 2). Participants were given the choice to either keep their eyes closed or open, whichever helped them feel more comfortable, in order to be as accurate as possible. The aforementioned experimental procedure prior to the thermal matching task took approximately 30 minutes, giving participants the opportunity to acclimatise themselves before proceeding with the dynamic *thermal matching task*. Participants were asked to wear a disposable blindfold and to place their left arm on the table to complete the dynamic *thermal matching task*, following the method fully described in Method section above. Participants were asked to pay close attention to each reference temperature because they were given the possibility to feel it just once. Upon completion, participants removed the blindfold, and they were given a short break before beginning the *affective touch task*. As part of this task, they were familiarised with the pleasantness rating scale, and the experimenter identified and marked two identical areas of 9x4 cm on the left forearm and palm with a washable marker, as was done in previous studies (Crucianelli et al., 2013; 2016; 2018). This was performed to control the stimulated area and the pressure applied during the touch by checking that the tactile stimulation was applied just inside the marked areas (more pressure would result in a wider spreading of the brush, that is, the tactile stimulation would be applied outside of the marked borders). Alternating the stimulated areas would counteract the fatigue of the CT fibres (McGlone et al., 2012). Participants were asked to wear the blindfold again for the entire duration of the affective touch task. Next, participants could take a break from wearing the blindfold before starting the *static temperature detection task*. No break was taken between the cold and warm blocks, but participants were only allowed to remove the blindfold at the very end of the task. The last part of the experimental procedure consisted of the *static pain detection task*, for which participants were asked to wear the blindfold once again. All the experimental tasks were conducted on the left, non-dominant hand or forearm. The starting location for each task was alternated between the forearm and the palm (e.g., participants starting one task on the palm next completed the task with the forearm; those who started one task with the forearm completed the following task with the palm). The order of the tasks was kept constant (with internal randomisation) (Figure 1 and Table 2). The pain detection task was performed last as to not arouse the body or cause hypoalgesia, which could affect performance on the other tasks (Gröne et al., 2012). The entire experimental procedure lasted approximately one hour, and participants were offered a wipe to remove the marker from the skin and were provided with a full debriefing at the end of the session. Testing took place in a testing room with constant temperature and humidity, with no significant changes in temperature between the beginning (M = 22.55°C, SD = 0.49) and the end (M = 23.10°C, SD = 0.47) of the testing session.

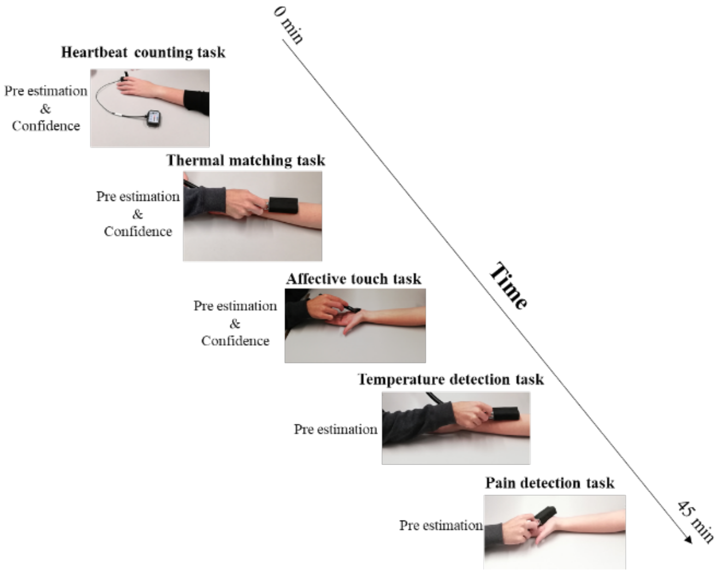


Figure 1. The experimental procedure. The heartbeat counting task was conducted using the BioNomadix system of a wearable wireless device connected to a Biopac MP150 system. The thermal matching task, temperature detection task and pain detection task were conducted using the thermode connected to the Somedic thermal stimulator. In the affective touch task, tactile stimulation was delivered with a soft brush. All the tasks were repeated on the forearm and on the palm in a randomised order.

Table 2. Overview of the structure of the different tasks. The basic tasks are described in the order that they were completed during the experimental procedure. Each row represents a task, and each column describes one step of each task, starting with pre-task estimation (or prior belief of performance), followed by the name of the actual task with its description in terms of method (number of trials and body sites) and outcome measures (interoceptive accuracy). The final column refers to the participants' performance confidence, the data of which were collected after each trial of the heartbeat counting task, dynamic thermal matching task and affective touch task only.

Interoceptive modality	Pre-task estimation	Interoceptive task	Task description	Outcome measures (interoceptive accuracy)	Post-trial confidence
Questionnaires	*N/A*	**Interoceptive sensibility**	Body Awareness Questionnaire Body Perception Questionnaire	Values between 18 - 126 Values between 12 - 60	*N/A*
Cardiac	*How well are you going to perform on this task? (0, not well at all - 100, very well)*	**Heartbeat counting task**	3 trials (25 s, 45 s, and 65 s)	Values between 0 - 1	*How confident are you with your answer? (0, not at all - 10, very)*
Dynamic temperature		**Thermal matching task**	3 temperatures (30, 32, and 34°C) 2 body locations (palm and forearm) 2 staircase approaches per temperature (increasing and decreasing temperature)	Values between 0 - 1	
Tactile affectivity		**Affective touch task**	7 velocities (0.3, 1, 3, 6, 9, 18, 27 cm/s) 2 body locations (palm and forearm)	Pleasantness of touch 0-100 & tactile sensitivity (CT – non-CT)	
Static temperature		**Temperature detection**	Method of limit 5 trials for warm and 5 trials for cold	Detection temperature and standard deviations	*N/A*
Static pain		**Pain detection**	Method of limit 5 trails for warm pain	Detection temperature and standard deviations	

Design and plan of analysis

All data were analysed with the Statistical Package for Social Sciences (SPSS), version 26. The data were tested for normality by means of the Shapiro-Wilk test and were found to be non-normal ($p < .05$). Subsequent two-step approach transformations (Templeton, 2011) did correct for the normality violations (see Supplementary Materials); therefore, parametric tests were used to analyse the data (described below). The false discovery rate (FDR, Benjamini & Hochberg, 1995) was used to correct for multiple correlations (we reported the corrected values for the significant effects); this method is widely used when a large number of multiple comparisons is applied, and it controls the proportions of false rejections out of all rejections (Benjamini, 2010). Bonferroni-corrected post hoc comparisons were used to follow up significant effects and interactions. All *p* values are 2-tailed unless otherwise specified.

First, we focused on the analysis of each task separately. As in Garfinkel et al., 2016, we first assessed whether there was a relationship between the dimensions of interoception (accuracy, confidence, and prior beliefs) for each submodality separately (cardiac, dynamic and static temperature, affective touch, and pain). Then, we investigated the relationship between the different interoceptive submodalities and dimensions. Specifically, we ran correlational analyses to investigate the relationship between accuracy and confidence across the submodalities. In secondary analyses using parametric correlational analyses, we also explored the relationship between accuracy and prior beliefs of performance, as well as the relationships between the interoceptive dimensions and individual differences in the questionnaires probing self-reported interoceptive awareness and bodily awareness (interoceptive sensibility). The results of secondary analyses are reported in Supplementary Materials only, for brevity.

We also performed Bayesian correlations for our main analyses of interest (i.e., correlations between accuracy - objective performance - across different interoceptive modalities). Bayesian correlations produce a Bayes factor (BF) as the main output index. BF_{01} indicates the probability supporting the null over the alternative hypotheses (e.g., a $BF_{01} = 8$ means that H_0 is 8 times more likely to be true than H_1). By convention, BFs between 0.33 and 3 are considered inconclusive (see Lee & Wagenmakers, 2014; Biel & Friedrich, 2018 for guidance on the interpretation of BF).

Interoceptive accuracy

We calculated the cardiac interoceptive accuracy (*heartbeat counting task)* by means of the following formula that allowed us to compare the counted and recorded heartbeats (Schandry, 1981):

$$\frac{1}{3}\Sigma(1-\frac{|recorded\ \ heartbeat\ -counted\ \ heartbeats\ |}{recorded\ \ heartbeats})$$

For the other tasks, the focus was 1) to explore whether there was a significant effect of touch location (hairy vs. non-hairy skin) and 2) to obtain an accuracy value that could resemble, and therefore be compared to, the interoceptive accuracy measured by means of the heartbeat counting task. This was done to ensure that levels of accuracy were equated across the modalities.

For the dynamic *thermal matching task*, we used the following formula:

$$1-(\Sigma\frac{(|reported\ \ temperature\ \ -reference\ \ temperature\ \ |)/_{2}}{12})$$

where 12 represents the total number of options presented to participants (regardless of direction - overestimation or underestimation of temperature) across the three trials. Both of these formulas provide a value between 0 and 1, with 0 suggesting poor performance and 1 indicating optimal performance on the task. We kept the order of the increasing and decreasing stimuli separate given the different mechanisms and skin responses known to be involved when perceiving cooling and warming stimuli (Nordin, 1990; Wessberg et al., 2003; Olausson, Wessberg, Morrison, McGlone, & Vallbo, 2010, for a review). Thus, for each subject, we obtained one increasing and one decreasing accuracy value for the forearm and for the palm. We provide an additional control analysis that focused on the perception of the three temperatures separately (30, 32, and 34°C) in hairy and non-hairy skin in the Supplementary Materials.

The *affective touch task* was analysed as in previous studies (e.g., Crucianelli et al., 2018). We obtained the scores for pleasantness for the CT-optimal, borderline, and CT-non-optimal velocities by averaging the scores of tactile pleasantness in each of these categories. This allowed us to investigate the main effect of velocity and skin site on pleasantness by means of a repeated measures ANOVA. For the purpose of this study, our main variable of interest was the so-called ‘affective touch sensitivity’ (Crucianelli et al., 2018; Kirsch et al., 2020), which describes the individual’s ability to differentiate levels of pleasantness between affective and neutral touch, without taking into account the total pleasantness. Thus, we averaged the pleasantness scores for CT-optimal velocities and for CT-non-optimal velocities, and we calculated the differences between these two measurements to obtain one tactile sensitivity score for the forearm and one for the palm. This differential score was then used in the analysis to investigate the relationship with participants’ performance on the other interoceptive tasks.

Next, for both *static temperature detection* and *static pain detection*, we were interested in both the sensitivity (i.e., the smallest change in temperature a person could detect) and the consistency or precision (i.e., the variability in the individual responses across the different trials, quantified as standard deviations) of the detection across trials. As a proxy of interoceptive accuracy, we calculated the relationship between sensitivity and consistency and obtained one detection accuracy value for cold temperature, one value for warm temperature and one value for warm pain for both hairy and non-hairy skin using the following formula:

$$[\frac{\Sigma(|32 - detection\ temperature|)}{5}] * standard\ deviation$$

where 32°C is the baseline starting temperature, detection temperature is the temperature that participants recognise as different (warmer or cooler) from baseline, and 5 is the total number of trials; we multiplied by the standard deviation to account for the individual variability in responses across trials. We developed this formula to take into account both the accuracy (i.e., how many degrees are necessary for the participants to detect a change) and the precision (i.e., how consistent participants are in their performance across trials). We then used these detection accuracy values to investigate the relationship with the other interoceptive modalities.

Interoceptive metacognitive awareness: Confidence and prior beliefs

In terms of metacognitive interoception, we focused both on ‘offline’ insight into participants’ own abilities *before* they completed the tasks and on ‘online’ confidence in their own answers reported immediately *after* each trial of the heartbeat counting task, dynamic thermal matching task and affective touch task. Specifically, metacognitive awareness for each interoceptive modality was operationalised as the extent to which pre-estimation of performance on each task and confidence predicted accuracy (Garfinkel et al., 2015; 2016). This was analysed by means of multiple regressions, with pre-estimation and confidence as the main predictors and accuracy as the outcome variable. The offline metacognitive measure was computed separately for cardiac, dynamic thermal matching task, affective touch, static temperature and static pain detection responses to provide five measures of metacognitive awareness. The online metacognitive measure (i.e., confidence) was obtained only for the cardiac interoception, dynamic thermal matching, and affective touch tasks because the static temperature detection task and static pain detection task followed a standardised method-of-limits procedure; providing individual confidence ratings after each trial during the task would have disrupted the participants' actual performance. Confidence ratings were averaged over trials for all the tasks.

Results

Demographics and interoceptive sensibility

The mean scores and standard deviations for BMI, interoceptive sensibility (as measured by means of the BAQ and BPQ), EDE-Q and DASS scores are reported in Table 3. No effect of sex on any of these measures was found, except for the EDE-Q.

Table 3. Mean and standard deviations for the participants' body mass index (BMI); Body Awareness Questionnaire (BAQ) scores; Body Perception Questionnaire (BPQ) scores; Eating Disorders Examination Questionnaire (EDE-Q) scores; and the scores on the depression, anxiety and stress scales.

	BMI	**BAQ**	**BPQ**	**EDE-Q**	**Depression**	**Anxiety**	**Stress**
Total sample	22.87 (2.99)	79.79 (18.38)	29.90 (8.77)	1.42 (1.12)	4.13 (3.87)	4.02 (3.52)	5.76 (4.05)
Females (32)	22.19 (2.90)	79.66 (19.86)	30.00 (9.22)	1.70 (1.14)	4.16 (4.05)	3.38 (2.79)	5.88 (4.14)
Males (30)	23.60 (2.95)	79.93 (16.99)	29.80 (8.41)	1.11 (1.04)	4.10 (3.74)	4.70 (4.10)	5.63 (4.02)
***F (p)* values**	3.62 (0.06)	0.03 (0.95)	0.08 (0.93)	4.56 (0.04)*	0.03 (0.96)	2.23 (0.14)	0.05 (0.82)

Interoceptive accuracy across modalities

Heartbeat detection task

The mean cardiac interoceptive accuracy score was 0.64 (SD = 0.25) in the present sample. This value is in line with those reported in previous studies (e.g., Tsakiris, Jiménez & Costantini, 2011; Crucianelli et al., 2018). The mean confidence score was 5.77 (SD = 2.28). One-way ANOVA revealed no effect of sex on cardiac accuracy (F (1, 61) = 0.128, p = 0.722, $\eta p^2 = 0.002$).

(Dynamic) thermal matching task

As mentioned in the Methods section, we obtained one increasing (staircase) temperature accuracy value for the forearm and one for the palm and one decreasing (staircase) value for the forearm and one value for the palm. The results of the 2 (location: palm vs. forearm) x 2 (staircase: increasing vs. decreasing) repeated measure ANOVA revealed a significant main effect of location (F (1, 61) = 5.00, $p = 0.029$, $\eta_p^2 = 0.084$, Figure 2), with participants being more accurate in the detection of dynamic temperature in the forearm (M = 0.81; SD = 0.16) than in the palm (M = 0.76; SD = 0.17). No main effect of staircase (F (1, 61) = 0.142; $p = 0.707$, $\eta_p^2 = 0.002$) or significant interaction (F (1, 61) = 0.299; $p = 0.586$, $\eta_p^2 = 0.005$) was found. No effect of sex was found for any of the variables of interest as investigated by means of separate one-way ANOVAs (all F_s between 0.024 and 0.467; all p_s between 0.497 and 0.878); thus, sex was not considered in subsequent analyses.

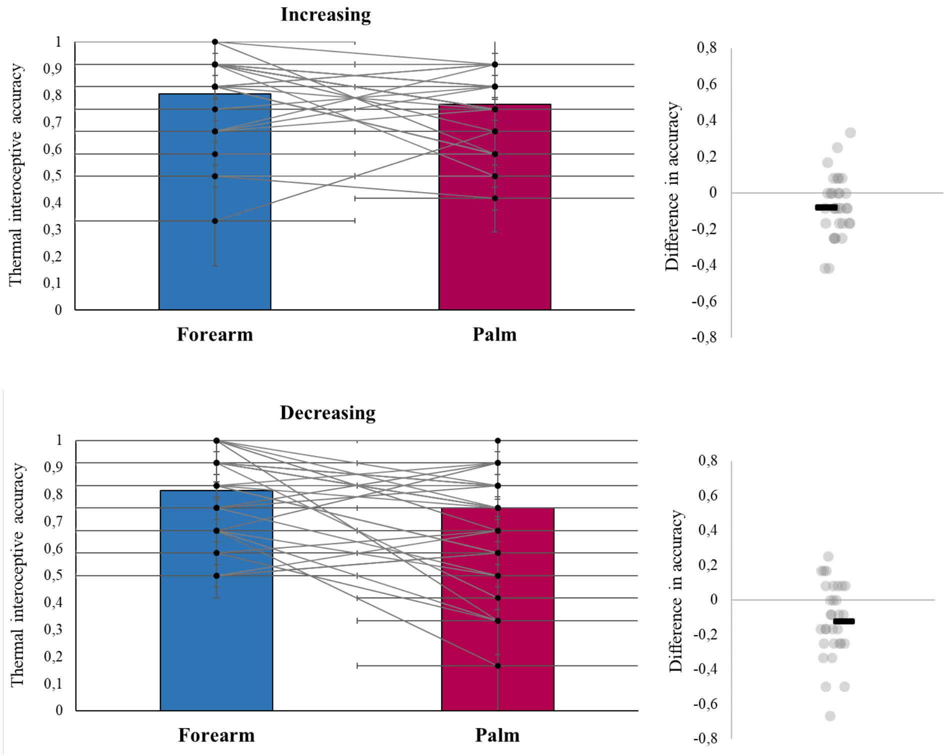
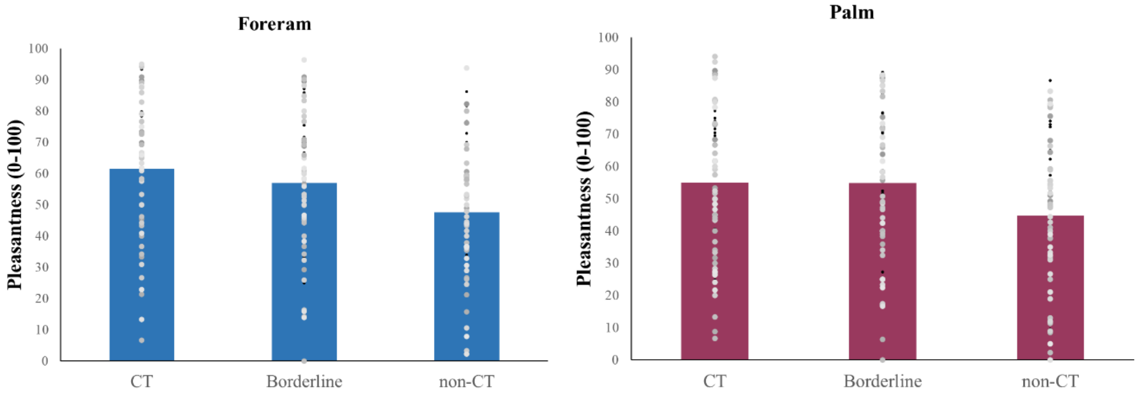


Figure 2. Mean, data distribution and standard errors for the dynamic thermal matching task, performed on the forearms (in blue) and palms (in burgundy) of the participants. The panel on top shows task performance during increasing trials, and the panel on the bottom shows task performance on decreasing trials. The graphs on the right-hand side represent the distribution of the differences between task performance regarding the forearm and palm for each participant.

Affective touch task

We averaged the CT optimal velocities (3 and 6 cm/s), borderline velocities (1 and 9 cm/s) and the CT-non-optimal velocities (0.3, 18 and 27 cm/s) to obtain three velocity variables. As expected, there was a main effect of velocity on touch pleasantness (F (2, 122) = 40.07, $p <$ 0.001, $\eta p^2 = 0.417$). Bonferroni corrected post hoc analysis ($\alpha = 0.017$) revealed that slow, CT-optimal touch was rated as more pleasant (M = 58.24; SD = 23.02) than fast, CT-non-optimal touch (M = 46.08; SD = 22.23; t(61) = 6.67; $p < 0.001$, Figure 3, Figure 1 in Supplementary Materials) and touch delivered at borderline velocities (M = 55.91; SD = 22.87; t(61) = 2.77; $p < 0.001$). There was also a significant difference between borderline and CT-non-optimal touch (t(61) = 6.47; $p < 0.001$). There was a main effect of location (F (1, 61) = 5.708, $p = 0.020$, $\eta p^2 = 0.092$), with touch being rated overall as more pleasant in the forearm (M = 55.32; SD = 22.61) than in the palm (M = 51.50; SD = 23.80), consistent with previous findings (Löken, Evert & Wessberg, 2011). There was a significant interaction between velocity and location (F (2, 122) = 4.896; $p = 0.009$, $\eta p^2 = 0.080$). Bonferroni corrected post hoc analysis ($\alpha = 0.017$) revealed a significant difference between the forearm and palm only in the perception of slow, CT-optimal touch t(61) = -2.93; $p = 0.005$), but not in the perception of borderline (t(61) = -1.19; $p = 0.241$) or CT-non-optimal touch (t(61) = -0.46; $p = 0.650$). No effect of sex on any of the touch pleasantness scores was found (all F_s between 0.002 and 2.394; all p_s between 0.127 and 0.966).



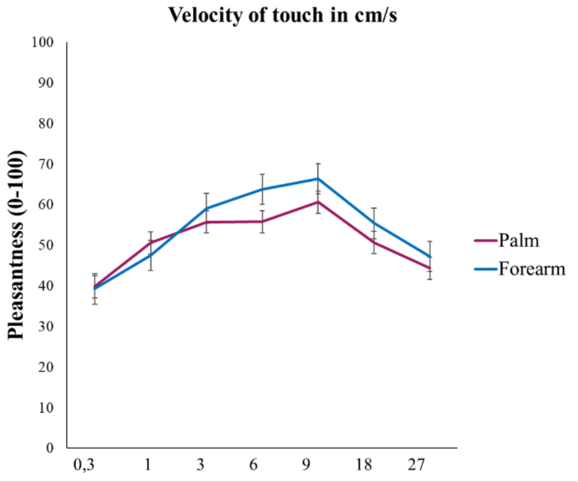


Figure 3. **Top panels**: Mean and data distribution for the pleasantness scores for CT-optimal, borderline and CT-non-optimal velocities for the forearm and palm. **Left panel**: Mean and standard errors for the same dataset of the affective touch task for each velocity (velocities are reported in cm/s), showing the main effect of velocity and location (forearm vs. palm) on touch pleasantness. A full account of the mean pleasantness for each velocity is reported in Figure 1 of the Supplementary Materials.

(Static) temperature detection task

We compared the smallest change in temperature participants could detect when temperature was increasing (warm) or decreasing (cool) from the neutral starting temperature of 32°C in both hairy (forearm) and non-hairy skin (palm). The results of the 2 (temperature: warm vs. cool) x 2 (location: forearm vs. palm) repeated measures ANOVA revealed a main effect of temperature (F (1, 61) = 67.74; $p < 0.001$, $\eta p^2 = 0.855$), suggesting that participants could detect cooling (M = 1.75°C; SD = 1.08) quicker or with a significantly smaller change in temperature compared to warming (M = 2.63°C; SD = 1.36, Figure 4). There was a non-significant main effect of location (F (1, 61) = 3.71; $p = 0.06$, $\eta p^2 = 0.066$), with participants needing a smaller but non-significant variation in terms of °C to detect changes in temperature in the forearm (M = 2.05°C; SD = 1.25) compared to the palm (M = 2.34°C; SD = 1.35, Figure 4). There was a significant interaction between temperature and skin site (F (1, 61) = 5.90; $p = 0.02$, $\eta p^2 = 0.060$). Bonferroni-corrected post hoc analysis ($\alpha = 0.025$) revealed a significant difference between hairy and non-hairy skin in the detection of cold temperatures ($t(61) = -3.47$, $p < 0.01$) but not warm temperatures ($t(61) = -0.18$, $p = 0.86$, see Figure 4).

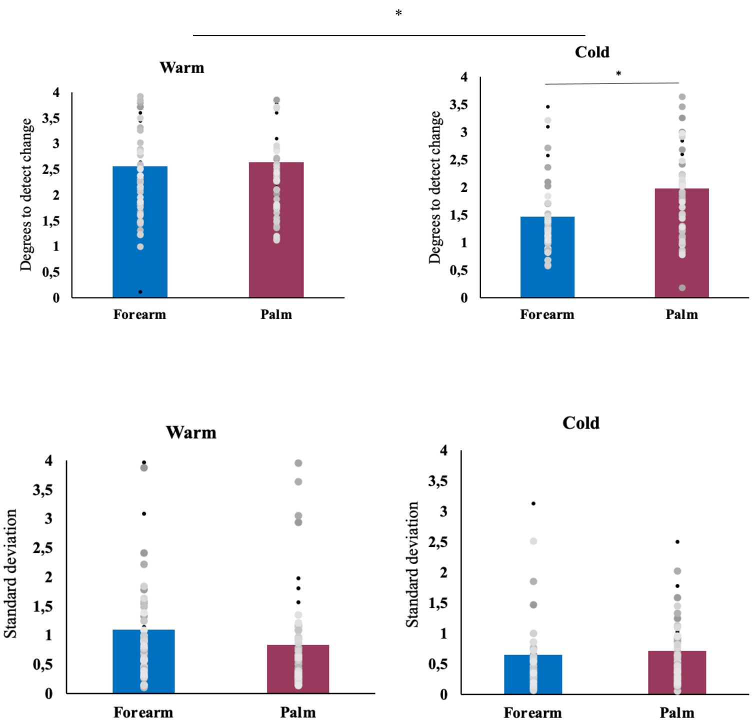


Figure 4. Means and data distribution for the static temperature detection task, showing the main effect of temperature on participants' ability to detect temperature, and significant difference between pam and forearm in detecting the cold, top panels (quantified as degrees to detect the change, measured in °C) and consistency in detecting changes in temperature (quantified as standard deviation), bottom panels, for warm and cold temperatures. * indicates significant differences, $p < 0.05$.

The main effect of sex on participants' temperature detection was (F (1, 61) = 3.97; $p = 0.051$) for warm, and (F (1, 61) = 3.88; $p = 0.053$) for cold temperatures on the palm, and (F (1, 61) = 2.56; $p = 0.115$) for warm and (F (1, 61) = 0.05, $p = 0.831$) for cold, on the forearm. That is, female participants could detect changes in temperature more promptly than male participants on the palm (female: M = 2.03, SD = 0.85; male: M = 2.66, SD = 1.61) but not on the forearm (female: M = 1.94; SD = 0.96; male: M = 2.15; SD = 1.20).

In terms of consistency (operationalised as the standard deviation) in the perception of thermal static stimuli, the results of the 2 (temperature: cool vs. warm) x 2 (location: forearm vs. palm) repeated measures ANOVA revealed a main effect of temperature (F (1, 61) = 7.09; $p = 0.01$, $\eta p^2 = 0.104$), suggesting that participants were more consistent in the detection of cold temperatures (M = 0.71; SD = 0.65) than warm temperatures (M = 0.96; SD = 0.68, Figure 4). No significant main effect of location (F (1, 61) = 1.19; $p = 0.28$, $\eta p^2 = 0.019$) or interaction (F (1, 61) = 2.16; $p = 0.15$, $\eta p^2 = 0.034$) was found. There was an effect of sex on the consistency in the detection of warm temperatures in both the palm (*F* (1, 61) = 6.514; *p* = 0.013) and forearm (*F* (1, 61) = 5.041; *p* = 0.028) but not for the detection of cold temperatures (palm: *F* (1, 61) = 0.094; *p* = 0.760; forearm: *F* (1, 61) = 0.018; *p* = 0.893). That is, female participants were significantly more consistent than male participants in the detection of static warming in the palm (female: M = 0.59; SD = 0.37; male: M = 1.09; SD = 1.04) and forearm (female: M = 0.84; SD = 0.74; male: M = 1.37; SD = 1.08).

(Static) pain detection task

Two paired sample t-tests were used to investigate differences between hairy (forearm) and non-hairy (palm) skin in the temperature necessary for participants to detect pain and the consistency (i.e., standard deviations) in reporting pain sensation. The results showed no significant main effects of body site on individual thresholds (*t*(61) = -1.12; *p* = 0.27; forearm, M = 42.26; SD = 4.47; palm, M = 42.72; SD = 4.50) or on consistency in detection (*t*(56) = -0.70; *p* = 0.49, see Figure 2 in Supplementary Materials). No effect of sex on pain detection was found (all F_s between 0.139 and 3.06; all p_s between 0.086 and 0.711).

Relationships across interoceptive modalities

Given the substantial number of analyses, we have applied FDR corrections (Benjamini-Hochberg adjusted *p* value = 0.18). No significant relationship was found between performance on the heartbeat counting task and the dynamic thermal matching task on the forearm (see Table 4) nor on the palm (see Table 5). BF_{01} indicated that the null hypothesis (cardiac accuracy not related to thermal accuracy) was more likely than the alternative hypothesis (cardiac accuracy related to thermal accuracy) ($BF_{01} > 1$), except for the relationship between cardiac accuracy and the thermal matching task in the forearm when temperature was decreasing ($BF_{01} < 1$) (see Lee & Wagenmakers, 2014; Biel & Friedrich, 2018 for guidance on the interpretation of BF).

In line with previous findings (Crucianelli et al., 2018), performance on the heartbeat counting task was not related to affective touch sensitivity, that is, the difference in pleasantness between slow and fast touch on the forearm (see Table 4) or on the palm (see Table 5 and Figure 3 in Supplementary Materials). BF_{01} indicated that the null hypothesis (cardiac accuracy not related to tactile sensitivity) was 7.38 (for the forearm) and 7.64 (for the palm) times more likely than the alternative hypothesis (cardiac accuracy related to tactile sensitivity) ($BF_{01} > 1$).

Cardiac interoceptive accuracy was not significantly related to the detection of static temperature on the forearm (see Table 4) or on the palm (see Table 5). BF_{01} indicated that the null hypothesis (cardiac accuracy not related to static temperature detection) was more likely than an alternative hypothesis (cardiac accuracy related to static temperature detection) (all BF$_{01}$> 1). Finally, no significant relationship was found between cardiac interoceptive accuracy and (warm) pain detection (see Table 4 for forearm data and Table 5 for palm data). BF$_{01}$ indicated that the null hypothesis (cardiac accuracy not related to pain detection) was more likely than an alternative hypothesis (cardiac accuracy related to pain detection) (all BF$_{01}$> 1).

Table 4. Correlational matrix describing the relationship between performance on the different interoceptive tasks (i.e., interoceptive accuracy) on the forearm. Thermal interoceptive accuracies when the temperature is decreasing (cooling) and increasing (warming) are significantly correlated. *P* values correspond to original FDR corrected values.

Forearm		**Heartbeat counting task**	**Thermal matching task**		**Affective touch task**	**Temperature detection**		**Pain detection**
			Increasing	**Decreasing**		**Warm**	**Cold**	
Heartbeat counting task		1						
Thermal matching task	**Increasing**	r = 0.06 p = 0.980 BF$_{01}$ = 9.47	1					
	Decreasing	r = 0.27 p = 0.180 BF$_{01}$ = 0.62	**r = 0.36** **p = 0.020*** **BF$_{01}$ = 0.02**	1				
Affective touch task		r = -0.09 p = 0.935 BF$_{01}$ = 7.38	r = 0.05 p = 0.852 BF$_{01}$ = 9.99	r = 0.06 p = 0.980 BF$_{01}$ = 8.58	1			
Temperature detection	**Warm**	r = -0.14 p = 0.840 BF$_{01}$ = 5.66	r = -0.13 p = 0.840 BF$_{01}$ = 5.07	r = - 0.05 p = 0.852 BF$_{01}$ = 9.99	r = -0.06 p = 0.892 BF$_{01}$ = 6.19	1		
	Cold	r = 0.05 p = 0.852 BF$_{01}$ = 9.38	r = -0.09 p = 0.987 BF$_{01}$ = 6.87	r = - 0.06 p = 0.927 BF$_{01}$ = 8.33	r = -0.33 p = 0.513 BF$_{01}$ = 0.30	r = 0.14 p = 0.784 BF$_{01}$ = 5.61	1	
Pain detection		r = 0.04 p = 0.818 BF$_{01}$ = 9.49	r = 0.06 p = 0.945 BF$_{01}$ = 10.02	r = -0.09 p = 0.940 BF$_{01}$ = 8.04	r = -0.01 p = 0.942 BF$_{01}$ = 6.07	r = 0.12 p = 0.863 BF$_{01}$ = 6.68	r = -0.06 p = 0.980 BF$_{01}$ = 8.92	1

Table 5. Correlational matrix describing the relationship between the performances at the different interoceptive tasks (i.e., interoceptive accuracy) on the palm. Thermal interoceptive accuracy when the temperature is decreasing (cooling) is negatively correlated with cold detection, and the performance in the warm detection task is significantly correlated with both cold detection and pain detection tasks in the palm only. *P* values correspond to original FDR corrected values. *indicates *p* values that are significant after correction for multiple comparisons (FDR).

Palm		**Heartbeat counting task**	**Thermal matching task**		**Affective touch task**	**Temperature detection**		**Pain detection**
			Increasing	**Decreasing**		**Warm**	**Cold**	
Heartbeat counting task		1						
Thermal matching task	**Increasing**	$r = 0.03$ $p = 0.851$ $BF_{01} = 9.67$	1					
	Decreasing	$r = 0.16$ $p = 0.711$ $BF_{01} = 6.31$	$r = 0.32$ $p = 0.105$ $BF_{01} = 1.2$	1				
Affective touch task		$r = -0.04$ $p = 0.840$ $BF_{01} = 7.64$	$r = -0.05$ $p = 0.865$ $BF_{01} = 9.55$	$r = -0.16$ $p = 0.801$ $BF_{01} = 5.34$	1			
Temperature detection	**Warm**	$r = 0.05$ $p = 0.952$ $BF_{01} = 9.20$	$r = -0.20$ $p = 0.513$ $BF_{01} = 1.89$	$r = -0.05$ $p = 0.921$ $BF_{01} = 6.29$	$r = -0.07$ $p = 0.990$ $BF_{01} = 8.11$	1		
	Cold	$r = 0.01$ $p = 0.990$ $BF_{01} = 10.02$	$r = -0.07$ $p = 0.990$ $BF_{01} = 9.15$	$r = -0.29$ $p = 0.140$ $BF_{01} = 0.30$	$r = -0.21$ $p = 0.577$ $BF_{01} = 2.92$	**$r = 0.41$** **$p = 0.021$*** **$BF_{01} = 0.04$**	1	
Pain detection		$r = 0.10$ $p = 0.950$ $BF_{01} = 7.31$	$r = -0.17$ $p = 0.798$ $BF_{01} = 5.21$	$r = -0.16$ $p = 0.770$ $BF_{01} = 6.41$	$r = =0.33$ $p = 0.840$ $BF_{01} = 8.54$	**$r = 0.34$** **$p = 0.042$*** **$BF_{01} = 0.25$**	$r = 0.12$ $p = 0.914$ $BF_{01} = 6.71$	1

The rest of the correlations among the skin-based interoceptive tasks are shown in Tables 4 and 5, and as can be seen there were mainly no significant relationships in line with relatively independent processing (see also Supplementary Figure 4 in the Supplementary Materials). Noteworthy the affective task showed little evidence for correlation with the thermal and nociceptive tasks, and the thermal and nociceptive tasks were uncorrelated on the forearm. The only significant correlation across modalities we observed was between warm temperature detection and pain (Table 5) in the palm.

However, as could be expected there were some significant correlations between tasks within sub-modalities. Performances on the thermal matching task in increasing and decreasing scales were significantly correlated on the forearm (Table 4) but not in the palm. Warm temperature detection was significantly correlated with cold detection in the palm (Table 5), and pain, as we just reported above.

Confidence across modalities

A similar approach of analysis was adopted for the confidence scores for cardiac awareness, dynamic temperature, and affective touch, whereby we focused first on the different tasks separately and then on the relationship of the participants' confidence in completing the different tasks. Confidence in one's own performance in the *heartbeat counting task* was not related to actual performance (r = 0.128; p = 0.323, see Figure 5 in the Supplementary Materials).

In the *thermal matching task*, the results of a 2 (location) x 2 (order) repeated measures ANOVA showed a significant main effect of location (F(1, 61) = 24.64; p < 0.001), with participants being more confident with their answers in the forearm (M= 6.73; SE = 0.18) than in the palm (M = 6.22; SE = 0.20). The order of presentation of temperature (staircase increasing/decreasing) did not have a significant effect (F(1, 61) = 0.184; p = 0.67) on confidence; the interaction between staircase and location was not significant (F(1, 61) = 1.54; p = 0.22). Regarding the relationship between performance and confidence in the thermal matching task, the only significant relationship was between confidence and performance in decreasing (cooling) temperature in the forearm (r = 0.287; p = 0.025, Figure 6). All the other relationships between confidence and accuracy in the thermal matching task were non-significant (increasing forearm: r = 0.21; p = 0.10; decreasing palm: r = 0.19; p = 0.12; increasing palm: r = 0.04; p = 0.73).

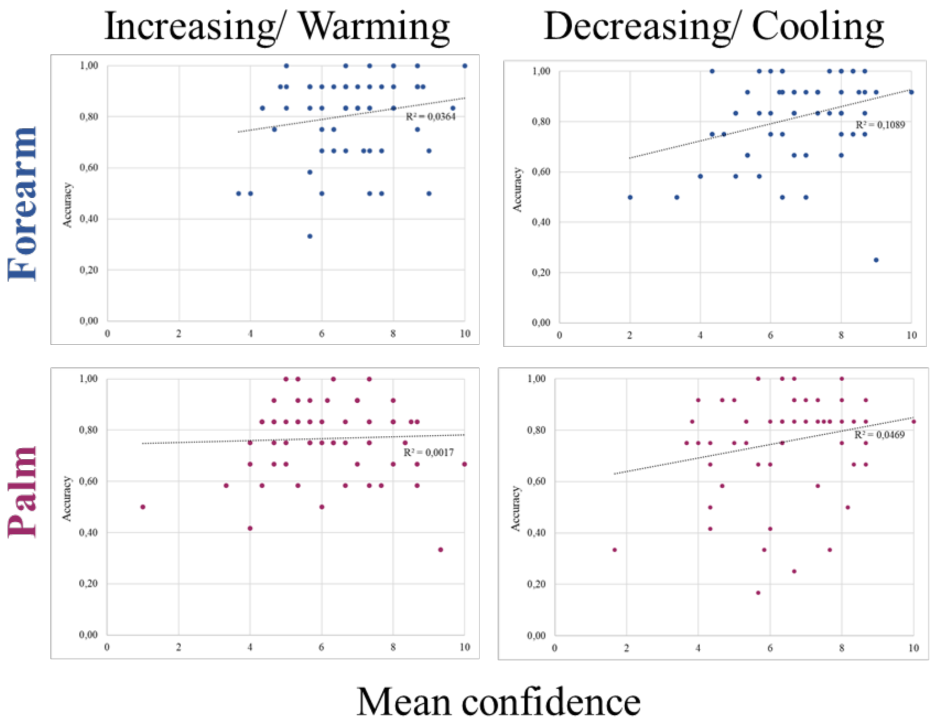


Figure 6: **Confidence-accuracy correspondence in the thermal matching task**. Only for the thermal matching task (TMT) on the forearm at decreasing (cooling) temperatures was there a correspondence between accuracy and the participants' average confidence rating; this indicated that, at the broad group level, subjective and objective dimensions were aligned. By contrast, there was no significant relationship between confidence and accuracy for performance on the TMT regarding the palm (in burgundy).

Finally, we focused on the *affective touch task*. The results of the 2 (location) x 3 (velocities) repeated measures ANOVA showed no main effect of location (F (1, 61) = 0.0; p = 1.00) or velocity (F (2, 122) = 1.72; p = 0.183) on participants' confidence in performance. The interaction between location and velocity was non-significant (F (2, 122) = 2.62, p = 0.077). Regarding the relationship between performance and confidence in the affective touch task, we found a significant relationship between confidence and perception of CT-optimal touch (r = 0.366; p = 0.003; Benjamini-Hochberg adjusted p value = 0.009) and borderline touch (r = 0.289; p = 0.023; Benjamini-Hochberg adjusted p value = 0.03) for the forearm only (see Figure 6 of Supplementary Materials).

Next, we investigated whether the tendency to be confident in one's own performance accuracy was generally related across the submodalities. Confidence in cardiac interoception was significantly related to confidence in thermal matching task performance for both the forearm (see Table 6) and palm (see Table 7). The correlations between confidence in cardiac interoception and affective touch showed a significant relationship between the former and confidence in the perception of CT-optimal touch in the palm (see Table 7) but not in the forearm (see Table 6). In terms of confidence across the thermal matching task and affective touch, correlational analyses revealed a significant relationship between confidence when temperature was increasing and CT-optimal touch in the palm. The same applies for confidence when the temperature was decreasing in the palm (see Table 7). Similar results were found for the forearm (see Table 6).

Table 6. Correlational matrix describing the relationship between confidence on the different interoceptive tasks on the forearm. *indicates *p* values that are significant after correction for multiple comparisons (FDR).

Forearm		**Heartbeat counting task**	**Thermal matching task**		**Affective touch task**
			Increasing	**Decreasing**	
Heartbeat counting task		1			
Thermal matching task	**Increasing**	***r* = 0.542** ***p* = 0.01***	1		
	Decreasing	***r* = 0.607** ***p* = 0.01***	*r* = 0.36 *p* = 0.180 BF_{01} = 0.02	1	
Affective touch task		*r* = 0.147 *p* = 0.253	***r* = 0.260** ***p* = 0.05***	***r* = 0.315** ***p* = 0.02***	1

Table 7. Correlational matrix describing the relationship between confidence on the different interoceptive tasks on the palm. *indicates *p* values that are significant after correction for multiple comparisons (FDR).

Palm		**Heartbeat counting task**	**Thermal matching task**		**Affective touch task**
			Increasing	**Decreasing**	
Heartbeat counting task		1			
Thermal matching task	**Increasing**	***r* = 0.517** ***p* = 0.01***	1		
	Decreasing	***r* = 0.569** ***p* = 0.01***	*r* = 0.32 *p* = 0.105 BF_{01} = 1.2	1	
Affective touch task		***r* = 0.28** ***p* = 0.03***	***r* = 0.448** ***p* = 0.01***	***r* = 0.332** ***p* = 0.01***	1

Discussion

Summary of key findings

The four main findings of the current work were as follows: 1) perceptual accuracy measures of cardiac awareness, thermosensation, nociception, and affective touch were not significantly related (with the only exception of pain and warm detection in the palm). This suggests that interoception should be seen as a set of relatively independent sensory abilities and submodalities rather than a generalised process and single trait. 2) Beliefs in performance rated before the tasks were to a large extent correlated across interoceptive submodalities and with the confidence ratings in task performance rated after the tasks, which collectively suggest that these metacognitive levels of assessing interoceptive bodily awareness constitute more general cognitive processes. 3) We found greater affective touch sensitivity (accuracy), lower cold detection thresholds, and greater accuracy in the dynamic thermal matching task on the hairy skin (forearm) compared to the non-hairy skin (palm). These observations are consistent with the view that hairy skin might play a more important role in skin-based interoceptive functions. 4) Finally, we have shown that a novel thermosensory task—the dynamic thermal matching task—can be used to probe thermosensation as a skin-based interoceptive submodality and, thus, complement existing approaches. Collectively, our results suggest that interoception at the perceptual level is best quantified using a battery of tests that captures its various sensory channels to obtain a more comprehensive picture and that more attention should be given to thermosensation as skin-based interoceptive submodality in future research.

Interoceptive accuracy across modalities

Our results suggest that sensory signals from heartbeats, pleasant touch stimuli, and thermosensory and nociceptive stimuli on the skin are processed relatively independently, and interoceptive accuracy measures obtained from the different modalities do not correlate significantly across individuals. This finding contrasts with the relatively common view in the psychological literature of interoception as a single integrated function and generalised ability. Our studies differ from most previous work in that we use a relatively large number of tests across submodalities, with a particular focus on three different skin-based submodalities. Previous studies have compared the classic heartbeat detection tasks to a single or a few other visceral modalities (Whitehead & Drescher, 1980; Herbert et al., 2012; Azzalini, Rebollo & Tallon-Baudry, 2019; Garfinkel et al., 2016; Faull, Subramanian, Ezra & Pattinson, 2019; Monti, Porciello, Tieri & Aglioti, 2020). For example, Garfinkel et al., 2016 observed no significant relationship between cardiac interoception and respiratory awareness in terms of perceptual accuracy measures, and Crucianelli et al., 2018 found no significant relationship between accuracy in the heartbeat counting task and an affective touch sensitivity measure. Ferentzi et al., 2018 used a larger battery of tests that included cardiac interoception, gastric perception, pain, and taste (a non-interoceptive modality) and did not observe any significant correlations between the perceptual measures. Thus, our results underscore and extend these previous findings by showing that a lack of correlated perceptual sensitivity/accuracy measures is not restricted to the visceral versus skin divide but is also observed between three different skin-based submodalities and between these skin-based channels from hairy and non-hairy skin and cardiac perception.

However, whether these negative correlation findings are reliable and whether our and previous studies failed to detect weak but psychologically relevant relationships are important questions. First, note that we *did* observe some significant correlations in accuracy measures between tasks, which suggests that our tasks were well conducted and that the statistical power was sufficient to detect such relationships. Specifically, cold and warm temperature detection and pain and cold detection were correlated on the palm. Furthermore, the task measures were significantly correlated *within* the skin-based interoceptive submodalities when we correlated accuracy measures across the palm and forearm (see Supplementary material, Table 4). Furthermore, in a recent follow-up study, we found a similar nonsignificant correlation between accuracy measures in the thermal matching task and the heartbeat counting task as in the current study (Radziun, Crucianelli & Ehrsson, 2022). Future studies could pool data across experiments and conduct meta-analyses to further investigate how strong the evidence is against a lack of relationship between accuracy measures across interoceptive submodalities.

We should note that interoceptive tasks are different for the obvious reason that each task has been optimised to probe a different sensory channel. Thus, the tasks put somewhat different demands on memory and executive functions, and this might add variability to the measures, in addition to the differences involved in basic sensory and perceptual processing. In the introduction, we acknowledged the limitations with the heartbeat counting tasks, and the static temperature and pain detection tasks put less demands on memory than the thermal matching task. Nevertheless, these methodological issues considered, we find little evidence that interoceptive perceptual abilities generalise across submodalities, and we suggest that it is more useful to think about these as separate abilities.

The current study investigated interoception using an individual differences approach, but we have not directly targeted the mechanisms behind interindividual variability in the various interoceptive submodalities. One can theorise that individual differences in interoceptive accuracy measures are driven by peripheral factors, such as different receptor densities, differences in central processing from the spinal cord to the brain (including differences in myelination of fibre tracts or differences in grey matter thickness in cortical and thalamic regions), or differences in high-level cognitive processing in terms of how different brain regions work together as functional circuits and the interplay between bottom-up and top-down factors. Future behavioural and neuroscience studies could explore the underlying mechanisms of such interindividual differences in interoceptive submodality processing.

How should we think about the current findings with respect to the neuroanatomical and neurophysiological studies that have shown that the insula processes different kinds of visceral and C-fibre signals from the skin? It is entirely plausible that the neural processing of information from the different interoceptive submodalities can remain relatively independent at lower sensory and early perceptual levels and be implemented in different cortical sections and separate neuronal populations within the posterior insula. We speculate that the neural basis for this separation may well be preserved up until at least the posterior insula, at which point such signals gradually become increasingly integrated with each other and with exteroceptive information and other sources of information (cognition, emotion) in higher brain areas, such as the anterior insula, cingulate cortex and orbitofrontal cortex, and give rise to more complex "interoceptive emotions", such as subjective pain, thermal distress and comfort, and subjective tactile pleasure (Crucianelli & Ehrsson, 2022).

Differences in affective touch and thermosensation between hairy and non-hairy skin

The observed differences in performance on the thermal tasks between hairy (forearm) and non-hairy (palm) skin could be due to fundamental differences in thermoreceptor densities on hairy and non-hairy skin and, for the affective touch task and perhaps the thermal matching task, differences in the engagement of the CT system (see below) (Vallbo, Olausson & Wessberg, 1999; Watkins et al., 2020). This conclusion is in line with recent behavioural findings showing higher thermal sensitivity in hairy skin than in glabrous skin (Filingeri et al., 2018). Notably, both the thermal matching task and the temperature detection task showed a similar pattern of results with regard to the perception of cold; the cold detection thresholds were lower for hairy skin than for non-hairy skin when touch was both dynamic and static. The fact that we have a higher sensitivity to cooling than warming could be explained by the greater abundance of cold receptors throughout our entire body (1.3–1.6 times stronger sensitivity to cooling than to warming; Luo et al., 2020). We also replicated earlier studies showing greater affective touch sensitivity (Crucianelli et al., 2018; Kirsch et al., 2020) on the forearm compared to the palm, in line with the notion of more numerous CT afferents in hairy skin (e.g., McGlone et al., 2012).

We suggest that these observed differences in thermal sensitivity on hairy and non-hairy skin fit the recent theoretical proposal that skin-based interoceptive signals from the hairy skin might have a privileged role in social thermoregulation and maintenance of homeostasis (IJzerman et al., 2015; Morrison, 2016; Burleson & Quigley, 2021). In contrast, we theorise that thermal signals detected through the non-hairy skin of our body (e.g., palm) might potentially have a more discriminatory role and might therefore be important for experiencing the temperature of grasped objects, for instance, a role that is less related to thermoregulation and more related to exploring the properties of external objects (Vallbo & Johansson, 1984; Johansson & Flanagan, 2009; Corniani & Saal, 2020). Furthermore, we hypothesise that thermal dynamic sensations (and in particular, those at neutral temperatures typical of skin-to-skin contact) play a different role in daily social interaction compared to static thermal sensations. The characteristics of CT optimal stimulation (i.e., slow velocity, light pressure, and neutral temperature) closely resemble those typical of affiliative touch (McGlone et al., 2014; Burleson & Quigley, 2021; Fotopoulou, von Mohr & Krahé, 2022); thus, we theorise that thermosensory and CT signals from hairy skin during pleasant touch stimulation at neutral skin temperature might work in concert to promote social connection, which is of vital importance for our survival.

Some findings from the non-hairy skin on the palm are worth commenting on. There were significant correlations between performance on the static temperature detection task and pain detection task on the palm only. One possible interpretation could be more integration of static thermal signals and pain in the palm compared to the forearm, where the processing of such signals remains more segregated. Previous studies have reported that hairy and glabrous skin share similar nociceptive afferents, with non-significant differences in pain sensations or brain potentials in terms of latency and amplitude (Iannetti, Zambreanu, & Tracey, 2006) and similar thresholds for cooling and warming in the forearm and the palm of the hand (Luo et al., 2020). These observations are in line with the current findings of non-significant differences in heat pain detection thresholds for the palm and forearm and suggest that the significant correlation between pain and warm detection in the palm is probably not due to basic differences in nociceptor density or pain thresholds across the two skin sites. We speculate that people learn to combine or pair painful and thermal sensations from the palm and digits when manipulating and grasping objects, as objects can sometimes cause pain. Such learned functional correlations could be less pronounced on hairy skin, which is typically not used when we explore objects.

Dynamic thermal matching task

The results from the thermal matching task reveal interesting differences between hairy and non-hairy skin that suggest greater thermal sensitivity in the former skin type for relatively weak cold and warm stimuli. We argue that this could reflect greater innervation of thermoreceptors on the forearm and perhaps the engagement of CT afferents. Ackerley et al. (2014) investigated the CT responses to light tactile stimuli delivered at different speeds and temperatures; the study showed that the maximum firing rate of the CT afferents from which they were recording using microneurography was found for mechanothermal stimuli delivered in the range of velocities between 1–10 cm/s and at neutral temperature (32°C, typical of human skin; Arens & Zhang, 2006). Moreover, the characteristic significant correlation between pleasantness ratings and CT discharge rates across velocities was found only for thermoneutral stimuli. Thus, we think that it is possible that CT signals may have contributed to the performance on the thermal matching task by providing additional information about how the stimulation felt in terms of affective sensations. Alternatively, the subjects may have ignored the possible changes in pleasantness and focused only on the thermal sensations. If this is the case, the CT contribution to performance on the thermal matching task would be neglectable, and the task would only probe thermosensation. Future studies could explicitly test this by varying stroking velocities (CT-optimal and CT-non-optimal velocities), testing temperature matching within and outside CT-optimal temperatures, and asking participants to match temperatures, pleasantness, or the ‘overall feeling’.

During affective touch in natural situations, the combination of the thermoneutral experiences in the thermal comfort zone are combined with tactile pleasantness into an overall experience of social touch. In interoceptive terms, we speculate that the CT system might thus contribute to how the skin affectively ‘feels’ during social touch. However, the fact that we did not find a relationship between performance on the thermal matching task and the affective touch task is in line with thermosensation and affective touch being relatively independent submodalities and recent evidence suggesting that affective touch pathways outside the spinothalamic pathway signalling pain and temperature may contribute to tactile pleasantness (Marshall et al., 2019). Although the results from the dynamic matching task are by no means conclusive with respect to the possible involvement of CT signals in the task, they suggest that greater attention should be given to potential interactions between thermal experiences and affective touch during social physical interactions in future studies.

Interoceptive ability across metacognitive dimensions

In terms of the metacognitive dimension, our results highlight a general relationship between prior beliefs in performance across tasks (as in Beck et al., 2019). That is, people who had higher beliefs in their upcoming performance on the heartbeat counting task or thermal matching task also had higher beliefs of performance on the affective touch and pain detection task. This might reflect the fact that this metacognitive dimension of interoception is related to domain general cognitive abilities and therefore is mainly driven by top-down beliefs that are relatively independent from the perceptual processes in the tasks. Similarly, the confidence ratings of performance obtained after the heartbeat counting task, the affective touch task, and the thermal matching tasks were correlated across modalities (note that such ratings were not obtained for the change detection tasks for reasons described in the methods). This suggests that the ability to judge task performance, presumably by recalling subjective awareness and response decisions (matching, counting, and rating pleasantness), is a generalised ability. Taken together, our results show a striking difference between metacognitive and perceptual levels of interoception in that only the former show evidence of significant and systematic correlations across submodalities (see Figure 7).

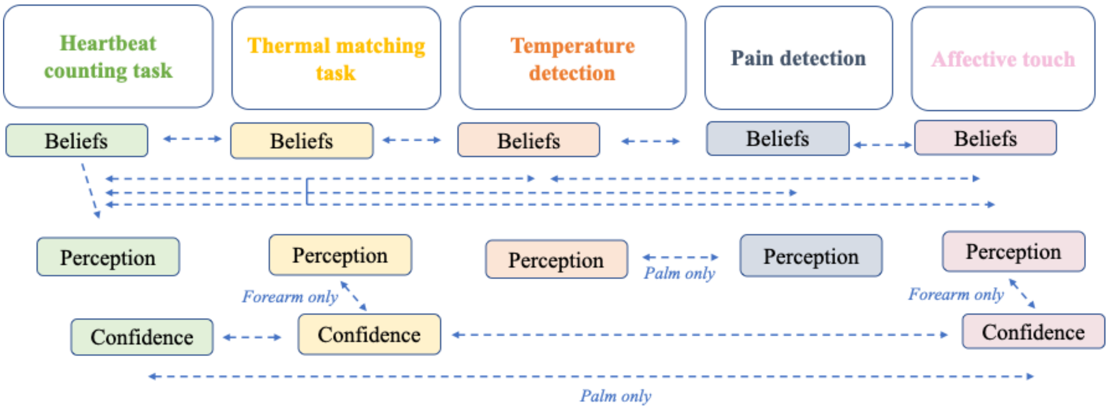


Figure 7. Overview of the findings across modalities. The dashed line indicates a significant correlation.

With respect to the question of how the metacognitive measures were related to perceptual accuracy, we found that higher confidence was related to better performance on both the thermal matching task and the affective touch task in hairy skin (forearm) only, in keeping with recent findings arguing that such 'metacognitive sensitivity' is higher in hairy skin than in non-hairy skin (von Mohr, Kirsch, Loh & Fotopoulou, 2019). This evidence might suggest that we are more precise in or aware of our ability to detect such stimuli on hairy skin (Morrison, 2016; Filingeri, Zhang & Arens, 2018) and provide yet another example of differences between hairy and non-hairy skin that is relevant to the current data. The reason for this is not clear, but we speculate that it may be related to affiliative and thermoregulatory processes being more closely linked to hairy skin. The belief ratings regarding task performance on the heartbeat counting task significantly correlated with accuracy on the heartbeat counting task (Supplementary Material); however, this was the only significant correlation we found between beliefs and accuracy measures, so overall, the connection between this metacognitive ability and task performance was rather poor.

In terms of *interoceptive sensibility*, we used both the Body Awareness Questionnaire (Shields, Mallory & Simon, 1989) and the Body Perception Questionnaire (Porges, 1993), which are two commonly used scales. In line with these questionnaires probing metacognitive levels of interoception, no significant correlations with accuracy measures were found for the Body Awareness Questionnaire scores (Table 2 in Supplementary Materials), and the Body Perception Questionnaire scores were correlated only with the affective touch task on the palm (see Table 3 in Supplementary Materials).

In contrast, these scales correlated with the confidence ratings for several tasks, but this was more apparent with the Body Awareness Questionnaire, in that scores on this scale were positively correlated with this metacognitive dimension for cardiac interoception, the thermal matching task (both palm and forearm) and the affective touch task on the palm. In contrast, Body Perception Questionnaire scores were positively correlated with confidence only for the affective touch task on the palm and forearm. Scores on both questionnaires showed little relationship with the belief ratings in task performance; scores on the Body Perception Questionnaire were correlated only with beliefs in pain detection only, and scores on the Body Awareness Questionnaire were correlated only with beliefs in temperature detection.

Nevertheless, these observations are reasonably well in line with previous claims that questionnaires mainly capture aspects of interoception at metacognitive levels (see Garfinkel et al., 2015; Fairclough & Goodwin, 2007; Schulz et al., 2013 for similar approaches). Here, we extend this observation to the current battery of five tasks, including multiple skin-based submodalities and the observation that the most convincing relationships seem to be found between scores on the Body Awareness Questionnaire and confidence ratings rather than belief ratings. Since confidence ratings relate to memory and awareness of task performance, we speculate that this may indicate that the questionnaires tap into such mnemonic and attentional processes in everyday experiences of interoceptive cues.

We believe that in future studies, it could be valuable to also include the standardised Multidimensional Assessment of Interoceptive Awareness scale (Mehling, Price, Daubenmier, Acree, Bartmess & Stewart, 2012), which is organised into eight separate subscales (e.g., emotional awareness, body listening, and self-regulation) and could potentially target different facets of self-reported interoception and their possible relationships with interoceptive accuracy and metacognitive awareness. Another valuable alternative is the recently developed Interoceptive Accuracy Scale (IAS, Murphy et al., 2020), which aims to distinguish the attention component from the accuracy component in interoceptive self-report measures.

Even though we did not find significant relationships between the questionnaires and the interoceptive accuracy measures in the present study, this does not mean that the former does not provide important information or should not be used in future studies. For instance, interoceptive sensibility has proven to be clinically relevant since some individuals have shown a dissociation between their self-report abilities to experience their body's physiological and inner status and actual performance, such as in individuals with autism spectrum disorder, individuals with high levels of anxiety (e.g., Garfinkel et al., 2016) and individuals with an eating disorder (Pollatos & Georgiou, 2016; Eshkevari et al., 2014).

Limitations and future directions

One limitation with the dynamic thermal matching task is that the thermosensory stimuli are presented during mechanical stimulation of the skin by a moving object. This was a deliberate design choice as outlined in the introduction, but it also means that this task involves both thermal and exteroceptive stimulation on the skin. Future studies could attempt to investigate the interoceptive nature of thermosensation by completely eliminating tactile inputs during the task (e.g., Ackerley et al., 2018). For example, stimulating thermoreceptors by means of heat lamps or lasers can allow us to deliver contactless thermal stimulation. Another approach can be to explicitly formulate the perceptual judgements about the interoceptive dimension of thermosensation, such as asking participants to report "which limb feels warmer/colder" or match thermal comfort or discomfort sensations. Nevertheless, all thermosensory stimuli have an intrinsic interoceptive dimension, we argue, given the dual nature of thermosensation as both exteroception and interoception and the fact that thermal signals are processed in the spinothalamic pathway and reach the posterior insula regardless of the nature of the psychological task.

Future studies should also focus on validating the thermal matching task by exploring more body sites, adding more trials, and investigating the test-retest reliability of the task. It would also be interesting to explore the relationship between the thermal matching and detection tasks and cold pain sensitivity, since here we investigated only heat pain. We did not continuously record the skin temperature during the current tasks but only at the beginning, so we could not explore possible dynamic interactions between skin temperature and task performance. However, our skin temperature data showed no significant variations between skin sites or across participants at baseline, so we do not think that this factor played a significant role in the current experiments (also the thermal stimulation was mild and brief and unlikely to cause significant changes in skin temperature). Finally, with the current battery of tests, we decided to present the experimental tasks in a fixed order for reasons explained in the methods section. As tasks were not counterbalanced, we cannot exclude order effects. However, since accuracy measures are well protected against cognitive bias, we did not observe significant correlations between accuracy measures across the individual tasks, and our individual task performance is well in line with previous studies that have tested these tasks in isolation or in different experimental contexts, we do not think this was a significant issue in the current study.

Conclusions

Taken together, our results suggest that it is possible to broaden the testable interoceptive modalities beyond cardiac signals to include skin-based interoceptive submodalities, including temperature perception. Our findings from the thermal matching task and the temperature detection task suggest that more attention should be given to differences between hairy and non-hairy skin because the former is likely to play a more important role in thermoregulation and interoceptive dimensions of thermosensation, as we have argued. The lack of significant relationships between performance on interoceptive tasks across all modalities and skin types tested (i.e., cardiac accuracy, affective touch, temperature, and pain detection; palm and forearm; with the only exception being cold and pain detection in the palm) supports the idea that interoception might be better conceptualised as a modular construct with relatively independent processing in parallel streams. Thus, just as in the case of exteroception, distinct interoceptive submodalities might not necessarily be related to one another, and the capacity to perceive different kinds of interoceptive signals may vary within an individual. Consequently, future basic and clinical studies could benefit from using batteries of interoceptive tests that comprise multiple interoceptive modalities, which can collectively provide a complete understanding of interception in health and disease.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationship that could be construed as potential conflicts of interest.

Authors contribution

Conceptualisation: LC, HHE; Data curation: LC, AE; Formal analysis: LC; Funding acquisition: HHE, LC; Investigation: LC, AE; Methodology: LC, HHE; Project administration: LC, HHE; Resources: HHE; Visualisation: LC, AE; Writing – original draft: LC; Writing – review & editing: LC, AE, HHE

Data availability statement

Data of this study are available as a supplementary file.

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