BODY REPRESENTATION AND INTEROCEPTIVE AWARENESS: COGNITIVE, AFFECTIVE, AND SOCIAL IMPLICATIONS

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EDITORIAL
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Editorial: Body Representation and Interoceptive Awareness: Cognitive, Affective, and Social Implications

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Editorial on the Research Topic

Body Representation and Interoceptive Awareness: Cognitive, Affective, and Social Implications

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INTRODUCTION

Following Descartes, we are not in our bodies as pilots are in their vessels (Descartes, 2008). Indeed, when something happens to the body, we actually feel it from within. Most of the scientific interest in understanding how the body is represented in the brain arose from this peculiarity and generated a significant corpus of studies in different research fields.

Converging evidence from body ownership illusion paradigms (e.g., the Rubber Hand Illusion) and patients with peripheral or central nervous system damage strongly suggests that the representation of one's own body arises from the integration of visual, vestibular, tactile, proprioceptive, interoceptive, and motor information (Berlucchi and Aglioti, 2010; Suzuki et al., 2013; Park and Blanke, 2019; Boccia et al., 2020). An efficient body representation (BR) is thought to be central to adequately acting in the environment, constructing the sense-of-self, and interacting with others, with important cognitive, affective and social implications (Goldman and de Vignemont, 2009; Ferroni et al., 2019; Macpherson et al., 2021). BR concerns and disturbances can be determined by disorders of interoceptive processing and multisensory integration, and by implicit and explicit habit-body memory deficits, impacting social and cognitive abilities (Besharati et al., 2016; Badoud and Tsakiris, 2017; Fossataro et al., 2018; Riva, 2018; Raimo et al., 2022).

Several aspects of BR development and dynamics across the lifespan remain to be investigated. Our Research Topic provides a state-of-the-art overview of current investigations, combining experimental psychology, psychiatry, psychophysics, and cognitive and affective neuroscience. In particular, recent BR research is progressively targeting interoceptive processing (i.e., the sense of the physiological condition of the body; Craig, 2002) as an important source of sensory input to bodily cognition. In this vein, the present Research Topic covers the relation between different types of BR and various interoceptive dimensions in motor, cognitive, affective, and social domains.

BODY REPRESENTATIONS AND INTEROCEPTIVE SENSIBILITY: COGNITIVE IMPLICATIONS

Interoceptive sensibility (IS) is a specific component of interoception, corresponding to the self-perceived tendency to focus on interoceptive signals as commonly assessed *via* self-report measures (Garfinkel et al., 2015). In the present Research Topic, four articles focus on IS in healthy individuals investigating (i) the relation with other interoceptive dimensions (i.e., accuracy and awareness) in different modalities (Horváth et al.), (ii) the association with different BR in adult lifespan (Raimo et al.), (iii) sex differences in IS neural correlates (Longarzo et al.), and (iv) IS role in higher-order cognitive functioning (Brown et al.).

Studying the three interoceptive dimensions (i.e., accuracy, sensibility, and awareness) in cardiac and proprioceptive modalities, Horváthet al. suggest that these dimensions are dissociable and modality-specific.

Raimo et al. provide new evidence on the relation between IS and BR, in terms of action-oriented (i.e., body schema) and non-action-oriented (i.e., body structural representation and body semantics) BR, across the adult lifespan. Age-related effects were evident both in action and non-action-oriented BR. Also, higher IS levels were significantly related to worse performance in a task tapping the body schema in older adults.

Along with age, sex differences are another source of interindividual IS variability. Accordingly, Longarzo et al. find both behavioral and neuroanatomical sex differences in IS. Indeed, women reported stronger attention in perceiving inner body sensations. Differences were also found in the strength of the correlation between IS scores and gray matter volumes in specific brain areas, since only in women IS scores and gray matter volumes in the left insula were associated.

A novel contribution to the role of bodily feeling/perception in shaping moral decision-making is offered by Brown et al. Higher IS scores were associated with more intuitive responses and reduced aversion to harmful actions in a task tapping the ability to override intuitive or "gut" responses to counterintuitive problems (i.e., the Cognitive Reflection Task). By implication, this study suggests that higher IS may indicate people's intuitive thinking preference in processing moral dilemma.

BODY REPRESENTATIONS AND INTEROCEPTION: PSYCHOPATHOLOGICAL AND AFFECTIVE IMPLICATIONS

Our Research Topic provides insight into the role played by BR and interoceptive processing in psychiatric and affective disorders, namely in eating disorders (Khalsa et al.) and depression (Schultchen et al.). Other studies focus on the body-space relation in psychopathologies (Rabellino et al.), and on the interindividual BR variability as a function of schizotypal and autistic traits (Michael et al.; Kuroki et al.) or empathic abilities (Heydrich et al.).

Schultchen et al. find lower interoceptive accuracy in individuals with depression than in healthy controls, a clinically relevant finding since interoceptive abilities can be improved through different methods, including mindfulness.

Khalsa et al. address the safety and tolerability of the Reduced Environmental Stimulation Therapy in anorexia nervosa. This timely paper highlights the need for a more effective form of treatment for anorexia nervosa, and shows the significant effect of this approach in improving interoceptive awareness, and reducing affective symptoms and body image disturbances.

Rabellino et al. provide an overview of the space-body relations, focusing on peripersonal space (PPS). Consistent with a conceptualization of PPS as a protective zone surrounding one's body, authors review studies investigating the relation between PPS, personality traits, and psychopathologies. In particular, they suggest that specific PPS alterations are present in trauma-related disorders.

Michael et al. investigate the relation between the perception of spontaneous sensations, serving to locate the bodily spatial boundaries, and embodiment as seen in schizotypal personality. Higher schizotypal traits were associated with the more frequent perception of spontaneous sensations, signaling altered body boundaries and suggesting that embodiment is required to feel oneself correctly.

Kuroki and Fukui explore how autistic traits modulate performance in hand laterality judgment and self-other discrimination tasks. In men, higher autistic traits were positively correlated with higher reaction times in the hand laterality judgment task. In contrast, in the self-other discrimination task, women with lower autistic trait scores reacted faster to a self-image than to other's images.

Heydrich et al. investigate if adopting another person's perspective can be altered by manipulating interoceptive cues. Participants had to imagine taking the perspective and position of a virtual body presented on a computer screen and to indicate which hand was marked; in the meantime, a silhouette surrounding the virtual body flashed either synchronously or asynchronously with the participants' heartbeats. The effect of synchronous cardio-visual stimulation on visuospatial perspective-taking was only present in participants with high empathic ability, suggesting that interoceptive processing, perspective taking, and empathy are inherently interlinked.

BODILY SELF-CONSCIOUSNESS AND MULTISENSORY INTEGRATION: SOCIAL IMPLICATIONS

Four studies focus on multisensory integration and bodily self-consciousness.

Studying the effect of tactile input on multisensory integration, Tanner, Orthlieb et al. investigate how proprioception interacts with artificial sensory substitution. Participants performed a simple proprioceptive estimation task under four tactile feedback conditions: hover, touch, electrotactile, and vibrotactile. Only the electrotactile and vibrotactile sensory substitutions succeed in multisensory integration when applied to the dominant hand, suggesting that sensory substitution may hinder positional ability in practical application, such as prosthetics.

Tanner, Newman et al. investigate the effect of changing the grip orientation with respect to gravity on the perception of slip direction during active grip, showing that precision grip responses are modulated by task context as seen in forces, latencies, and orientation sensitivity. These findings provide insight for research exploring (own-) body perception and bodily self-awareness and can have implications for future clinical studies in individuals with body modifications (e.g., amputation).

Bekrater-Bodmann et al. explore the relationship between exteroceptive and interoceptive information underlying the feeling that the self is located within the borders of one's own body. By manipulating participants' perspective of their own body (first- vs. third-person perspective) as well as the synchrony of visuotactile stimulation (synchronous vs. asynchronous), the authors found that participants reported out-of-body experiences, particularly under third-person perspective combined with synchronous visuotactile stimulation. Better interoceptive awareness was associated with lower effects of exteroceptive inputs on body perception. Overall, this study nicely shows that bodily self-location, a key component of bodily self-consciousness, relies on the interaction of higher-order interoceptive abilities and exteroceptive input.

Previous research indicated that bodily self-consciousness is also linked to the self-others distinctions, as highlighted in the opinion paper by Pacholik-Żuromska, who discusses how bodily self-consciousness, in terms of sense of ownership and agency, shapes propositional self-others-knowledge (i.e., a specific type of metacognition pivotal in understanding intentions and ascribing mental states to other individuals). Specifically, the author provides a new model of how self-others-knowledge is constructed, assigning a pivotal role to proprioception. This opinion paper calls for more integrative research accounting for the social mind as shaped by the body and its interaction with the world.

CONCLUSION

We believe that the collection of articles in this Research Topic underscores the value of combining different perspectives to address body representation and will stimulate further in-depth investigations of such fascinating matter.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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Hunger Bias or Gut Instinct? Responses to Judgments of Harm Depending on Visceral State Versus Intuitive Decision-Making

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Empirical investigation into the emotional and physiological processes that shape moral decision-making is vast and growing. Yet, relatively less attention has been paid to measures of interoception in morality research despite its centrality in both emotional and physiological processes. Hunger and thirst represent two everyday interoceptive states, and hunger, in particular, has been shown to be influential for moral decision-making in numerous studies. It is possible that a tendency to focus on internal sensations interoceptive sensibility (IS), as well as the emotional and physiological states associated with visceral states, could be important in the relationships between hunger, thirst, and moral judgments. This cross-sectional online research (n = 154) explored whether IS, hunger, thirst, and emotional state influenced appropriateness and acceptability judgments of harm. The moral dilemma stimuli used allowed the independent calculation of (1) people's tendency to avoid harmful action at all costs and (2) people's tendency to maximize outcomes that benefit the greater good. The Cognitive Reflection Task (CRT) was implemented to determine whether an ability to override intuitive responses to counterintuitive problems predicted harm-based moral judgments, as found previously. Hunger bias, independent of IS and emotional state, was influential for non-profitable acceptability judgments of harmful actions. Contrary to dual-process perspectives, a novel finding was that more intuitive responses on the CRT predicted a reduced aversion to harmful actions that was indirectly associated with IS. We suggest that IS may indicate people's vulnerability to cognitive miserliness on the CRT task and reduced deliberation of moral dilemma stimuli. The framing of moral dilemmatic questions to encourage allocentric (acceptability questions) versus egocentric perspectives (appropriateness questions) could explain the divergence between hunger bias and intuitive decision-making for predicting these judgments, respectively. The findings are discussed in relation to dual-process accounts of harm-based moral judgments and evidence linking visceral experiences to harm aversion and moral decision-making.

Keywords: interoception, moral judgment, hunger, decision-making, moral dilemmas

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INTRODUCTION

Our current homeostatic needs provide a context for decision-making (Gailliot, 2013; Yam et al., 2014; Craig, 2015). Important decisions sometimes with serious consequences, such as prescribing antibiotics (Linder et al., 2014), judicial rulings (Danziger et al., 2011), and voting behavior (Gomez et al., 2007), can be influenced by regularly occurring trivialities, such as the time of day (Danziger et al., 2011; Linder et al., 2014), bad weather (Gomez et al., 2007), carbon-dioxide levels (Satish et al., 2012), and how hungry we are (Gailliot, 2013). The connection between how we feel right now and the decisions we make is no coincidence. Interoception refers to our perception and interpretation of visceral sensations associated with homeostatic regulation inside the body, such as those originating in the cardiovascular, respiratory, and gastrointestinal systems (Garfinkel and Critchley, 2013; Craig, 2015). Brain areas responsible for the perception of visceral states (e.g., feeling hot, cold, full) are also implicated in the integration of this information to initiate drive states (e.g., hunger, thirst, sex drive) that in turn affect how we feel (Craig, 2015). The vagus nerve communicates the majority of information from visceral centers to the brain stem (Hellström and Näslund, 2001) coordinating adaptive fight/flight responses on the one hand and emotional expression and social engagement processes on the other, depending on the physiological state of the body (Porges, 1993). There is considerable crossover in brain areas responsible for interoception, emotion, and social cognition (Adolfi et al., 2017), and empirical advances in the field of embodied cognition continue to illuminate how cognitive products of the mind can be rooted within the body (Häfner, 2013). Furthermore, individual differences in how we perceive internal sensations have been shown to be important in the link between visceral processes and decision-making (Dunn et al., 2010; Häfner, 2013).

Visceral states such as hunger can influence ethical decisions in the laboratory (e.g., Yam et al., 2014) and the real world (e.g., Gailliot, 2013). Hunger is the subjective experience of food deprivation comprising visceral sensations in the stomach area, an emotional desire or wanting to eat, and cognitive states associated with eating, food, and hunger (Stevenson et al., 2015). Thirst is a comparatively understudied but related drive, largely regulated by food intake (Mckiernan et al., 2009), and comprises a desire or wanting to obtain and drink water, often accompanied by sensations such as dryness of mouth (Ramsay and Booth, 2012). Incidental emotional states can influence moral decision-making (Valdesolo and Desteno, 2006); sensitivity to moral norms (Gawronski et al., 2018) and emotional-regulation difficulties predict a bias toward immoral judgments (Zhang et al., 2017a). Differences in blood glucose levels have also shown to predict prosocial intentions (Gailliot et al., 2007). Danziger et al. (2011) found the probability of court judges to provide less favorable rulings was increasingly likely before the provision of a food/rest break compared to afterward. However, other researchers (Weinshall-Margel and Shapard, 2011) have contested this, suggesting that the order of cases seen by judges was partly responsible for this observation.

Laboratory-based research has been more effective at substantiating a link between hunger and moral judgments as hunger can be objectively manipulated. Vicario et al. (2018) found hunger reduced moral disapproval ratings for ethical violations, suggesting hunger bias may reduce the harshness of moral judgments. A dispositional sensitivity toward feelings of disgust was also found to increase the severity of moral disapproval ratings of ethical violations. Vicario and colleagues suggested hormonal reactions and interoceptive signals triggered by eating may evoke feelings of nausea interpreted as disgust (Tracy et al., 2019), which subsequently inform moral judgments. This is consistent with other work (Wheatley and Haidt, 2005; Horberg et al., 2009), including Schnall et al. (2008), who found disgust manipulations encourage harsher judgments of ethical violations and is strongest for those with a greater tendency to pay attention to interoceptive sensations. Despite large variations in interoceptive sensitivities between people and daily fluctuations in interoceptive states, individual differences in interoception is an underexplored area in the link between moral decision-making and visceral states such as hunger (Dunn et al., 2006).

Damasio's et al. (1996) somatic marker hypothesis (SMH) was among the first theoretical frameworks to reveal the neuropsychological foundations that connect fundamental visceral processes with higher-level moral cognitions. The SMH (Damasio et al., 1996) describes how changes in bodily states have the potential to alter our emotional state and bias our thinking processes to support adaptive behavioral responses to the environment (Craig, 2015; Barrett, 2016). The ventromedial prefrontal cortex is believed to be responsible for the representation of homeostatic information (including emotional state) when evaluating ethical violations (Damasio, 1994; Moretto et al., 2010). Damage to this area is associated with emotional deficits in guilt and empathy (Anderson et al., 2013), reduced physiological responses to moral decisions, and greater acceptance of moral violations (Moretto et al., 2010). The insula is a key center for interoceptive integration (Adolfi et al., 2017) and is implicated in processing negative emotional states, particularly disgust sensitivity (Calder et al., 2007), which can bias moral decision-making (Greene et al., 2004). It is possible people with superior ability to perceive interoceptive processes could be more influenced by this information when forming moral judgments. For example, in research using the Iowa Gambling Task (a card-choosing task measuring decision-making under uncertainty), people with a superior ability to detect internal sensations were more influenced by concurrent somatic signals even when those signals unhelpfully guided them toward high-risk card decks (Dunn et al., 2010).

Historically, research exploring emotional influences in moral decision-making has focused on harm-based moral dilemmas such as the Trolley (Thomson, 1985) and Footbridge (Foot, 2003) problems, as particularly emotive moral conflicts to consider (Greene et al., 2001). In these dilemmas, participants judge whether it is acceptable to cause fatal harm to one person either directly (Footbridge) or indirectly (Trolley), as a necessary means to saving the lives of more (>1) people. Judgments can be influenced by an emotional reaction to the harmful *action* toward the one person intentionally harmed ("deontology") or to the *outcomes* of the action for the many people who would be harmed otherwise ("utilitarianism") (Cushman, 2013; Miller et al., 2014). This traditional moral dilemma paradigm places utilitarianism and deontology on opposite ends of a bipolar scale, preventing us from determining whether someone chooses to harm the one person because he/she has a weakened aversion to harming others or because he/she is more motivated to save the lives of more people (Conway and Gawronski, 2013). A more recent process-dissociation approach (Conway and Gawronski, 2013) uses moral dilemma stimuli that allow the measurement of people's outcome-maximization (utilitarian) and harm-aversion (deontological) motivations independently. This method works by calculating the probability that someone chooses to condone harming others when harm results in a "greater good" overall and when it does not. Although people's tendencies to avoid harm or maximize outcomes do not necessarily represent people's abstract views about deontological and utilitarian philosophies (Kahane et al., 2018), these terms are used for clarity.

Deontological moral judgments associated with the rejection of harmful action have been associated with more visceral and intuitive decision-making processes than utilitarian decisions (Greene et al., 2001; Park et al., 2016). Greene's et al. (2004) dual-process account of morality proposes deontological judgments are driven by automatic and emotional responses associated with activation of emotional centers in the brain, whereas utilitarian judgments are driven by more reflective, cognitive processes and are associated with activation of brain areas implicated in cognitive control (Greene et al., 2004). In support of a dual-process conceptualization, emotional arousal predicts deontological preferences (Szekely and Miu, 2015), and performing or witnessing harmful actions correlates with measures of cardiac arousal (Cushman et al., 2012; Parton and McGinley, 2019). More calculative reasoning styles have been associated with utilitarian response tendencies (Patil et al., 2020), and successful performance on the Cognitive Reflection Task (CRT; Frederick, 2005) is associated with increased utilitarian judgments, potentially due to its association with cognitive deliberation (Baron et al., 2015). The CRT task includes questions that have both correct and "intuitive" answers and can be scored according to correct versus intuitive responses (Erceg and Bubić, 2017). Successful performance on this task requires some reflection to avoid the intuitive lures and determine the correct solutions. As such, this task is believed to provide an indication of a person's ability to "override" their gut response to counterintuitive problems (Frederick, 2005). Byrd and Conway (2019) suggest that arithmetic-reflection ability (captured by the CRT) is responsible for the association with utilitarian preferences, possibly because it indicates a greater numerical focus (i.e., saving *more* lives) when weighing up moral decisions, whereas Park et al. (2016) suggest strong utilitarian preferences may reflect poorer integration of visceral signals into the decision-making process, leading participants to place more weight on the outcomes of harmful action.

The physiological, emotional, and cognitive processes implicated in moral decision-making are relevant to consider in the context of hunger and thirst, as changes in our psychophysiological states have the potential to bias decision-making processes (Critchley and Garfinkel, 2018). Food deprivation is often associated with increased physiological arousal (e.g., Chan et al., 2007; Ribeiro et al., 2009). Ghrelin (the "hunger" hormone) appears to play a role in regulating our responses to stressors potentially by increasing anxiety (see Korbonits et al., 2004) and relationship with the stress hormone cortisol (Sarker et al., 2013). Although there has been less empirical interest in thirst, available evidence suggests hydration levels do not affect cardiovascular reactivity (Schwabe et al., 2007) but can affect blood reactivity to stress (Rochette and Patterson, 2005). Cardiovascular arousal is of particular interest, as arousal represents a core component of emotional experience (Russell and Barrett, 1999), which can intensify the processing of emotionally salient information (McGaugh, 2015) and can influence moral decision-making (Greene et al., 2001). Heartbeat signals alone can directly influence cognition and facilitate the detection of fearful and threatening stimuli (Garfinkel and Critchley, 2016). In addition, the sound of "quickening" heartbeat feedback has shown to predict moral decision-making (Gu et al., 2013), demonstrating how even a belief that we are physiologically aroused can influence our moral choices. Hunger sensations or sensations associated with hunger-induced physiological arousal may manifest as different psychological states (Barrett et al., 2004; MacCormack and Lindquist, 2016), depending on individual differences in perception (Dunn et al., 2010; Herbert et al., 2012) and interpretation (Domschke et al., 2010) of these interoceptive processes. For example, brain regions associated with the conscious awareness of interoceptive states are also implicated in subjective emotional experience (Zaki et al., 2012), and individuals who are better at detecting heartbeat sensations experience more arousal-focused emotional experiences (Barrett et al., 2004). Furthermore, preliminary evidence suggests hunger could actually provide a context for more accurate perception of visceral sensations due to changes in the autonomic nervous system that alter cardiac activity (Herbert et al., 2012). Therefore, although subjective hunger and thirst states may be influential for moral decision-making due to the physiological experiences typically accompanying them, it is likely that individual differences in interoceptive sensitivities will shape how these visceral states translate into psychological and emotional states.

Interoceptive sensibility (IS) is one construct that could influence the psychological manifestation of visceral states and is a measure of a person's tendency to focus on internal sensations, independent from their ability to objectively detect internal sensations (Garfinkel and Critchley, 2013). Although some evidence suggests heartbeat detection accuracy corresponds with increased sensitivity to bodily information (Duschek et al., 2015), other research indicates interoceptive accuracy and sensibility are unrelated (Ainley and Tsakiris, 2013; Ferentzi et al., 2018). Individual differences in IS have shown to be important in the link between our visceral experiences and subjective appraisals of these experiences (Häfner, 2013) and could potentially shape the interpretation of visceral sensations present during moral decision-making. Individuals high in body awareness typically direct more attention toward visceral sensations, increasing the likelihood they will observe and misinterpret physiological changes as meaningful, which can influence emotional state (Palomba and Stegagno, 1995) and increase anxiety (Clark et al., 1997; Domschke et al., 2010). Paulus and Stein (2010) suggest that visceral sensations detected by people with high levels of anxiety can be intensified and associated with bad or aversive outcomes and is consistent with the finding that IS can increase risk-averse behavior when bodily information is present (Salvato et al., 2019). Overall, the link between anxiety and moral judgments of harm presents a mixed picture. Anxiety facilitates increased vigilance to threats and has been associated with unethical behavior (Kouchaki and Desai, 2015). There is some evidence to suggest that self-oriented anxiety associated with empathy can increase people's tendency to reject harm in traditional moral dilemmas (Sarlo et al., 2014). Trait anxiety has shown to specifically predict moral goodness ratings of utilitarian action in the Footbridge dilemma, whereas mild anxiety-inducing manipulations appear to have less of an impact on moral judgments (Zhao et al., 2016). It is plausible that a greater attentional focus on bodily sensations could heighten sensitivity to arousal-based physiological sensations accompanying hunger or thirst, which, if interpreted as meaningful and anxiety-evoking (Paulus and Stein, 2010), could influence moral decision-making (Sarlo et al., 2014; Zhao et al., 2016).

Importantly, prior studies exploring the relationship between hunger and moral judgments have measured judgments of ethical violations, which require people to make allocentric judgments about the acceptability of other people's morally dubious actions (e.g., Vicario et al., 2018). However, moral dilemmas used to explore people's aversion to harm typically ask questions that facilitate an egocentric perspective, e.g., "Would **you**, carry out X action. . . in order to?" (e.g., Thomson, 1985; Foot, 2003; Conway and Gawronski, 2013). Several studies have found discrepancies between whether people judge another person's actions to be morally acceptable and whether people agree that they would perform "immoral" actions themselves (Tassy et al., 2013; Pletti et al., 2017). An egocentric perspective that is putting ourselves in the shoes of the agent committing an immoral act encourages us to consider the self-relevant consequences of our actions (Sood and Forehand, 2005). Egocentric moral judgments, but not allocentric judgments, have been associated with activation of the amygdala, suggesting these judgments rely on emotional processes that allocentric judgments do not (Berthoz et al., 2006). Therefore, it is possible that imagining ourselves personally performing harmful acts could influence how likely we are to refer to bodily and emotional cues when forming moral judgments. Extending previous work, we explored whether the roles of hunger, interoceptive process, and emotional state were associated with moral appropriateness (egocentric) and moral acceptability (allocentric) judgments of harm in the same way. Furthermore, comparing people's tendency to judge harmful acts as morally acceptable from an allocentric perspective when harm results in a greater good, and when it does not, has not been previously explored.

We do not yet have a clear understanding of how incidental visceral and emotional states may interact and exert influence over moral judgments in the moment, as the relationships between these variables are complex and multidirectional. Food deprivation can affect physiological arousal (e.g., Korbonits et al., 2004; Chan et al., 2007) and emotional processes (MacCormack and Lindquist, 2016), which are known to influence moral judgments regarding the harm of others (Damasio et al., 1990; Greene et al., 2001; Cushman et al., 2012; Parton and McGinley, 2019). Hunger also influences interoceptive processes and may even heighten our awareness of changes in cardiac arousal (Herbert et al., 2012). A heightened awareness of internal sensations associated with hunger/thirst may increase the availability of bodily cues (Domschke et al., 2010). Hunger states could therefore influence moral decision-making, e.g., by reducing the harshness of moral acceptability judgments (e.g., Vicario et al., 2018), but the direction of this effect has not been previously investigated with harm-based moral judgments. Emotional state is fundamentally linked with interoceptive processes and hunger (Macht and Simons, 2000; Barrett, 2016; MacCormack and Lindquist, 2016), and can affect moral judgments (e.g., Valdesolo and Desteno, 2006; Zhang et al., 2017b). People's current emotional experiences could therefore modulate the relationship between hunger/thirst and moral decision-making. We also explored the influence of sex, age, and individual differences in anxiety for predicting moral judgments. Women and older people are more likely to reject harmful action in hypothetical moral dilemmas (Armstrong et al., 2019; McNair et al., 2019). Anxiety is associated with heightened cardiac arousal, which can affect how we process threatening information (Garfinkel and Critchley, 2016), and is a psychological correlate of both hunger (Herman et al., 1987) and IS (Domschke et al., 2010). The role of anxiety in moral decision-making appears mixed. Anxiety has shown to increase unethical behavior in some circumstances (Kouchaki and Desai, 2015), with trait anxiety and self-focused emotional distress demonstrating varying influences on moral judgments (Sarlo et al., 2014).

The current study aimed to assess the interdependent relationships between IS, hunger, and moral judgments of harm with the following research questions (the protocol was registered on the Open Science Framework; Brown et al., 2019).

R1. Does felt hunger or thirst bias responses to a moral judgment task?

R2. Does IS moderate the relationship between hunger/thirst and moral judgments of harm?

R3. Does emotional state moderate the relationship between hunger and moral judgments of harm?

R4. Does sex, age, and/or anxiety predict moral judgments of harm?

MATERIALS AND METHODS

Design

This was a within-subjects cross-sectional study ($n = 154$) testing preregistered research questions and exploratory hypotheses in a series of regression analyses. Moral appropriateness and moral acceptability judgments were the dependent variables. Hunger, thirst, IS, incidental emotional state, and performance on the CRT (Frederick, 2005) were the independent variables. The influence of age, sex, and anxiety for predicting moral judgments was also explored.

Measures

Demographics

Participants completed a brief demographic form indicating their sex, age, nationality, and ethnicity. Collecting sex data was preferred over gender, as physiological sex differences were more relevant because of known sex differences in interoceptive abilities. Experience in mindfulness/mediation practice was collected as a control variable because of its associations with body awareness (Bornemann et al., 2015), which could inform interpretation of the results. The item read: "Are you an experienced meditator or regularly practice mindfulness?" with the following response options: No/Practice mindfulness or mediate occasionally/Yes, coded for analysis.

Health Questionnaire

A brief health questionnaire was used to assess participants' general health on the day prior to and day of the experiment in the interest of managing any outliers that could influence the dependent and independent variables, e.g., feelings of nausea, sickness. Only one of the questions regarding "current state of health" was coded for analysis as it was deemed more relevant to the participant's current emotional state. The item read: "How is your overall health at this moment?" and response options included: Very bad/Unwell, Slightly unwell, No complaints, Fine, Very good. These were numerically coded 1 to 5 before the analysis to create a measure of "current health."

Anxiety

State and trait anxiety were measured using the State and Trait Anxiety Scale (Spielberger and Gorsuch, 1983). This consists of two identical 20-item scales that ask participants to rate how they feel *right now* (state anxiety) and how they feel *in general* (trait anxiety). Participants were asked to indicate their agreement (Not at all/Somewhat/Moderately so/Very much so), with 20 different statements, e.g., "I feel calm," "I feel tense," "I feel at ease." The scales include positively and negatively coded items to calculate two cumulative scores representing state and trait anxiety.

Interoceptive Sensibility

Interoceptive sensibility (IS) concerns individuals' beliefs about their sensitivity to normal bodily processes (Garfinkel and Critchley, 2013; Ferentzi et al., 2018) and was measured using the Private Body Consciousness subscale of the Body Consciousness Questionnaire (Miller et al., 1981). This subscale offers a parsimonious measure of IS, focusing specifically on bodily sensations, and is commonly used in interoception research e.g., (Werner et al., 2009; Sze et al., 2010; Ainley and Tsakiris, 2013). The entire Body Consciousness Questionnaire (Miller et al., 1981) was used in the interest of maintaining scale validity. Only scores for the Private Body Consciousness subscale (PBCQ) were calculated for analysis, which includes five questions measuring how often people typically notice or pay attention to interoceptive sensations. Subscale items include the following: "I know immediately when my mouth or throat gets dry," "I am sensitive to internal bodily tensions," and "I am quick to sense the hunger contractions in my stomach." Participants indicated how characteristic each statement was of themselves on a scale (extremely uncharacteristic/uncharacteristic/neutral/characteristic/extremely characteristic). Items were numerically coded 1 to 5, resulting in a maximum possible score of 25. Mean scores were calculated for all participants before analysis.

State Emotion

State emotion was measured using the Positive and Negative Affect Scale (PANAS; Watson et al., 1988). Positive affect (PA) and negative affect (NA) represent two independent subscales of subjective emotional experience. Each subscale consists of 10 items and demonstrates high internal reliability (PA: Cronbach $\alpha = 0.89$, NA: Cronbach $\alpha = 0.85$; Crawford and Henry, 2004).

Moral Judgment Stimuli

Conway and Gawronski's (2013) moral dilemma stimuli were used to assess independent response-tendencies of harm aversion and outcome maximization separately. Harm aversion represents the tendency to reject the moral appropriateness of carrying out harmful actions regardless of the consequences of harm, whereas outcome maximization represents the tendency to condone the moral appropriateness of harmful action, if harm results in a greater good overall (e.g., saving more lives). Participants respond with a yes or no response (**Table 1**). Their text-based procedure includes 20 moral dilemmas made up of 10 story pairs, which are matched in story content, but the amount of "greater good" resulting from a harmful action is manipulated. This makes it possible to measure harm-aversion tendencies while controlling for people's tendency to maximize outcomes. A harm-aversion and outcome-maximization score is calculated for each person, based on the probability that they accepted/rejected harm when harm resulted in a "greater good" and when it did not (for full probability equations, see Conway and Gawronski, 2013).

Moral Acceptability Ratings

Moral acceptability ratings of allocentric ethical violations (Schnall et al., 2008) or moral goodness ratings of harmful actions (Sarlo et al., 2014) provide a useful scale measure of the strength of people's judgments of harmful actions. Here we implemented a moral acceptability measure, to capture the strength of people's allocentric moral judgments when harmful action results in a greater good and when it does not. Following each of the moral dilemmas, we asked participants to judge the moral acceptability of the harmful actions proposed in the previous moral dilemma (**Table 1**). The item read: "How morally acceptable or morally unacceptable do you find the proposed action to be?" Response options included: 1 = completely unacceptable, 2 = moderately unacceptable, 3 = slightly unacceptable, 4 = neither acceptable nor unacceptable, 5 = slightly acceptable, 6 = moderately acceptable, 7 = completely acceptable (adapted from Schnall et al., 2008).

TABLE 1 | Matched pair of moral dilemma stimuli from Conway and Gawronski's (2013) moral dilemma task.

Causing harm maximizes outcomes	Causing harm does *not* maximize outcomes
You are a soldier guarding a border checkpoint between your nation and one troubled by insurgent violence. You notice a young man in a cheap car approaching the checkpoint with a determined look on his face. You suspect he means to bomb the checkpoint, **killing all the soldiers inside.** He is rapidly approaching your station. **Question:** Is it appropriate for you to shoot and kill the approaching man? Yes/No	You are a soldier guarding a border checkpoint between your nation and one troubled by insurgent violence. You notice a young man in a cheap car approaching the checkpoint with a determined look on his face. You suspect he means to cross the border in order to **work illegally inside your country**. He is rapidly approaching your station. **Question:** Is it appropriate for you to shoot and kill the approaching man? Yes/No

Hunger and Thirst

Two separate, single-item visual analog scales were used to assess self-reported sensations of hunger and thirst on a scale of 1 to 9: "How hungry/thirsty do you feel at this moment?" (1 = not at all, 9 = extremely hungry/thirsty). Hunger and thirst were assessed last to avoid any priming effects before the moral judgment task.

Cognitive Reflection Task

The original CRT (Frederick, 2005) assesses participant's ability to override intuitive or "gut" responses to counterintuitive problems. The task involves three questions that have both an intuitive and correct answer, e.g., "A bat and a ball cost $1.10 in total. The bat costs $1.00 more than the ball. How much does the ball cost?" Participants manually typed their answers, and response time was not capped. Successful performance on this task requires further deliberation of the questions to determine the correct solutions, and therefore, better performance is associated with a greater ability to override the "intuitive" or more obvious answer. This measure aimed to capture participant's intuitive versus analytic decision-making tendencies when faced with counterintuitive problems. There are many possible scoring methods for the CRT. As such, both the "regular" scoring method (totaling only correct answers) and the "intuitive" scoring method (totaling only intuitive answers and disregarding incorrect answers) were used (Erceg and Bubić, 2017), to inspect correlations between these alternative calculations.

Procedure

Following approval from University of Bath Psychology Ethics Committee, 154 participants were recruited online via advertisements displayed on University of Bath research participation portal and social networking sites. The experiment was developed in Qualtrics and accessible via an anonymous web link. All partially completed questionnaires were excluded from analysis. We exceeded our target sample size of 120 participants, which was based on *a priori* power calculations using G*Power for multiple linear regression models, assuming $\alpha = 0.95$, $\beta = 0.8$, and $f^2 = 0.10$ (df = 8). Inclusion criteria for participation were guided by a literature review of physiological and psychological confounds known to influence the primary independent variables, namely, hunger, thirst, and interoception. Participants were required to be aged 18 + years; with no current mental health issues; no history of disordered eating, diabetes, thyroid conditions, gastrointestinal or heart conditions, or previous surgery to those areas; and no current health conditions or medication that affected diet, weight, or exercise. Eligibility criteria were emphasized on the research advertisements and participant information sheet.

Potential participants accessing the experiment in Qualtrics were first presented with a study information sheet. They were then asked to confirm they met eligibility requirements and encouraged to contact the experimenter with any questions or concerns about taking part. Participants then completed an online consent form and were made aware they could enter their names into a prize draw at the end of the experiment in exchange for their participation. Participants worked through a series of questionnaires in the order outlined below with instructions provided before each questionnaire. The experiment took roughly 30 min to complete and could be mostly carried out at the pace of the respondent. The moral dilemma task was the only timed element of the experiment, whereby the text for each moral dilemma story would time out after 45 s and was followed by the moral judgment questions. Participants could advance to the questions after 20 s with a button click. This ensured reading time for each moral dilemma was roughly standardized and was clearly signposted in the instructions before starting the task. Upon completion of the study, participants were thanked for their time and provided with some further information about the study and experimenter contact details. They were then asked if they would like to enter the prize draw to win one of four 25 Amazon vouchers, by entering their details via an anonymous link to a raffle survey in Qualtrics.

RESULTS

Data Reduction and Descriptive Analysis

The sample was 31.8% male, and the ages of participants ranged from 18 to 70 years [median = 31, standard deviation (SD) = 12.21]. Statistical analysis was carried out with SPSS v.24. A Pearson bivariate correlation analysis including all of the variables was conducted first, followed by a series of ordinary least squares regression analyses to address preregistered and exploratory hypotheses. The SPSS scripts for moderation, mediation, and conditional process analyses (PROCESS) were adopted from Hayes (2018). For all moderation analyses carried out in PROCESS, interactions are probed at the 16th, 50th, and 84th percentiles by default. As females were considerably overrepresented in this sample, a bootstrapping method was adopted for all regression analyses (5,000 × bootstrapping samples, 95% confidence interval) to generate standard error estimates that do not rely on parametric assumptions (Hayes, 2018).

Dependent Variables: Moral Judgments and Moral Acceptability Ratings

The four moral judgment–dependent variables included (1) harm aversion and (2) outcome maximization tendencies and moral acceptability ratings for (3) congruent and (4) incongruent trials. Raw harm-aversion and outcome-maximization scores were standardized into *Z* scores as suggested (see Supplementary Material; Conway and Gawronski, 2013). As expected, harm-aversion and outcome-maximization scores showed only weak negative correlation ($r = -0.092$, $p = 0.259$), confirming the independence of these response tendencies. To explore whether people judged harmful actions (from an allocentric perspective) as more morally acceptable for trials where harm maximized outcomes and when it did not, moral acceptability ratings for the harmful actions proposed in each moral dilemma were averaged for trials where harm did not maximize outcomes (congruent) and trials where harm maximized outcomes (incongruent) (**Table 1**). This resulted in two average moral acceptability scores for each participant: (1) acceptability_incongruent and (2) acceptability_congruent. Each acceptability score represented 10 moral acceptability ratings. Moral acceptability scores for congruent and incongruent trials were strongly positively correlated ($r = 0.640$, $p < 0.001$). This indicates people were relatively consistent in how morally acceptable they judged harmful actions to be from an allocentric perspective across all trials, when harm maximized outcomes and when it did not.

The distribution of studentized residuals of the dependent variables was inspected. Outcome-maximization scores and acceptability_incongruent scores were fairly normally distributed. Harm-aversion scores sat slightly higher than the mean on average; however, only mild skewness was identified. A log10 transformation was carried out on acceptability_congruent scores to adjust for a strong positive skew. For all regression analyses, a casewise diagnostic was performed on studentized residuals to identify outliers affecting the values of the estimated regression coefficients. Only three outliers ± 3 SDs were identified overall and removed from the associated regression analysis. A Cook distance and Levene test confirmed no leverage values or unusual data points in each regression model. All other regression assumptions were met.

Scale Reliability

The state emotion and trait and state anxiety measures showed high internal reliability. Coefficient *a* values were 0.87 for positive affect 0.89 for negative affect (0.82 for the entire PANAS measure) 0.94 for state anxiety, and 0.95 for trait anxiety. Adequate internal consistency was found for the private body consciousness subscale (five items) of the Body Consciousness Questionnaire ($a = 0.65$) and is comparable to prior research (Christensen et al., 1996). Scores for the CRT were coded for the presence of correct answers (regular scoring) and intuitive answers (intuitive scoring) and demonstrated very high negative correlation ($r = -0.910$, $p < 0.001$). Correlations for the independent variables can be found below in **Table 2**.

Hunger and Thirst

The mean hunger rating was 3.24 (SD = 2.09) and 4.07 for thirst (SD = 1.96), and the mode being 1 for hunger and 3 for thirst. As expected, hunger and thirst were positively correlated ($r = 0.294$), and both scores positively predicted how many hours it had been since participants reported eating. Hunger and thirst scores were relatively normally distributed, although participants typically reported less felt hunger than the median response option. Thirst was positively correlated with interoception ($r = 0.247$, $p < 0.001$), suggesting that people who were more likely to focus on internal sensations were also more likely to report subjective experiences of thirst.

Anxiety, Emotion, and Interoceptive Sensibility

Both state and trait anxiety strongly positively correlated with negative affect and were negatively correlated with positive affect (**Table 2**), which is expected as subjective arousal comprises a core component of affective experience (Russell and Barrett, 1999). More anxious people were more likely to report feeling unwell, and although the direction of the relationship is unclear, correlation between anxiety and health-related concerns is consistent with other work in this field (Domschke et al., 2010; Paulus and Stein, 2010). A noteworthy observation was that self-reported frequency of mindfulness practice (see *Demographics*) was positively correlated with IS ($r = 0.274$, $p = 0.001$), suggesting people with a tendency to focus on bodily sensations engaged in mindfulness more often. Therefore, people exhibiting a greater tendency to notice bodily sensations in this study may have demonstrated a healthier, more adaptive attentional style toward bodily sensations as opposed to a more anxious preoccupation with bodily sensations.

Analyses

R1. Hunger, Thirst, and Moral Judgments of Harm

R1 tested whether felt hunger or thirst biased moral judgments of harm. Hunger and thirst ratings were entered as predictor variables in four multiple linear regression models. Outcome maximization, harm aversion, and moral acceptability for congruent (acceptability_congruent) and incongruent trials (acceptability_incongruent) were the dependent variables. Contrary to our hypothesis, neither hunger ($b = 0.072$, $p = 0.402$) nor thirst ($b = 0.036$, $p = 0.675$) predicted participant's harm aversion scores (R^2 chng = 0.010, $F(2,149) = 0.597$, $p = 0.552$). Moreover, hunger ($b = 0.043$) and thirst ($b = -0.043$) did not predict participant outcome-maximization scores (R^2 chng = 0.003, $F(2,149) = 0.195$, $p = 0.823$). Therefore, participants who were more hungry or thirsty were not more or less likely to accept/reject harm or maximize outcomes on the moral dilemma task than those who were less hungry or thirsty. Hunger ($b = 0.118$, $p = 0.170$) and thirst ($b = -0.052$, $p = 0.544$) also did not predict acceptability_incongruent scores (where harm results in a "greater good") (R^2 chng = 0.013, $F(2,148) = 0.973$, $p = 0.380$). Hunger did negatively predict acceptability _congruent scores ($b = 0.226$, $p = 0.008$) in the model (R^2 chng = 0.049, $F(2,148) = 3.841$, $p = 0.024$) but thirst did not ($b = -0.116$, $p = 0.167$). Therefore, hungrier participants were

TABLE 2 | Pearson coefficients for all independent variables in vertical order: hunger, thirst, state anxiety, trait anxiety, positive affect, negative affect, interoceptive sensibility, Cognitive Reflection Task score (regular), age, sex (male = 1, female = 2), current health (*$p < 0.05$; **$p < 0.01$).

	Thirst	State anxiety	Trait anxiety	Positive affect	Negative affect	Interoceptive sensibility	CRT	Age	Sex	Health
Hunger	0.289**	−0.30	−0.089	−0.031	−0.071	0.152	−0.069	0.000	0.041	0.050
Thirst		0.165	0.136	−0.117	0.140	0.247**	0.012	−0.061	0.064	−0.154
State anxiety			0.726**	−0.197*	0.454**	0.038	−0.045	−0.318**	0.119	−0.430**
Trait anxiety				−0.284**	0.454**	0.121	−0.008	−0.294**	0.227**	−0.325**
Positive affect					−0.072	−0.125	0.057	0.143	−0.156	0.204*
Negative affect						0.083	−0.023	−0.205*	0.230**	−0.148
Interoceptive sensibility							−0.216**	−0.004	0.093	−0.072
CRT								0.047	−0.121	−0.029
Age									−0.253**	0.155
Sex										−0.040

more likely to judge the moral acceptability of harmful actions as less "wrong," but only for trials where harmful actions resulted in no greater good overall. Finally, as hunger and thirst are related sensations often physiologically interlinked, a *post hoc* mediation analysis was conducted to assess whether hunger (*a*) influenced acceptability_congruent scores through experiences of thirst (*b*). A bootstrap confidence interval for the indirect effect ($ab = -0.0421$) included zero (-0.0059 to 0.0005), indicating that hunger did not influence moral acceptability ratings on congruent trials through related experiences of thirst. Despite the positive correlation between hunger and thirst ratings, how thirsty participants felt did not appear influential for moral acceptability ratings across all trials.

R2. Moderating Role of Affective State

In R2, we explored the moderating role of affective state in the relationship between hunger and moral judgments of harm. Against our predictions, no significant correlations were found between hunger, thirst, and positive or negative emotional state or between emotional state and moral judgments (**Table 2**). Non-significant relationships between hunger/thirst and moral judgments were not probed for moderation effects of emotional state. A moderating role of positive affect (R^2 chng = 0.0118, $F(1,147) = 1.82$, $p = 0.1793$) and negative affect (R^2 chng = 0.012, $F(1,147) = 1.853$, $p = 0.1755$) was not found in the relationship found between hunger and acceptability_congruent ratings found in R1. A further mediation analysis was carried out to rule out the possibility of hunger influencing acceptability_congruent ratings through changes in emotional state. Bootstrap confidence intervals of the indirect effect of hunger through positive affect (-0.0012 to 0.0012) and negative affect (-0.0013 to 0.0008) on acceptability_congruent ratings were entirely below zero, ruling out any mediation effects. Together this indicates the influence of hunger on moral acceptability ratings of unprofitable harmful acts cannot be explained by hunger-associated changes in emotional state. A two-step hierarchical regression controlling for the effects of positive affect, negative affect, and state anxiety also confirmed hunger significantly influenced acceptability_congruent ratings ($b = 0.197$, $p = 0.016$). Therefore, the influence of hunger on non-profitable judgments of harm was independent of affective experience.

R3. Moderating Role of Interoceptive Sensibility

In R3, we proposed that greater IS (tendency to focus on bodily sensations) could increase the availability of visceral sensations associated with hunger or thirst that could moderate the relationship between hunger/thirst and moral judgments. Contrary to R3, a moderation analysis yielded no interaction effect between hunger and interoception for outcome-maximization tendencies (R^2 chng < 0.001, $F(1,147) = 0.054$, $p = 0.817$), harm-aversion tendencies (R^2 chng = 0.0179, $F(1,147) = 2.719$, $p = 0.101$), acceptability_incongruent scores (R^2 chng = 0.0064, $F(1,147) = 0.964$, $p = 0.328$), or acceptability_congruent scores (R^2 chng = 0.003, $F(1,147) = 0.455$, $p = 0.501$). Similarly, no moderation effect of interoception was found between thirst and outcome maximization (R^2 chng = 0.000, $F(1,147) = 0.064$, $p = 0.799$), harm-aversion tendencies (R^2 chng = 0.0026, $F(1,147) = 0.395$, $p = 0.531$), acceptability_incongruent scores (R^2 chng < 0.001, $F(1,147) = 0.002$, $p = 0.961$), or acceptability_congruent scores (R^2 chng < 0.001, $F(1,147) = 0.005$, $p = 0.979$). Therefore, the influence of sensations of hunger or thirst on participant's moral acceptability and moral appropriateness judgments did not vary as a function of their tendency to focus on bodily sensations.

R4. Influence of Sex, Age, and Anxiety on Moral Judgments

Age and sex were inputted as predictors in multiple linear regression models of all of the dependent variables (harm aversion, outcome-maximization tendencies, acceptability_congruent, and acceptability_incongruent ratings). We found participants' age ($b = 0.216$, $p = 0.009$) and sex ($b = 0.220$, $p = 0.008$) significantly predicted harm-aversion tendencies, with females and older participants showing greater harm-aversion tendencies irrespective of the consequences of harm ($R^2 = 0.071$, $F(2,148) = 5.656$, $p = 0.004$). Neither age nor sex predicted outcome-maximization tendencies, i.e., acceptance of harm in the interests of the "greater good" ($R^2 = 0.003$, $F(2,148) = 0.215$, $p = 0.807$). Age and sex also did not predict acceptability_congruent (R^2 = 0.022, $F(2,148)$ = 1.626, p = 0.200) or acceptability_incongruent ratings (R^2 = 0.026, $F(2,148)$ = 1.959, p = 0.145). Therefore, age and sex did not influence how morally acceptable people judged harmful actions to be, despite the differences in harm-aversion tendencies overall. In partial support of the role of anxiety in moral judgments, state anxiety negatively correlated with harm aversion (r = −0.177, p = 0.03), indicating people who were more anxious at the time of the experiment were less likely to reject causing harm in the moral dilemmas. However, a hierarchical regression model confirmed that state anxiety did not significantly predict harm-aversion scores when controlling for the effects of sex and age (R^2 chng = 0.091, $F(3,147)$ = 4.911, b = −0.150, p = 0.078). State anxiety was significantly negatively correlated with age (r = 0.318, p < 0.01), with younger people more likely to report both state and trait anxiety. Therefore, age appears to account for much of the variation in state anxiety that predicted harm rejection judgments toward the moral dilemmas.

Exploratory Analyses

EH1. CRT Performance and Moral Judgments

We tested the hypothesis that more accurate performance on the CRT task would positively predict more utilitarian response tendencies in line with prior research (Baron et al., 2015; Byrd and Conway, 2019).

Contrary to EH1, CRT performance showed significant positive correlation with harm aversion (r = 0.235, p = 0.004) but not outcome-maximization tendencies (r = 0.048, p = 0.562). As gender differences have been found for CRT performance (Ring et al., 2016), a multiple linear regression controlling for the effects of age and sex confirmed that CRT scores significantly predicted harm-aversion tendencies (R^2 chng = 0.135, $F(3,147)$ = 7.655, b = 0.255, p = 0.001). This finding was sustained when inputting alternative CRT scores representing the presence of "intuitive" answers as opposed to correct answers. Therefore, participants who were more likely to provide "intuitive" answers on the CRT were more likely to accept causing harm in moral dilemmas, irrespective of the outcomes.

EH2. CRT Performance, Interoceptive Sensibility, and Harm Aversion

Following EH1, we explored the predictive relationship between IS and the performance on the CRT task. We further investigated the possibility of a mediation effect of IS through intuitive decision-making processes (captured by the CRT) on harm-aversion responses.

Following identification of moderate correlation between CRT scores and IS (r = −0.216, p = 0.008), a linear regression model confirmed that higher IS predicted more incorrect and intuitive responses on the CRT (R^2 chng = 0.046, $F(1,149)$ = 7.264, p = 0.008). A mediation analysis explored the presence of an indirect effect of IS (a) on harm-aversion scores, through more "intuitive" decision-making processes on the CRT (b). The direct effect of interoception on harm-aversion scores was not significant (t = −0.272, p = 0.786). However, a bootstrap confidence interval of the indirect effect (ab = −0.0802) was entirely below zero (−0.1718 to −0.0110), suggesting that people with a greater tendency to focus on internal sensations provided more intuitive responses on the CRT and were more likely to condone harmful actions. Therefore, IS explains a significant amount of variance in "intuitive" CRT responses, which subsequently predicts participants acceptance of harmful actions.

DISCUSSION

An unexpected and novel discovery in this study was that hunger bias appeared uniquely influential for acceptability judgments of non-profitable harmful actions, whereas "intuitive" decision-making tendencies exclusively predicted appropriateness judgments of harm. These independent effects suggest that a metaphorical "gut instinct" and gut-related visceral experiences of hunger have distinct influences on harm-based moral cognition. We do have the capacity to be morally hypocritical; although we may judge an action to be morally appropriate, we can equally judge that act to be morally unacceptable (Tassy et al., 2013). Framing questions such as "is it appropriate to. . .?" versus "how morally acceptable do you find. . .?" assume different perspectives of the judge, and inconsistencies have been found between these types of judgments previously (Tassy et al., 2013; Pletti et al., 2017). Choice judgments such as "Would you do. . . in order to. . .?" involves forming a judgment from an egocentric perspective and makes self-relevant consequences more salient (Sood and Forehand, 2005; Tassy et al., 2013). Choice judgments are akin to the moral appropriateness judgments in this study, which encouraged people to adopt the perspective of the person carrying out the harmful action in the story (**Table 1**), whereas moral acceptability judgments provide a more abstract or allocentric perspective to evaluate a harmful act and create distance from the self and refer to the moral acceptability judgments in this study (Frith and De Vignemont, 2005). These two types of judgments may rely on distinct neural bases associated with differing degrees of agency. For example, egocentric moral judgments, but not allocentric, have been associated with activation of the amygdala, suggesting these judgments activate emotional processes associated with weighing up the consequences of our own actions for ourselves (Berthoz et al., 2006). Moreover, experiencing oneself as the cause of action has shown to activate areas of the anterior insula (Adolfi et al., 2017), whereas experiencing someone else as the cause of action is associated with activation of the inferior parietal cortex (Farrer and Frith, 2002). The importance of "where we are" in relation to harm has also come to light in virtual-reality studies that find discrepancies between hypothetical moral judgments people make and the harmful behaviors they perform when confronted with more realistic moral dilemmas (e.g., Francis et al., 2016).

In R1, we found less hungry people rated harm as more wrong in instances where harm did not result in any "greater good" overall, although this predictive relationship was relatively weak. This suggests hunger may be uniquely influential for allocentric judgments about unprofitable harmful acts. In line with prior research, the physiological changes associated with hunger states could bias how severely we judge the acceptability of moral violations from an allocentric perspective (Vicario et al., 2018), but the exclusivity of this effect for non-profitable harmful actions is a novel finding for harm-based moral dilemmas. Arguably, acceptability judgments for the trials where harm did not result in a "greater good" provides a judgment of the "wrongness" of excessive harm, as there is no moral justification to judge harm that is without benefit as morally acceptable. However, clearly people did judge certain types of harm to be more acceptable than other types, and this appears to have been influenced by their level of hunger. This is discussed further below. Moral appropriateness judgments, however, may reflect more stable aversions people have to characteristically harmful actions (action aversion) and witnessing the pain of others (outcome aversion) (Miller et al., 2014), which are more impervious to temporary hunger states. Alternatively, the binary yes/no option may simply prevent us from understanding the true strength of appropriateness judgments. Surprisingly, in R3, we found emotional state did not moderate the relationship between hunger and moral judgments. IS also did not moderate any relationships between hunger, thirst, and moral judgments, contrary (R2). Null findings for R2 and R3 suggest that hunger "acted alone" to influence non-profitable moral acceptability judgments of harm and cannot be explained by differences in people's tendency to focus on visceral sensations such as hunger or incidental emotional state (e.g., Valdesolo and Desteno, 2006).

Perhaps most surprising was that CRT performance (directly) and IS (indirectly) predicted people's harm-aversion tendencies. This may suggest a discrete influence of intuitive decision-making processes and IS for judgments of harm when adopting an egocentric viewpoint of the actor causing harm. This finding contradicts exploratory hypothesis EH1 and prior research showing a positive relationship between CRT performance and outcome maximization or "utilitarian" tendencies (Baron et al., 2015; Byrd and Conway, 2019). Although a logical reflection measure has correlated with harm-aversion tendencies before, arithmetic reflection (assessed by the CRT) has not (Byrd and Conway, 2019). The fact that more arithmetically correct answers on the CRT predicted the rejection of harmful action when harm resulted in a "greater good" and when it did not challenges the view that a more arithmetic focus is responsible for moral judgments that prioritize the number of lives saved (Byrd and Conway, 2019; Patil et al., 2020). An association between CRT performance and harm aversion is also counterintuitive to dual-process perspectives (Greene et al., 2001) that propose the rejection of harmful actions is associated with a faster, more emotional decision-making pathway that we might expect to negatively correlate with intuitive responses on the CRT (e.g., Kahneman and Frederick, 2002). People with higher IS were more likely to provide "intuitive" answers on the CRT task, suggesting greater bodily awareness impeded successful performance on this task. Furthermore, in EH2, we found IS indirectly predicted harm-aversion tendencies through its influence on CRT performance, whereby heightened IS appeared to reduce people's ability to resolve counterintuitive problems on the CRT, which subsequently increased the likelihood they would condone harmful actions on the moral dilemma task. There is some support for the notion that an awareness of somatic states could actually enhance our representations of ourselves in relation to our moral responsibilities (Immordino-Yang, 2011), but the findings here suggest a heightened focus on visceral sensations may somehow contribute to a weakening of our aversion to harmful actions.

In R4, we found age and sex were the strongest predictors of harm aversion but not outcome-maximization tendencies. As found previously, older participants and female participants were most likely to reject causing harm (Armstrong et al., 2019; McNair et al., 2019), but these age and sex differences did not extend to moral acceptability ratings – a distinction that has not been clarified before. There was partial support for a role of state anxiety in predicting harm-aversion tendencies, with more anxious people more likely to accept causing harm regardless of the outcomes. This is somewhat consistent with a previous finding (Kouchaki and Desai, 2015) and is potentially due to how anxiety influences how we process threatening information (see Garfinkel and Critchley, 2016). However, the predictive value of state anxiety appeared to be mostly explained by variation in age, with younger people significantly more likely to report higher levels of state anxiety.

Hunger and Moral Acceptability Ratings

We did find hungrier people were more likely to judge non-profitable harmful actions as more morally acceptable, although the magnitude of effect was relatively weak and should be interpreted with caution. An absence of a relationship between hunger and state anxiety suggests these appraisals were not based on hunger-induced arousal (e.g., Korbonits et al., 2004; Chan et al., 2007). Indeed, hunger may not always induce physiological arousal in a negative sense (e.g., Michalsen, 2010), and hunger and state anxiety were, in fact, slightly negatively correlated in this study. Psychophysiological arousal has shown to predict an aversion to harmful actions (Cushman et al., 2012). Therefore, if arousal cues were reduced in hungrier individuals, it is possible this lessened the severity of their acceptability judgments and is consistent with the finding that hunger can actually reduce threat tolerance and promote riskier decision-making in animals (Ghosh et al., 2016). As the majority of people reported lower levels of hunger, it is possible that our sample did not include enough "very-hungry" participants to generate the hormonal and physiological responses associated with hunger-induced arousal. This subsequently reduces the probability of observing individual differences in state anxiety or negative affect associated with hunger that may have been influential.

As people who were less hungry reported to have eaten more recently, a "fullness"-based explanation is perhaps more likely and is consistent with some prior research (Vicario et al., 2018). Nausea symptoms often correlate with post-eating gastric emptying (Halawi et al., 2017) and can be interpreted emotionally as disgust (Tracy et al., 2019), which can influence moral judgments (see Haidt et al., 1994). However, this is a novel finding for harm-based moral judgments (Horberg et al., 2009). Nevertheless, this explanation is consistent with research finding positive correlations between hunger and acceptance of moral violations (Vicario et al., 2018), and between disgust sensitivity and disapproval of moral violations (Horberg et al., 2009; Vicario and Rafal, 2017). Unfortunately, as we did not measure disgust or fullness, these hypotheses remain speculative, although only 3% of the sample reported any nausea or gastrointestinal distress in a prestudy health questionnaire. Importantly, nausea associated with gastric dysrhythmias is not unique to visceral signaling processes associated with eating and can occur during hunger states and stomach emptiness (see Levine, 2005 for a review). However, why exactly hunger was influential only for moral acceptability judgments of harm that did not result in any "greater good" overall is unclear and requires further investigation.

Interoceptive Sensibility

Interoceptive sensibility did not moderate the relationship between hunger and acceptability judgments of non-profitable harm (R2). As people's tendency to focus on visceral sensations did not change the relationship between hunger and moral judgments, this implies that the psychophysiological processes proposed to underlie this relationship (e.g., Vicario et al., 2018) do not strengthen with higher levels of attention directed toward internal sensations. However, it is conceivable that people with higher levels of IS had lower thresholds for detecting sensations of hunger and thirst (Stevenson et al., 2015) and were more likely to overestimate "true" homeostatic states of hunger/thirst. This was evident for thirst at least, as a moderate correlation between thirst and IS ($r = 0.247$, $p < 0.01$) indicated people with a greater sensitivity to bodily sensations were more aware of thirst-type visceral sensations. Similarly, hunger was positively correlated with IS ($r = 0.152$) but was non-significant. It could be argued that the hunger and thirst ratings scales provided a measure of IS themselves, as they asked people to consciously assess and report subjective visceral states, which will of course depend on the availability of this information. Although problematic levels of multicollinearity between hunger/thirst and IS were not identified in the regression analyses, if changes in IS were met with corresponding changes in hunger/thirst ratings, this would reduce the likelihood of observing any moderation effects of IS in the relationship between hunger and moral judgments. Future work using a larger sample could generate more statistical power to uncover any small effect sizes of IS in the link between hunger and moral acceptability judgments not found here.

Role of Emotional States and Anxiety

Interestingly, neither anxiety nor emotional state correlated with hunger or thirst providing no support for any association between these constructs found previously (see MacCormack and Lindquist, 2016). Agreeing on the archetypical symptoms and psychophysiological experiences of hunger and thirst is challenging, because of variations in eating contexts (Ribeiro et al., 2009) and the variation of visceral and emotional expressions of hunger and thirst people report (e.g., Michalsen, 2010). For example, a large proportion of people do not experience abdominal emptiness when hungry (Harris and Wardle, 1987), and some even report positive psychological experiences from food deprivation (Watkins and Serpell, 2016), which could partially explain why we did not find the anticipated relationships between hunger, thirst, and emotional states in this study. Alternatively, the null finding for R3 is perhaps due to the low variation in hunger and thirst ratings in this sample.

State anxiety negatively predicted harm-aversion tendencies on the moral judgment task but fell from significance when controlling for age and sex. Trait anxiety did not correlate with harm-aversion tendencies, which contradicts an earlier finding (Zhao et al., 2016) and is surprising considering that measures of dispositional threat reactivity have predicted people's aversion to harmful actions (Cushman et al., 2012), with momentary anxiety inductions having less of an effect on moral judgments (Zhao et al., 2016). Anxiety can facilitate the processing of threatening information (Mathews, 1990) and increase anticipation of aversive outcomes (Paulus and Stein, 2010) and may explain the negative association found between state anxiety and harm-acceptance tendencies found here. More anxious people may have perceived the hypothetical recipients of harm to be more threatening or considered the option of not carrying out harm (i.e., doing nothing) to be the riskier option compared to less anxious people, but the link between anxiety, physiological arousal, and moral judgments is likely much more complex. Moreover, as emotion and anxiety were measured before participants completed the moral dilemmas, we can only speculate that any incidental feelings of anxiety or emotion were experienced as unrelated to the task as opposed to a reaction to the potential consequences of their choices on the task (see Baumeister et al., 2012).

CRT, Interoceptive Sensibility, and Harm Aversion

While interoceptive accuracy (on a heartbeat detection task) has shown to influence CRT performance under certain conditions (Lugo et al., 2017), a relationship between IS and CRT performance is novel. Empirical work surrounding IS and cognition is limited. There is some evidence to suggest IS can influence risk-taking behavior (Salvato et al., 2019), but this does not appear related to impulsivity in decision-making (Herman et al., 2018). IS also indirectly predicted harm-aversion tendencies through its influence on CRT performance. Both IS (Paulus and Stein, 2010) and egocentric moral judgments are associated with forms of self-referential processing (Sood and Forehand, 2005), which is one speculative explanation of the indirect association between IS and harm aversion in this study. People scoring higher on IS may engage in self-referential processing to a greater extent, which possibly reduces their inclination to engage in computationally demanding decision processes when faced with counterintuitive problems like the CRT. Therefore, these people may be more likely to rely on intuitive heuristics to form their answer (Kahneman and Frederick, 2002), which may also have consequences for moral decision-making. Consistent with this hypothesis, perhaps the most parsimonious account for why the CRT was a predictor of harm-aversion bias here is because it taps into our general tendency toward being "cognitive misers" – preferring the processing option that requires least energy expenditure (Tversky and Kahneman, 1974; Toplak et al., 2011). More intuitive responses on the CRT task could suggest reduced engagement or deliberation of items across the whole experiment, including the moral dilemmas where harmful actions do not result in a greater good overall. For these "congruent" dilemmas, weighing up the consequences of harmful action arguably requires slightly more scrutiny of the story content at times. If participants did not fully consider the specific content of the stories, they could have mistakenly condoned harmful actions due to misreading or overlooking story information, which would provide a negatively skewed measure of harm aversion for these people. Therefore, rather than poorer performance on the CRT task representing stable differences in intuitive thinking styles, it is possibly more a reflection of intuitive "preference" (Pennycook et al., 2016) based on the computational resource available or utilized at that moment (Toplak et al., 2011).

Sex and Age Effects

In line with prior research using traditional moral dilemma paradigms, older participants demonstrated greater harm-aversion preferences which has been linked to a greater propensity to experience negative emotions (McNair et al., 2019) and/or a reduced ability to overcome affective cues when making judgments (Hess et al., 2000). Older participants in this study reported lower negative affect and state/trait anxiety than younger participants, and no age-related differences were found for IS. Therefore, incidental negative affect (unrelated to the task) or greater attentional focus toward affective cues in the body does not appear to underlie the finding here, but a more negative emotional response to the moral dilemma stimuli from older participants cannot be ruled out. Similarly, although some research has shown men demonstrate stronger utilitarian preferences (Tinghög et al., 2016), the finding that females scored similarly to men on utilitarian preferences but higher on harm-aversion tendencies is in line with cumulative research findings in this field (Armstrong et al., 2019). Explanations for gender differences typically center around differences in socialization practices (Wood and Eagly, 2012), as well as evolutionary pressures and physiological differences (see Armstrong et al., 2019 for a review), which may engender greater social and emotional responses to the prospect of harming others in women.

LIMITATIONS

Online research into hunger and thirst has the advantage of gathering data from people in their natural eating environments but does not guarantee variation in visceral experiences or the presence of real physiological changes associated with hunger and thirst. It is possible that low variability of hunger (3.24 ± 2.09) and thirst ratings (4.07 ± 1.96) prevented us from uncovering individual differences in the impact of visceral and emotional states on moral decision-making. In addition, relying on self-report measures cannot provide an objective understanding of the physiological conditions accompanying these subjective states, and some research has found intraindividual inconsistencies using visual analog scales of appetite (e.g., Flint et al., 2000). One indication of reliability of our measure is that hunger significantly predicted hours since eating, providing the expected relationship between hunger states and reported ingestive behavior. Although we can never know what hungry or thirsty "feels" like to different people or guarantee a consistent impact of food-deprivation manipulations on visceral experiences (Michalsen, 2010; Stevenson et al., 2015), using fasting manipulations (Vicario et al., 2018) or measures of blood-glucose (Gailliot et al., 2007) would allow the objective investigation of the impact of homeostatic depletion on moral decision-making.

A second limitation was the measure of IS used PBCQ: Porges, 1993). Although popular in interoception research (e.g., Ainley and Tsakiris, 2013; Duschek et al., 2015; Garfinkel et al., 2015), the PBCQ provides a one-dimensional trait measure of perceptual awareness of bodily symptoms. An important distinction between body awareness attention styles (Mehling et al., 2018) is not captured by this measure and limits our understanding of IS in this context. A more negative attentional style is associated with anxiety and somatization (Domschke et al., 2010; Ginzburg et al., 2014), whereas a more adaptive attentional focus on the body can enhance self-regulatory processes associated with bodily sensations and is prevalent in mindfulness-style practices such as body scanning (Bornemann et al., 2015). As participants self-reported mindfulness practice positively correlated with IS, it is possible that participants on the higher end of the IS scale exhibited a "healthier" attentional focus on bodily sensations, which could explain the absence of any relationship between IS and anxiety. Future work using a Multidimensional Assessment of Interoceptive Awareness (Mehling et al., 2018) would provide a more nuanced understanding of the attentional and emotional regulation styles of people with higher levels of IS.

The CRT (Frederick, 2005) is a popular but controversial measure, inherently confounded with numeracy ability. It is possible the CRT provides an indication of people's tendency to think in less effortful ways as opposed to reflecting stable individual differences in thinking styles (Toplak et al., 2011). A recent study found CRT scores did not reflect thinking styles or intuitive ability that was distinct from a general intelligence measure (Blacksmith et al., 2019), whereas other research suggests the CRT is valid for measuring reflective but not intuitive thinking styles (Pennycook et al., 2016). Ambiguity about whether the CRT taps into stable psychological constructs or more temporary psychological processes can make the interpretation of results difficult. Future replications could clarify whether the CRT's power in predicting harm-aversion judgments was due stable individual differences in intuitive or rational thinking styles using measures such as the Rational–Experiential Inventory (Pacini and Epstein, 1999). Finally, our sample was a moderate size and well-represented in terms of age but contained a disproportionate number of women. Considering small effect sizes and several null findings in this study, a more substantial and representative sample would increase the power to uncover effects of visceral states and interoceptive processes on moral judgments if they do exist.

CONCLUSION

When making difficult moral decisions, we may refer to a metaphorical "gut instinct" to explain our choices, a feeling we locate in our stomach area that steers us one way or another. Hunger is one such sensation fundamentally linked with our gastrointestinal system that appears to play a role in allocentric judgments of harmful acts and other moral transgressions, potentially due to its link with disgust (Schnall et al., 2008; Vicario et al., 2018). We also associate "gut feelings" with a felt sense of intuition. Intuition is easily linked with interoceptive processes, when we cannot consciously access the homeostatic valuations happening between the brain and body that can bias our decision-making processes (Damasio et al., 1996; Craig, 2015). Here, we found intuitive thinking preference on the CRT was associated with a tendency to pay attention to interoceptive sensations and a reduced aversion to harmful actions. Together, these findings suggest hunger bias and intuitive thinking preferences may represent independent processes shaping different types of moral judgments. It is possible that the presence of "intuitive" responses on the CRT may instead represent an absence of deliberative thinking processes (e.g., Toplak et al., 2011), and we speculated that increased monitoring of bodily sensations associated with body awareness could interfere with more effortful thinking processes due to the demand on attentional resources. Further work using validated measures of intuitive thinking (e.g., Pacini and Epstein, 1999) could clarify this supposition. Interestingly, incidental emotion and anxiety states did not moderate any relationship between hunger, interoception, CRT performance, and moral judgments. This suggests that emotional state at the time of making harm-based moral judgments did not provide any significant contribution to these effects, contrary to our hypotheses (Valdesolo and Desteno, 2006). Future work measuring people's emotional state before and after the task could clarify whether a change in emotional state is more predictive of moral judgments than incidental emotional state. The findings of this study have gone some way in clarifying the influence of incidental visceral states, emotion, and IS on moral judgments of harm. Interoception is significantly understudied in morality research, which provides many more research opportunities to explore the complex relationships between interoceptive processes, emotion, and moral decision-making.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by University of Bath Psychology Ethics Committee. The participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

HB conceived the study idea, carried out the research, and conducted data analysis and manuscript writing. DS and MP supervised the entire project, piloted the research, and provided feedback and ideas on the study design, data analysis, and written manuscript. All authors contributed to the article and approved the submitted version.

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Reduced Environmental Stimulation in Anorexia Nervosa: An Early-Phase Clinical Trial

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Reduced Environmental Stimulation Therapy (REST) alters the balance of sensory input to the nervous system by systematically attenuating sensory signals from visual, auditory, thermal, tactile, vestibular, and proprioceptive channels. Previous research from our group has shown that REST *via* floatation acutely reduces anxiety and blood pressure (BP) while simultaneously heightening interoceptive awareness in clinically anxious populations. Anorexia nervosa (AN) is an eating disorder characterized by elevated anxiety, distorted body representation, and abnormal interoception, raising the question of whether REST might positively impact these symptoms. However, this approach has never been studied in eating disorders, and it is unknown whether exposure to floatation REST might worsen AN symptoms. To examine these possibilities, we conducted an open-label study to investigate the safety and tolerability of REST in AN. We also explored the acute impact of REST on BP, affective symptoms, body image disturbance, and interoception. Twenty-one partially weight-restored AN outpatients completed a protocol involving four sequential sessions of REST: reclining in a zero-gravity chair, floating in an open pool, and two sessions of floating in an enclosed pool. All sessions were 90 min, approximately 1 week apart. We measured orthostatic BP before and immediately after each session (primary outcome), in addition to collecting BP readings every 10 min during the session using a wireless waterproof system as a secondary outcome measure. Each participant's affective state, awareness of interoceptive sensations, and body image were assessed before and after every session (exploratory outcomes). There was no evidence of orthostatic hypotension following floating, and no adverse events (primary outcome). Secondary analyses revealed that REST induced statistically significant reductions in BP ($p < 0.001$; Cohen's d, 0.2–0.5), anxiety ($p < 0.001$; Cohen's d, >1) and negative affect ($p < 0.01$; Cohen's d, >0.5), heightened awareness of cardiorespiratory ($p < 0.01$; Cohen's d, 0.2–0.5) but not gastrointestinal sensations, and reduced body image dissatisfaction

($p < 0.001$; Cohen's d, >0.5). The findings from this initial trial suggest that individuals with AN can safely tolerate the physical effects of REST *via* floatation. Future randomized controlled trials will need to investigate whether these initial observations of improved anxiety, interoception, and body image disturbance occur in acutely ill AN populations.

Clinical Trial Registration: ClinicalTrials.gov; Identifier: NCT02801084 (April 01, 2016).

Keywords: eating disorder, floatation therapy, interoception, stress, body image, body awareness, interoceptive awareness

INTRODUCTION

Anorexia nervosa is an unusually deadly disorder with the highest mortality risk of all psychiatric disorders (Sullivan, 1995; Suokas et al., 2013), carrying an estimated standardized mortality rate two to three times higher than schizophrenia, bipolar disorder, and unipolar depression (Arcelus et al., 2011; Hoang et al., 2014). Disability from AN peaks during the second and third decades of life, jeopardizing developmental milestones including adult individuation and educational and occupational achievements. Although many AN patients die from complications associated with starvation, others die as a result of suicide (Keshaviah et al., 2014). Of those remaining, 20% are chronically ill (Steinhausen, 2002; Bulik et al., 2007; Lock, 2010; McElroy et al., 2015), with relapse rates as high as 30–50% following inpatient treatment (Khalsa et al., 2017; Berends et al., 2018).

Individuals with AN show evidence of heightened anxiety expression, including premorbid anxious personality traits, and the disorder shares a high degree of comorbidity (nearly 60–80%) with anxiety disorders and depression (Bulik et al., 1997; Kaye et al., 2004). The diagnosis of an anxiety disorder has been observed to increase the subsequent risk of developing AN (Meier et al., 2015), suggesting the possibility of shared etiological mechanisms or common pathophysiological pathways. However, medical treatments for anxiety and mood disturbances show limited efficacy in AN, with serotonergic agents being the primary long-term medication treatment option (Himmerich and Treasure, 2018). One especially concerning finding is that anxiolytic medications that are effective at reducing anxiety over the short term in anxiety-disordered patients, such as benzodiazepines, are ineffective in lowering the anxiety associated with AN (Steinglass et al., 2014). Alternative anxiolytic medications, such as beta-blockers, are often contraindicated in these patients due to the compensatory bradycardia that often follows chronic caloric restriction in AN patients. Therefore, additional treatments which can effectively ameliorate affective disturbances in AN are needed.

One pathophysiological model of AN posits that these individuals have a fundamentally disturbed relationship between the way that afferent internal bodily signals are processed in the brain, and that this disturbance causally contributes to the emergence of aversive visceral sensations and emotions when exposed to food or food-related stimuli (Kaye et al., 2009, 2011). For example, individuals with AN show evidence of exaggerated perceptual processing of anxiety-associated cardiac and respiratory sensations (e.g., heightened feelings of palpitations and dyspnea) (Khalsa et al., 2015), as well as abnormal neural activation in interoceptive brain regions such as the cingulate and insular cortices (Kerr et al., 2016; Berner et al., 2017). However, the evidence for causal influences of interoception on the development and expression of AN and other eating disorders is limited by a lack of basic and clinical studies focusing on mechanistic underpinnings (Martin et al., 2019).

Reduced Environmental Stimulation Therapy *via* floatation is a relatively unexplored non-pharmacological intervention that has recently begun to be investigated for potential anxiolytic effects (Jonsson and Kjellgren, 2016; Feinstein et al., 2018a,b). The REST experience is calibrated so that input from exteroceptive sensory channels (e.g., visual, auditory, olfactory, gustatory, thermal, and tactile) is minimized, as is most vestibular, gravitational, and proprioceptive input, movement, and speech. As a first step toward exploring whether floatation-REST could help individuals with anxiety and depression, we conducted an open-label trial in 50 anxious and depressed individuals, spanning a range of different anxiety and stress-related disorders (including posttraumatic stress disorder, generalized anxiety disorder, social anxiety disorder, panic disorder, and agoraphobia) (Feinstein et al., 2018b). A single 1-h session of floatation-REST was well tolerated by the anxious sample, with no major safety concerns or adverse events. Regardless of diagnosis, the float experience induced a strong short-term reduction in state anxiety and a substantial improvement in mood. In a recent follow-up study using a within-subject crossover design, we recruited 31 participants with clinically elevated levels of anxiety to undergo a 90-min session of floatation-REST and an exteroceptive comparison condition (watching a relaxing documentary film) (Feinstein et al., 2018a). Measures of self-reported affect and interoceptive awareness were collected before and after each session, and BP was measured during each session. Floatation-REST generated a significant anxiolytic effect relative to the comparison condition that was characterized by reductions in state anxiety and muscle tension and increases in feelings of relaxation and serenity. In addition, significant BP reductions were evident throughout the float session. Despite the observed anxiolytic effects in

Abbreviations: AN, Anorexia nervosa; BAS-2, Body Appreciation Scale Version 2; BISS, Body Image States Scale; BMI, Body Mass Index; BP, blood pressure; DBP, diastolic blood pressure; DSM-5, Diagnostic and Statistical Manual Version 5; EDE-Q, Eating Disorder Examination Questionnaire; ICC, intraclass correlation coefficient; IQR, interquartile range; LIBR, Laureate Institute for Brain Research; LMM, linear mixed-effects models; PANAS-X, Positive and Negative Affect Schedule Version X; POMP, Percent of Maximum Possible; PRFS, Photographic Figure Rating Scale; REST, Reduced Environmental Stimulation Therapy; SBP, systolic blood pressure; STAI, Spielberger Trait Anxiety Inventory.

these individuals, exposure to the float environment significantly enhanced awareness for interoceptive (cardiac and respiratory) sensations, a finding that we attributed to a process of reciprocal inhibition (Wolpe, 1968).

Based on our initial findings with anxious individuals, we wondered whether REST *via* floatation might positively impact affective and interoceptive symptoms in individuals with AN. However, there have been no studies documenting the safety or tolerability of the procedure in eating disorders populations (acutely ill or remitted/recovered), and we could find only one brief theoretical review of the topic suggesting that "there are some qualities of REST that make it particularly appropriate for the treatment of eating disorders" (Barabasz, 1993). Moreover, we were uncertain whether exposure to REST might worsen AN symptoms. We therefore aimed to conduct an open-label clinical trial to assess the safety and tolerability of REST in AN, and secondarily, to explore the impact of this procedure on clinically relevant symptoms related to affective experience, body image disturbance, and interoception. With no previous studies of REST in eating disorder populations, we focused our recruitment for this initial study on partially weight-restored AN individuals drawn from outpatient settings (1) in case the intervention was anxiety provoking or non-therapeutic and (2) preclude imminent fall risk under normal physical activity levels (as can occur in AN individuals who are severely underweight).

The primary objective of the study was to investigate whether there is evidence of negative health consequences associated with exposure to the REST environment in partially weight-restored AN. We selected orthostatic hypotension as our primary outcome for safety since (1) our prior research (Feinstein et al., 2018a) identified reductions in BP as an acute effect associated with floating, (2) orthostatic hypotension could increase fall risk when transitioning from laying to standing (an action occurring at the end of each float) (Sachs et al., 2016), and (3) orthostatic hypotension is a major medical condition associated with acute dehydration that is especially common in underweight and even partially weight-restored AN (Lanier et al., 2011). We hypothesized that floating would be safe and well tolerated by individuals with AN and predicted that there would be no adverse physical effects (e.g., no orthostatic BP reductions, or falls, upon standing). We chose several secondary outcome measures including anxiety, stress, mood, body representation, and interoceptive awareness (introduced further in the next section) and investigated the effects of floating on these subjective measures using two-tailed hypothesis tests and Cohen's *d* effect size.

MATERIALS AND METHODS

Aim

The primary objective of this study was to determine whether individuals with partially weight-restored AN would exhibit evidence of orthostatic hypotension following REST. We defined orthostatic hypotension (primary outcome) as a drop of $\geq$20 mmHg in SBP or a drop of $\geq$10 mmHg in DBP when measured shortly after transitioning from lying down to standing, according to consensus guidelines (Kaufmann, 1996). The secondary objective of this study was to examine the acute effects of REST on BP during floating and subjective measures of emotional experience (including anxiety and mood), body image disturbance, and interoception. These secondary aims were exploratory and intended to provide information on the subjective changes induced by REST in individuals with AN, assisting in the identification of potentially useful targets for future studies.

Participant Recruitment

Participants were recruited *via* online and print advertisements and *via* referral from eating disorder treatment providers in the local community. To be included in the study, participants were required to have met the *Diagnostic and Statistical Manual 5* (DSM-5) criteria for a lifetime diagnosis of AN during an interview with a board-certified psychiatrist. Additionally, all participants were required to be partially weight restored to a BMI range above the cut-off for a current diagnosis of AN according to ICD10 (World Health Organization, 1993), defined as having a BMI of $>$17.5. Exclusion criteria included the presence of any schizophrenia spectrum disorder, other psychotic disorder, and bipolar and related disorders. Inpatients were excluded, as were individuals reporting active suicidal ideation with intent or plan (as determined by psychiatric interview). Subjects who exhibited orthostatic hypotension prior to REST (defined as a drop of $\geq$20 mmHg in SBP or a drop of $\geq$10 mmHg in DBP when measured shortly after transitioning from lying down to standing) were excluded. We chose to examine BP changes between lying and standing, as these measures provide the greatest postural differences and were considered to be the most sensitive measure of orthostasis. Participants were also excluded if they reported use of any psychoactive drugs within the past week (e.g., marijuana, cocaine, ecstasy, psilocybin, phencyclidine, and ketamine), any alcohol consumed within the previous 12 h, and any caffeine or nicotine consumed within the previous 3 h for each float. For all other medications, participants were required to be stably medicated prior to participation, defined as having taken the medication for 6 weeks or longer. Participants were also screened for a history of unstable liver or renal insufficiency, glaucoma, diabetes, significant and unstable cardiac, vascular, pulmonary, gastrointestinal, endocrine, neurologic, hematologic, dermatologic, rheumatologic, or metabolic disturbance and excluded if they reported any of these conditions. All study procedures were approved by the Western Institutional Review Board. All participants provided written informed consent prior to participation and received compensation for study participation.

Clinical Assessments

After providing informed consent, all participants underwent diagnostic verification *via* a clinical history and evaluation by a board certified psychiatrist (SSK or SEM) with the application of DSM-5 criteria (American Psychiatric Association, 2013). During this session, participants completed a measurement of their BMI, medical history, medication assessment, and vital sign measurements including orthostatic BP.

Experimental Protocol

In this single group open-label pre–post-study design, all participants were provided access to four sequential REST sessions involving supine floating: reclining in a comfortable zero-gravity chair (chair-REST), followed on three occasions by floating in a pool of water (floatation-REST). The pool floats also followed a sequential protocol whereby participants first floated in an open pool (floatation-*REST*, open) before floating in an identically sized pool with an enclosure (floatation-*REST*, enclosed). For each session, participants were encouraged to float for the full 90 min, but they could also stop the experience at any time. These procedures were intended to help participants accommodate to the float environment and to ensure they were in full control over the experience. Sessions were spaced approximately 1 week apart. To ensure there were no external distractions, participants removed all personal belongings (including cellular phones) before each float.

Session 1: Chair-REST

Participants first reclined in a zero-gravity chair (Human Touch Perfect Chair PC510, Classic Power, Series 2) in the supine position for up to 90 min (**Figure 1**). The chair was ergonomically designed to take pressure off the spinal cord and contained memory foam backing to help the chair conform to each participant's body shape. A motorized lever allowed the participant to recline the chair to a comfortable position. The chair was located in a dimly lit room using the same light as that used in the float pool. Participants could turn the light on and off using an infrared air switch. Participants remained clothed throughout (unlike the typical floatation-REST procedure, in which individuals are typically naked), and consequently, the room was maintained at a normal room temperature of approximately 23.3°C.

Session 2: Floatation-REST, Open

Participants floated in a supine position for up to 90 min in an open circular fiberglass pool (2.44 m diameter, 0.28 m depth), custom designed for research purposes by Floataway (Norfolk, United Kingdom) (**Figure 1**), a design that we selected to optimize the float experience for individuals with heightened anxiety and claustrophobia (see Feinstein et al., 2018b). The pool contained water filled with approximately 816 kg of USP-grade Epsom salt (magnesium sulfate), creating a dense saltwater solution maintained at a specific gravity of ~1.26, allowing participants to effortlessly float on their back. The room around the pool was constructed to be waterproof, soundproof, lightproof, and temperature controlled. Silent heaters were placed under the pool to maintain the water at a constant temperature and a dedicated heating, ventilation, and air conditioning system maintained the air at a constant temperature. The temperature of the water and air approximated the surface temperature of the skin (~35.0°C), and could be adjusted remotely by the experimenter in a nearby control room. An intercom system allowed the participant to freely communicate with the experimenter throughout the float session should any issues arise, and specialized speakers placed around the perimeter of the pool allowed the experimenter to communicate with the participant and play music to signal the end of the session.

Sessions 3 and 4: Floatation-REST, Enclosed

Participants then floated in a supine position for up to 90 min in an enclosed pool with the same dimensions as the open pool (2.44 m diameter, 0.28 m depth) that was also fitted with a rounded wall and a 2.44-m domed ceiling. We included the enclosed condition as this procedure reflects the manner in which most recreational float pools are designed. The experience between the open and enclosed pools was essentially identical, with the exception that the enclosed pool allowed us to calibrate humidity with greater precision. Thus, the room dimensions, temperature controls, and intercom system for this room were identical to the open pool (see **Figure 1** for a visual comparison of both pools). No physiological recordings were made during session 3 to allow each participant one "naturalistic" experience of the floatation-REST environment without any concurrent physiological measurements.

Outcome Measures

Blood Pressure Measurements

During each session, orthostatic BP was measured before and after each float. Prior to initiating the first BP measurement,

FIGURE 1 | REST at LIBR. **(Left)** Chair-REST. **(Middle)** Floatation-REST in an open pool. **(Right)** Floatation-REST in an enclosed pool. The open **(middle)** and enclosed **(right)** pools are both 2.44 m in diameter and 0.28 m in depth. The domed pool contains an enclosure with a 2.44-m domed ceiling. Each pool contains 11 in. of reverse osmosis water saturated with ~816 kg of USP grade Epsom salt (magnesium sulfate), creating a dense saltwater solution that is maintained at a specific gravity of ~1.26, allowing participants to effortlessly float on their back while the water hovers just above the ears. The temperature of the water and the temperature of the air are both calibrated to match the temperature of the skin (~35.0°C). For more details about how our float pools were engineered to minimize exteroceptive sensory stimulation to the nervous system, please see Feinstein et al. (2018a; 2018b).

participants were asked to lay quietly for 5 min, to ensure that they had accommodated to their true resting physiological state for that session. Following the first lying BP measurement, all other measurements were taken after a 1-min delay during each position (sitting, then standing) to ensure that participants had equilibrated to the position, and so that readings were not artificially influenced by physical activity. Prefloat BP measurements were taken with a clinical-standard device CASMED 740 (CAS Medical Systems Inc., Branford, CT, United States) that is commonly utilized for vital sign measurement in inpatient hospital settings. In order to obtain BP measurements during the float environment, we used the QardioArm wireless BP monitor (Qardio Inc., San Francisco, CA, United States), an FDA-cleared automated sphygmomanometer which uses the Oscillometric method to achieve a measurement range of 40–250 mmHg and an accuracy of ±3 mmHg. The QardioArm has been clinically validated according to ANSI/AAMI/ISO 81060–2:2009 as well as the European Society for Hypertension International Protocol Revision 2010 (O'Brien et al., 2010). Thus, each participant underwent orthostatic BP measurement with both the CASMED and QardioArm devices during the prefloat condition, to ensure comparability between the devices. For each measurement, the BP cuff was positioned approximately 1 in. above the elbow, so that it was situated at the same level as the heart. During each float, participants were instructed to keep their arms positioned along the side of their body. A LimbO Waterproof Protector (Limbo USA, Portland, ME, United States) was placed over the QardioArm BP device in order to prevent water from reaching it during the pool float sessions (in which case all QardioArm BP measures were obtained with this sleeve applied, to avoid any external influences on the pre- and post-float data points). After collecting orthostatic BP measurements with the QardioArm, to characterize BP responses during the float, nine additional BP measurements were collected once every 10 min (less if the participant exited the float before the full 90 min)[1]. The initial BP measurement of this sequence occurred approximately 5 min into the float session. All BP data from the QardioArm was wirelessly transmitted in real time *via* Bluetooth 4.0 to an iPad tablet located in the adjacent control room. Each BP measurement took 30–60 s to complete and was initiated remotely by the experimenter using an application on the iPad. Since application of an intermittently inflating BP cuff represents a departure from the naturalistic experience of floatation-REST, after completing their first pool float participants were given the opportunity to experience the next float without any instrumentation applied. As a result, pre- and post-float BP data were available for only three sessions: the chair float, the first pool float, and the third (final) pool float.

Self-Report Measures

All self-report measurements were administered electronically to participants *via* an electronic tablet (Apple iPad). Survey measures were obtained using Research Electronic Data Capture (REDCap[2]), a secure Web-based application for electronic collection and management of research and clinical trial data. All self-report measures were administered during the pre- and post-REST time periods, before and after the primary outcome measures had been collected (**Figure 2**), for each of the four sessions. Several different types of self-report measures were administered before and after each session of REST, as described next.

State-Trait Anxiety Inventory-State Form

The Spielberger State Anxiety Inventory (Spielberger et al., 1983) is a widely used 20-item self-report questionnaire intended to assess an individual's level of anxiety at the present moment with total scores ranging from 20 to 80. The items assess for the presence or absence of current anxiety symptoms, and the measure has been shown to have excellent internal consistency and good convergent and discriminant validity (Spielberger et al., 1983). Participants completed the State-Trait Anxiety Inventory (STAI) immediately before and after each REST session.

Positive and Negative Affect Schedule—Expanded Form

The Positive and Negative Affect Schedule—Expanded Form (PANAS-X) (Watson et al., 1988) is one of the most commonly used measures of mood, with high internal consistency, and good convergent, discriminant, and construct validity. We chose the expanded form, which has several subscales measuring general dimensions of affect (positive and negative), as well as basic emotions (e.g., fear, sadness, joviality, etc.). We included the negative affect, positive affect, joviality, fatigue, and serenity subscales. Each subscale uses the same 5-point Likert-type response scale to collect ratings, ranging from 1 (very slightly or not at all) to 5 (extremely). The positive affect subscale

[1]Participants were not informed of the temporal intervals between BP measurements, to prevent them from estimating the duration of each float. Instead, they were informed they might feel the BP device inflate "periodically, from time to time." Furthermore, the exact inflation interval was jittered randomly up to 1 min by the experimenter.

[2]www.project-redcap.org

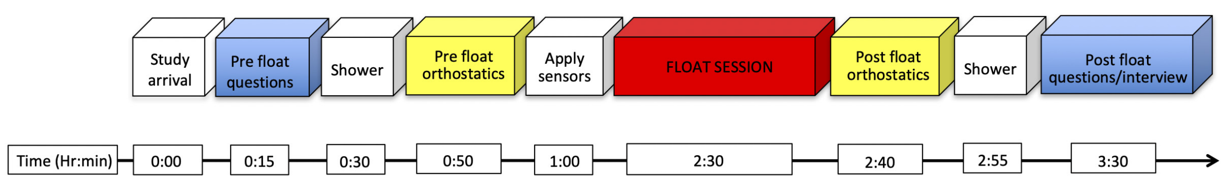

FIGURE 2 | Approximate timeline of assessments during each REST session. Sensor application included the application of a wireless blood pressure monitor and waterproof cast. The total duration of each session was approximately 3.5 h.

has participants rate how *active*, *alert*, *attentive*, *determined*, *enthusiastic*, *excited*, *inspired*, *interested*, *proud*, *and strong* they feel at the present moment. The negative affect subscale has participants rate how *afraid*, *scared*, *nervous, jittery*, *irritable*, *hostile*, *guilty*, *ashamed*, *upset*, *and distressed* they feel at the present moment. The joviality subscale has participants rate how *happy*, *joyful*, *delighted*, *cheerful*, *lively*, *and energetic* they feel at the present moment. The fatigue affect subscale has participants rate how *sleepy*, *tired*, *sluggish*, *and drowsy* they feel at the present moment. Finally, the serenity subscale has participants rate how *calm*, *relaxed*, and *at ease* they feel at the present moment. Participants completed the PANAS-X immediately before and after each REST session.

Visual Analog Scales

Participants completed several Visual Analog Scale (VAS) measures where they rated how they currently felt on a 100-point scale that went from 0 (Not at all/None) to 100 (Extremely/The most I have ever felt). Each scale contained a digital slider that participants could move along a horizontal axis. We included affective VAS measures for *relaxation*, *stress*, *refreshed*, and *energy*. The Relaxation VAS asked, "How relaxed do you feel right now?" The Stress VAS asked, "How stressed or anxious do you feel right now?" The Refreshed VAS asked, "How refreshed do you feel right now?" The Energy VAS asked, "How much energy do you have right now?" Participants completed the VAS measures immediately before and after each REST session.

Interoceptive Awareness Measures

Participants completed several interoceptive awareness VAS measures assessing the intensity of *heartbeat*, *breath*, *and stomach/digestive* sensations immediately before and after each REST session, on a 100-point scale that went from 0 (Not at all/None) to 100 (Extremely/The most I have ever felt). For the pre session questions, the heartbeat VAS asked, "How intensely do you feel your heartbeat right now?" The breath VAS asked, "How intensely do you feel your breath right now?" The stomach VAS asked, "How intensely do you feel your stomach or digestive system right now?" For the post session questions, the heartbeat VAS asked, "How intensely did you feel your heartbeat while floating?" The breath VAS asked, "How intensely did you feel your breath while floating?" The stomach VAS asked, "How intensely did you feel your stomach or digestive system while floating?"

Body Appreciation Scale 2

The Body Appreciation Scale (Tylka and Wood-Barcalow, 2015) was developed to assess an individual's trait level of positive acceptance of attitudinal characteristics toward their body. The Body Appreciation Scale 2 (BAS-2) was modified from its original version (to remove sex-specific terms and body dissatisfaction-based language), with 10 items using a 5-point Likert scale from 1 (Never) to 5 (Always), with total scores ranging from 10 to 50. Participants completed the BAS-2 once prior to floating (at baseline), and again immediately following each REST session. As a trait measure, the BAS-2 trait instructs participants to "Please indicate whether the question is true about you never, seldom, sometimes, often or always." However, since each REST session reflected a state measurement, we modified the post-REST instructions for the BAS-2 accordingly. Thus, the postsession measures instructed participants: "For each of the questions below, please rate how you felt during the float."

Body Image States Scale

The BISS (Cash et al., 2002) was developed to assess an individual's level of negative attitudinal characteristics toward their body, *via* six items that query feelings about physical appearance, body size, shape, weight, and attractiveness. Participants choose among nine options that best describe how they feel "right now at this very moment" from "Extremely dissatisfied" to "Extremely satisfied" (or *vice versa*), with total scores computed as the mean of the six items after reverse scoring three of the positive-to-negative items. Participants completed the BISS immediately before and after each REST session.

Photographic Figure Rating Scale

The PFRS (Swami et al., 2008) was developed to assess an individual's visual perceptual preference for different body types. It consists of 10 photographic images of different women (with the head obscured), each with BMI measurements that vary from emaciated to obese. Participants are instructed to select the body type that they perceive most accurately reflects (1) their current body type and (2) their ideal body type. A body dissatisfaction score is then calculated by subtracting the participant's ideal self-rating from their current self-rating. The measure has been reported to demonstrate good construct validity (Swami et al., 2008) and good test–retest reliability on repeated administrations (Swami et al., 2012). Participants completed the PFRS immediately before and after each REST session.

Eating Disorder Examination Questionnaire 6.0

The Eating Disorder Examination Questionnaire 6.0 (EDE-Q 6.0) (Fairburn and Beglin, 2008) is a commonly used 28-item self-report measure based on the eating disorder examination interview used by clinicians to diagnose and assess severity of an eating disorder. The EDE-Q 6.0 consists of a global eating disorder score (total of four facets averaged), as well as four groups of eating disorder symptoms, which include eating restraint, eating concerns, shape concerns, and weight concerns, with each ranging from a score of 0 to 6 (higher scores are considered to index greater illness severity, with normative studies suggesting that a score of 2.2 or greater is indicative of symptoms above the 65th percentile; Luce et al., 2008). For the purposes of this study, we collected and report EDE-Q 6.0 total scores during the initial prefloat baseline assessment in order to provide an indication of self-reported illness severity.

Presession Instructions

Prior to each session, all participants were instructed that they could remain in the session "for up to 90 min" and that they could stop at any time. During each session, participants were encouraged to try to remain still and to try not to fall asleep. Participants were encouraged to experience each session with the lights turned off, but they were also reminded that they were free to turn the lights on whenever they needed them. The full instruction set can be found in the **Supplementary Material**.

Postsession Interviews

After each REST session, participants completed a debriefing interview with an experimenter to assess their experience. Questions were open-ended and asked about how the session went, their general experience, as well as questions about positive and negative thoughts or experiences during each session. These interviews were recorded and transcribed.

Setting

All assessments were conducted at the Laureate Institute for Brain Research facilities.

Sample Size Calculation

Sample size was estimated based on the primary outcome (orthostatic hypotension). We intended to obtain an estimate on the proportion of orthostatic hypotension with a margin of error <15%. Assuming no participant would show orthostatic hypotension, we calculated that $N = 19$ participants would provide an exact one-sided 95% confidence interval of 14.6%. Our recruitment assumed a 20% incompletion rate (i.e., 23 participants needed).

Statistical Analysis

Primary Outcome

The standing-vs.-lying changes in BP were calculated for each participant, and the proportion of participants demonstrating orthostatic hypotension was evaluated using the exact binomial method.

Secondary Outcomes

The secondary outcomes were obtained on the same participants repeatedly across REST sessions, which were analyzed using LMM. Three different LMM's were built according to the availability of outcome measures, with the inference of interest focused on time of floating (for BP) or post-vs.-pre-REST changes (for all other secondary outcomes). Before assessing the secondary outcome measure of BP, we evaluated the reliability of the QardioArm vs. CASMED devices was evaluated for each session and each position using the Pearson correlation coefficient, and for all sessions and positions combined using the intraclass coefficient (ICC), determined by the sum of between-subject random-effect variance components divided by the total (between- and within-subject) random variance components obtained from a random-effects model with fixed intercept and random intercepts of subject, session, and measure (lying, sitting, and standing). The secondary outcome of BP measures were obtained during REST and were modeled by a LMM with session, time, and/or session-by-time interaction as potential fixed effects, and random subject and/or session intercepts, with a potential first-order autoregressive (AR1) correlation structure. For each of the SBP and DBP measures, we fitted three fixed-effects options (time only; time and Session main effects; main effects plus time and Session interaction) × 5 random-effects/correlation-structure options (random subject intercepts only; random session intercepts only; random subject and session intercepts; random subject and session intercepts plus random time slope; random subject and session intercepts plus AR1 correlation structure) = 15 combinations. The final models of optimal fixed and random effects were chosen by the smallest values of Bayesian Information Criterion (BIC). To make all other secondary outcome measures consistent in scale, each participant's raw and change scores for state anxiety, affect, body image disturbance, and interoceptive awareness were first converted into standardized units representing the percent of maximum possible (POMP) for each measure ranging from 0 to 100% (Cohen et al., 1999), a procedure modeled after our previous study (Feinstein et al., 2018a). This step made all measures in the same scale as VAS ranging from 0 to 100%. For all secondary outcome measures (except the BAS-2 scale), these POMP scores were then fitted to a 2nd LMM with fixed session (pre vs. post) effect and random subject and session intercepts. The inference of interests was on the post-vs.-pre-POMP changes.

For the BAS-2 scale, its POMP was fitted to a 3rd LMM with 2 fixed-effect options [intercept only; session (baseline, Chair-REST, Flotation-pool open, Flotation-pool enclosed 1 and 2) main effect] × 3 random-effects/correlation-structure options (random subject intercept; random session intercept, random subject intercept and AR1 correlation structure across sessions) = 6 combinations. As before, the optimal fixed- and random-effects/correlation structure was determined by BIC.

Parameters in all LMMs were obtained using the restricted maximum likelihood (ReML) method, and the degrees of freedom were calculated using the Kenward–Roger method for LMM with only random effects but no AR1 correlation. The 95% confidence intervals (CIs) of the fixed-effect parameters were calculated by either the approximate method assuming normal distributions for the fixed-effects when AR1 correlation structure was evaluated, or otherwise by the percentile method using 500 parametric bootstrap samples. The overall time or session effects (i.e., variables with more than two levels) were assessed by the F-test *via* type III analysis of variance. Considering the early phase of the study and exploratory nature of the measures, no procedure was applied for multiple comparisons, and our inference focused on point and interval estimates. The whole analysis was performed on R version 3.5.2, using R packages lme4 version 1.1-21 (Bates et al., 2015) and nlme version 3.1-137 (Pinheiro et al., 2018) for LMM, lmerTest version 3.1-0 for the Kenward–Roger method (Kuznetsova et al., 2017), and emmeans version 1.3.5 for marginal means (Lenth, 2019).

RESULTS

Participant Demographics

Demographic characteristics for the 23 recruited partially weight-restored AN participants are listed in **Table 1**. During the structured clinical interview, the lifetime history of AN as defined by DSM-5 criteria was confirmed for all participants. The group showed an average age of onset of 15 years, an average illness duration of 9 years, and an average lowest self-reported BMI of

TABLE 1 | Demographics for the AN participant group.

Demographic	AN participants
Age	26.6 ± 9 years
Sex	22 females, 1 male
Education	14.9 ± 2.6 years
Age of illness onset	15.9 ± 4.9 years
Illness duration	9.0 ± 6.1 years
Lowest BMI	15.2 ± 1.9 units
Current Body mass index (BMI)	21.8 ± 2.7 units
Eating Disorder Examination Questionnaire Total score (range, 0–6)	2.26 ± 1.4 units
Spielberger Trait Anxiety Inventory (range, 20–80)	54.1 ± 8.8 units

Means ± standard deviation. AN, anorexia nervosa.

15.2. Although the current BMI average for the group was in the normal range, there was evidence of residual AN symptoms based on higher-than-normal EDE-Q global scores and elevated trait anxiety on the STAI-trait scale (**Table 1**).

Completion Rate

All 23 of the participants completed the chair and the open-pool sessions, but only 21 of them completed the two enclosed-pool sessions (see **Figure 3** for CONSORT diagram). Of the two participants who withdrew after the second session, one cited a lack of interest in the float pool environment, and the other did not give a reason and stopped responding to appointment requests.

Session Duration

The median and IQR (in bracket parentheses) of each session duration was 90 [82, 90], 90 [85, 90], 90 [90, 91], and 90 [85, 90] min for chair, open pool, and the two enclosed pool sessions, respectively (see **Supplementary Material**), demonstrating that participants were able to tolerate the 90 min sessions.

Reliability Check for Blood Pressure Measurement

Across all sessions and positions, the median and IQR of the Pearson correlation coefficients measured between the QardioArm and CASMED devices was 0.80 [0.75, 0.83] and 0.80 [0.73, 0.83] for SBP and DBP, respectively (see **Supplementary Material** for details). When all sessions and positions were considered together, the ICC for systolic BP was 0.70 and for diastolic BP was 0.73, indicating good reliability across devices.

Primary Outcome of Orthostatic Hypotension

None of the participants completing any float session exhibited evidence of meeting the established criteria for orthostatic hypotension, suggesting a one-sided 95% CI of 13% (upper tail) in this population. **Figure 4** displays the postfloat orthostatic BP measurements for each individual. At the group level, the median and range (in bracket parentheses) of the systolic and diastolic BP changes from lying to standing was 5 [−12, 30] and 11 [−5, 46] mmHg, respectively, across the three sessions (**Figure 5**). With respect to other safety measures, we did not observe any falls upon standing, and there were no reports of feeling lightheaded or dizzy. Additionally, there were no adverse events such as acute panic attacks, severe dysphoria, agitation, or increased suicidal ideation.

Secondary Outcomes

Blood Pressure Responses During REST

Systolic BP appeared to slightly increase during Chair-REST but showed a U-shaped pattern (decreased, remained stable, and then increased) during floatation-REST, with the largest decrease occurring during the final session (**Figure 6A**). Nonetheless, the differences across sessions were not substantial, and BIC suggested a LMM with only the time but not the session nor the session-by-time interaction fixed-effects. The LMM suggested the largest reductions (with 95% CI, t-statistic, and p value) ranged between 2.3 [(0.47, 4.13), $t(592) = -2.47$, $p = 0.014$] and 3.7 [(1.83, 5.49), $t(592) = -3.93$, $p < 0.0001$] mmHg between the 25th and 65th minutes of REST. Diastolic BP showed a more consistent decrease across both sessions of floatation-REST as compared with chair-REST (**Figure 6B**) and BIC also selected a LMM with only time as a fixed-effect. The LMM suggested the largest reductions ranged between 1.8 [(0.17, 3.48), $t(592) = -2.17$, $p = 0.030$] and 2.6 [(0.83, 4.39), $t(592) = -2.88$, $p = 0.004$] mmHg between the 25th and 65th minutes of REST.

State-Trait Anxiety Inventory-State Form

For the secondary outcome of STAI-state anxiety, the LMM suggested that the post-vs.-pre-POMP change was on average −15.2% (with a 95% CI of −18.3 to −12.1%) across all four REST sessions ($p < 0.0001$).

Positive and Negative Affect Schedule—Expanded Form

For the secondary outcome of PANAS negative affect, the LMM suggested that the post-vs.-pre-POMP change was on average −8.3% (with a 95% CI of −11.2 to −5.3%) across all four sessions ($p < 0.0001$). For the secondary outcome of PANAS positive affect, the LMM suggested that the post-vs.-pre-POMP change was on average 4.5% (with a 95% CI of 1.2 to 7.9%) across all four sessions ($p = 0.007$). For the secondary outcome of PANAS joviality, the LMM suggested that the post-vs.-pre-POMP change was on average 5.5% (with a 95% CI of 1.9–9.8%) across all four sessions ($p = 0.007$). For the secondary outcome of PANAS fatigue, the LMM suggested that the post-vs.-pre-POMP change was on average −13.9% (with a 95% CI of −20.2 to −8.4%) across all four sessions ($p < 0.0001$). For the secondary outcome of PANAS serenity, the LMM suggested that the post-vs.-pre-POMP change was on average 25.3% (with a 95% CI of 19.8, 31.5%) across all four sessions ($p < 0.0001$). Thus, participants reported reduced negative affect and fatigue from pre- to post-REST, whereas they reported increased positive affect, joviality, and serenity from pre- to post-REST.

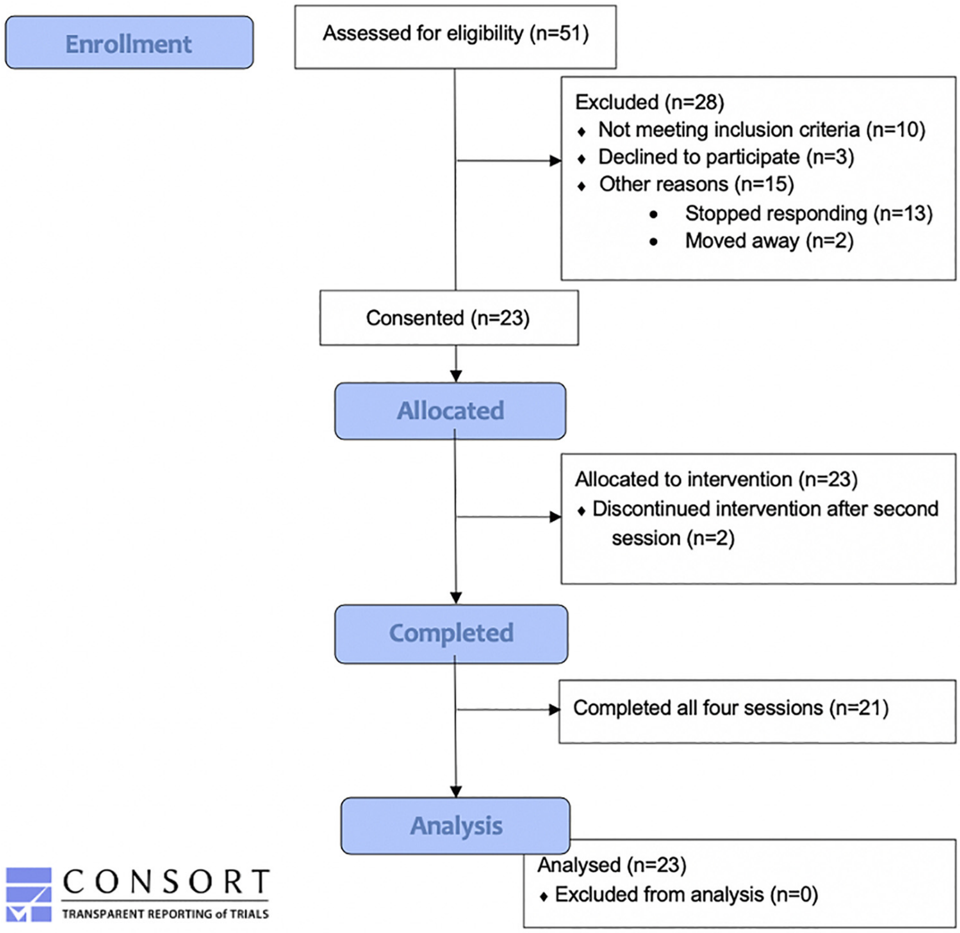

FIGURE 3 | Consort flow diagram. This figure illustrates the number of participants included in enrollment, the number allocated to the REST intervention, the number withdrawn, and the number included in the data analysis.

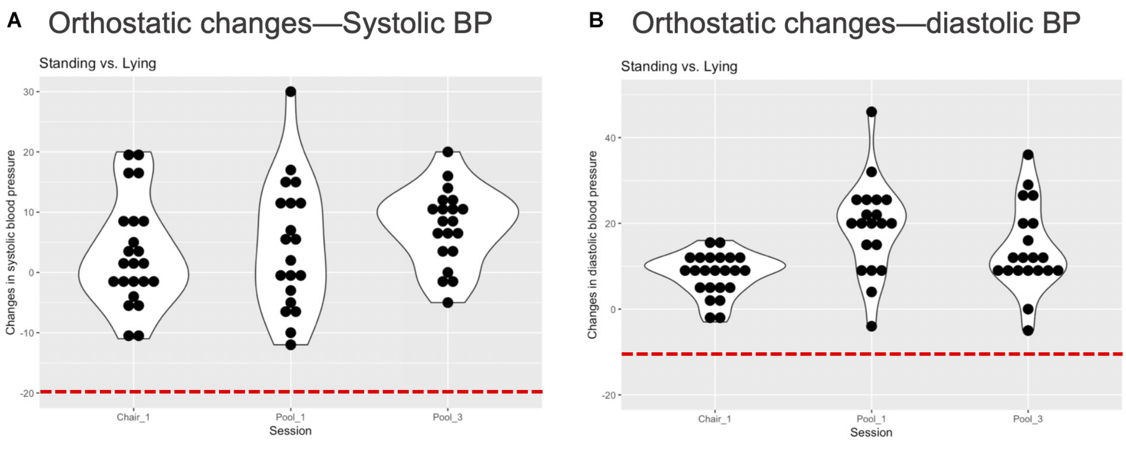

FIGURE 4 | Individual orthostatic blood pressure changes. **(A)** The figure displays each individual's change in systolic blood pressure (BP) from lying to standing at the end of each REST session. There was no evidence of systolic orthostatic hypotension in any individual, i.e., a reduction in systolic BP below 20 mmHg (red dashed line). **(B)** The figure displays each individual's change in diastolic BP from lying to standing at the end of each REST session. There was no evidence of diastolic orthostatic hypotension in any individual, i.e., a reduction in systolic BP below 10 mmHg (red dashed line). Note that BP was not measured during the second pool session and is therefore unlisted.

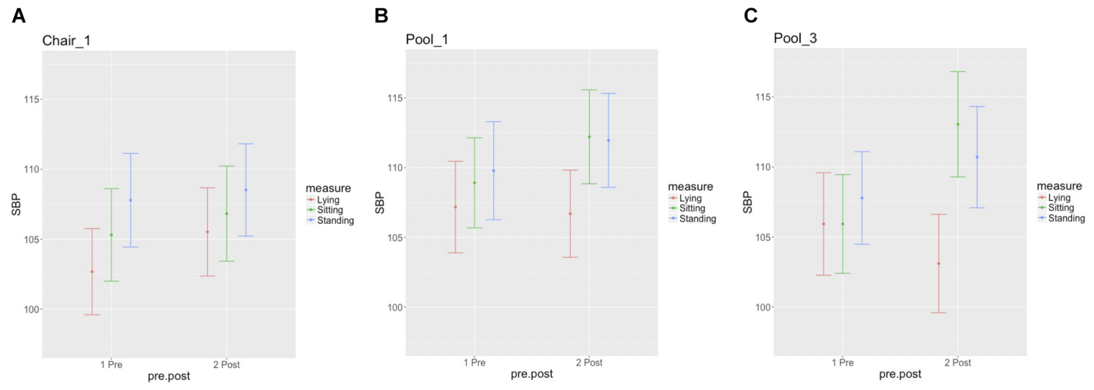

FIGURE 5 | Group summary of orthostatic blood pressure measures. Each figure displays the mean and standard error for the lying, sitting, and standing blood pressure measurements, at pre- and postsession intervals for the **(A)** chair-REST **(B)** the first and **(C)** final floatation-REST sessions.

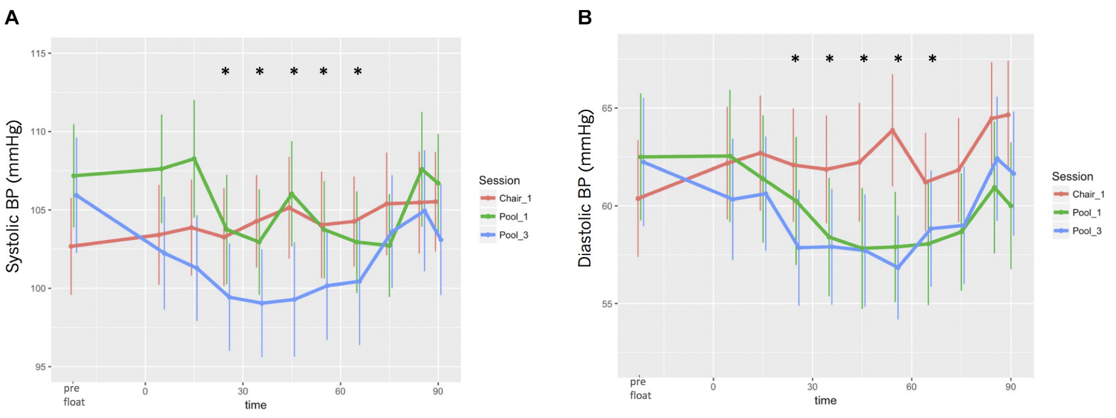

FIGURE 6 | Blood pressure responses during REST. **(A)** Systolic BP. **(B)** Diastolic BP. Significant reductions in both systolic and diastolic BP occurred between the 25th and 65th minutes of REST.

Visual Analog Scales

For the secondary outcome of VAS relaxation, the LMM suggested that the post-vs.-pre-POMP change was on average 21.9% (with a 95% CI of 17.3–26.1%) across all four sessions ($p < 0.0001$). For the secondary outcome of VAS stress, the LMM suggested that the post-vs.-pre-POMP change was on average −22.9% (with a 95% CI of −27.3 to −18.5%) across all four sessions ($p < 0.0001$). For the secondary outcome of VAS refreshed, the LMM suggested that the post-vs.-pre-POMP change was on average 32.0% (with a 95% CI of 27.0–36.4%) across all four sessions ($p < 0.0001$). For the secondary outcome of VAS energy, the LMM suggested that the post-vs.-pre-POMP change was on average 16.6% (with a 95% CI of 12.0–20.6%) across all four sessions ($p < 0.0001$). Thus participants reported reduced stress from pre- to post-REST, whereas they reported increased relaxation, refreshment, and energy from pre- to post-REST.

Interoceptive Awareness Measures

For the secondary outcome of heartbeat intensity, the LMM suggested that the REST-vs.-baseline POMP change was on average 10.6% (with a 95% CI of 2.7–17.9%) across all four sessions ($p = 0.0032$). For the secondary outcome of breath intensity, the LMM suggested that the REST-vs.-baseline POMP change was on average 8.8% (with a 95% CI of 2.7–14.8%) across all four sessions ($p = 0.0043$). For the secondary outcome of stomach/digestive intensity, the LMM suggested that the REST-vs.-baseline POMP change was on average −1.8% (with a 95% CI of −8.7–5.1%) across all four sessions ($p = 0.581$). Thus, during REST, participants reported feeling significant increases in the intensity of the sensations from their heartbeat and breath but not from their stomach/digestive system.

Body Appreciation Scale 2

For the BAS-2, the score increased by 0.26 (95% CI from −0.06 to 0.58), 0.10 (from −0.28 to 0.48), 0.10 (from −0.32 to 0.51), and 0.08 (from −0.34 to 0.50) across the four sessions of REST. The type III analysis of variance comparing the post-float assessments vs. the initial baseline assessment did not observe a statistically significant difference across sessions: $F(4,84) = 1.38$, $p = 0.25$, and BIC suggested a model without a session effect.

Body Image States Scale

For the BISS, a negative attitudinal body image secondary outcome measure, the LMM suggested that the post-vs.-pre-POMP change was on average 1.05% (with a 95% CI of 0.7–1.5%) across all four REST sessions ($p < 0.0001$), suggesting a statistically significant increase in more favorable body image state.

Photographic Figure Rating Scale

For body dissatisfaction ratings on the PFRS, a visual perceptual body image secondary outcome measure, the LMM suggested that the post-vs.-pre-POMP change was on average −4.66% (with a 95% CI of −6.58 to −2.67%) across all four float sessions ($p < 0.0001$). Thus, participants reported significantly reduced body image dissatisfaction from pre- to post-REST.

Effect Sizes for Secondary and Exploratory Outcome Measures

Effect size calculations (Cohen's *d*) for all secondary and exploratory outcome measures are listed in **Figure 7**. REST elicited moderate (0.5) to large (0.8 and greater) effects on ratings of state anxiety, stress, refreshment, serenity, relaxation, energy, and PFRS body dissatisfaction. REST elicited small (0.2) to moderate (0.5) effects on BP, heartbeat and breath intensity, and negative attitudinal body image. REST appeared to have minimal effects on stomach/gastrointestinal sensation intensity ratings and positive body appreciation ratings.

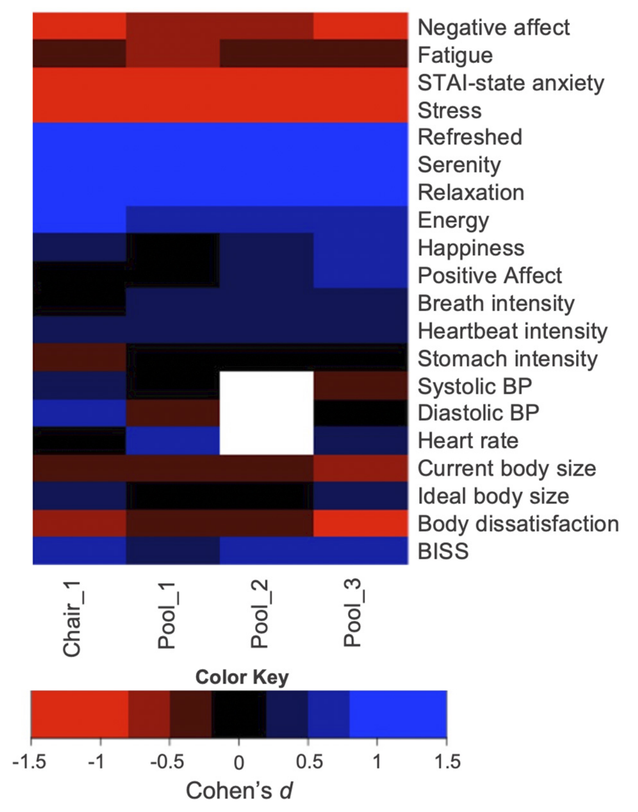

FIGURE 7 | Effect size estimates for the secondary outcome measures. Note that there were no blood pressure measures taken during the second pool float, and therefore that field is blank. A table showing the exact effect size estimates and associated confidence intervals is located in the **Supplementary Material**.

Postsession Interviews

A complete transcription of the post-REST interviews is provided in the **Supplementary Material**. Overall, most participants found the REST experience to be positive. Many participants stated that the idea of the REST environment elicited some apprehension, particularly during the initial minutes of exposure to REST or when they turned the lights off (in which case they kept the lights on during the session). These feelings were usually followed by a sense of physical relaxation and a slowing of their thought process. Many individuals spontaneously reported experiencing their heartbeat and breathing sensations more intensely, as well as a sense of weightlessness, particularly in the floatation pools. Many found that the REST environment elicited thoughts about their bodies and body image concerns, with a couple of individuals reporting performing body checking maneuvers, but more individuals noted that they experienced a positive change in their relation to their bodies during REST. For example, some individuals reported positively experiencing a sense that they could not feel their outer body limits or their stomach sensations at certain times, eventually moving their limbs or trunk to re-engage the sense of body ownership. A few reported consciously noting that their sense of distress and focus about their body image was lower during the sessions. When directly queried, there were more positive endorsements of the REST environments during each float than there were negative endorsements.

DISCUSSION

We conducted this single group open-label study with the primary aim of investigating the safety and tolerability of REST in AN. Secondarily, we aimed to explore the impact of REST on affective symptoms, body image disturbance, and interoception. Prior to the current study, there have been no studies documenting the safety or tolerability of the procedure in any eating disorders population, and we could find only one brief theoretical review of the topic (Barabasz, 1993). Therefore, this study represents the first empirical investigation of REST in eating disorders.

With respect to the primary outcome of safety, we did not observe any evidence of orthostatic BP reductions for either the systolic or diastolic measure. We also did not observe any falls or other signs of adverse experiences such as acute panic attacks, severe dysphoria, agitation, or suicidal ideation in response to the REST environment. Some participants reported mild apprehension with exposure to the dark, with thoughts about their body image, or with worry about having increased anxiety in the REST environment, but ultimately these were felt to be tolerable as evidenced by the significant reduction in state anxiety, comments provided during postsession interviews, and high rate of study completion (21 out of 23 individuals completing the entire four session protocol). Collectively, these results suggest that the participants in this study safely tolerated the REST environment and found it to be acceptable. The sample recruited for this study was composed of outpatients with a lifetime diagnosis of AN, with moderate levels of residual symptoms according to their scores on the EDE-Q, and heightened levels of trait anxiety according to the STAI. To reduce the risk of falling while in an unsupervised environment, future studies of more acutely ill individuals (e.g., inpatients) would need to demonstrate that they do not exhibit signs of orthostatic hypotension before commencing REST.

With respect to the secondary outcome measures, we observed significant reductions in several affective measures from pre- to post-float including self-reported state anxiety, stress, fatigue, and negative affect, as well as significantly increased positive affect, relaxation, joviality, refreshment, energy, and serenity. The observed reductions in state anxiety on the STAI are potentially noteworthy for several reasons: (1) current anxiolytic medications such as benzodiazepines (Steinglass et al., 2014) and behavioral treatments for anxiety in AN show limited efficacy, (2) the magnitude of the effect was large, and (3) they mirror our previous observation of acute anxiety reductions in a transdiagnostic group of individuals with heightened anxiety sensitivity (Feinstein et al., 2018a). At this juncture, it is important to emphasize that such observations are to be regarded as preliminary until they can be verified in subsequent studies employing control conditions and randomized participant assignment, to account for the potential impact of expectancies on responses to this novel behavioral intervention.

In the current study, we observed significant reductions in body dissatisfaction measured *via* the PFRS, with effect sizes ranging from small during the first few floats to large during the final float. This amounted to a POMP reduction of nearly 5%. We also observed an improvement in the BISS, a negative attitudinal measure of body image disturbance but to a much smaller extent (only about 1% POMP). There was also no effect of floating on the BAS, a positive attitudinal measure of body image. These results are important because it is well known that individuals with AN often retain body image disturbances long after achieving weight restoration, and body image disturbance has been identified as a predictor of relapse (Keel et al., 2005). Explanatory models of AN have traditionally focused on the roles of personality traits [e.g., obsessionality (Lilenfeld et al., 2006), perfectionism (Zucker et al., 2011), cognitive inflexibility (Friederich and Herzog, 2011)], culturally derived values [e.g., "thinness ideal" (Levine and Smolak, 2010)], or family environment (Klump et al., 2002). While such models have revealed key aspects of eating disorders, it has been suggested that treatments directed toward them yield only moderate recovery rates (Pike, 1998; Couturier et al., 2013; Galsworthy-Francis and Allan, 2014; Tchanturia et al., 2014), indicating that research into novel therapies is needed. The possibility that REST could have a therapeutic impact on measures of body image is potentially noteworthy, but it should also be noted that the observed effects were short term and were not compared against a control intervention.

We also observed significant changes in interoceptive awareness for heartbeat and breathing sensations (with a medium effect size) but not for the stomach/digestive system. Increased cardiorespiratory sensation changes during floatation-REST mirrored our previous observation with anxious individuals (Feinstein et al., 2018a), but the lack of change in stomach/digestive system changes was noteworthy given the predominant focus on such symptoms outside of meal times, such as fullness, bloating, and constipation (Robinson, 1989; Halmi and Sunday, 1991; Sato and Fukudo, 2015) in AN. While we cannot know whether this pattern of interoceptive changes is the source of their positive affective responses to REST, it would seem that changes in gastrointestinal (GI) sensation were not a major contributing factor. The fact that GI sensations were actually diminished during REST (and not heightened like other interoceptive sensations) is also important from a safety perspective, as it highlights that REST does not seem to exacerbate the intensity of their already uncomfortable GI sensations. Interestingly, several recent studies exclusively using self-report measures have suggested that interoceptive awareness may be positively associated with positive body image in adolescents and adults (Todd et al., 2019a,b). The current study extends this link *via* physical exposure of AN individuals to the REST environment, finding both increases in cardiorespiratory interoceptive sensations and improved positive body image measures.

Limitations

This study has several limitations that elicit considerations for future investigations. For this initial study, we recruited a relatively small sample that was partially weight restored, was composed of individuals with a lifetime history of AN (i.e., some did not have a current diagnosis of AN), and was thoroughly screened to exclude the presence of acute medical illness. We therefore cannot rule out the possibility that a larger or more clinically heterogeneous sample might have had a different outcome with respect to safety, tolerability, and subjective outcome. The lack of a control condition in our use of an open-label design means that the observed results could be susceptible to the effects of expectation. Although such effects can impact any type of clinical trial, they are especially important to consider when conducting non-pharmacological clinical trials. In the current study, we attempted to constrain such expectations by providing participants with only the minimum information necessary for them to consider the potential risks and time constraints involved in study participation. We also decided against randomizing to a control condition in this initial study based on (1) our primary interest in gathering safety and feasibility data and (2) ensuring in this initial study a gradual exposure to REST so as to minimize potential safety risks from a more rapid immersion directly into floatation-REST. Thus our approach followed the development principles of behavioral clinical trials optimization [e.g., the ORBIT model (Czajkowski et al., 2015)], in which the early-phase (akin to Phase I) relates to 'defining and refining' the intervention, leading to future proof-of-concept and pilot feasibility studies (akin to Phase II), and finally, late-phase efficacy trials (akin to Phase III). Now that there are some safety data available, we recommend that future studies investigating the efficacy of REST in modifying clinically relevant outcomes incorporate a randomized control condition (e.g., a wait-list control group) or a crossover design (Feinstein et al., 2018a). Other comparator options include employing a usual care group or attentional control group (Freedland et al., 2011); these latter approaches may be preferable on an inpatient unit, where usual care for AN is intensive and includes multiple forms of treatment such as pharmacotherapy and psychotherapy. Another consideration is the finding that the chair-REST condition exhibited effect sizes that were similar to floatation-REST for some of the secondary outcome measures, such as negative affect, anxiety, stress, relaxation, serenity, and refreshment, potentially raising questions about whether exposure to the pool environment would even be necessary to elicit some of these effects. However, the observed effects on body image (particularly, body dissatisfaction on the PFRS), interoception, BP, as well as positive affect could indicate some specificity to the float pool environment. Future trials employing a randomized controlled design can help disentangle whether specific types of REST (Suedfeld and Borrie, 1999) are more efficacious than others for treating AN. Finally, a third limitation relates to the lack of control for multiple comparisons when examining the numerous secondary objectives. With these considerations in mind, we regard these results as preliminary and hypothesis generating for future studies. We have chosen the emphasize the observed effect sizes (which also must be interpreted with caution given the aforementioned lack of a control group to manage potential influences of expectancy), in hopes that they are of use in the design of future studies.

CONCLUSION

Overall, the findings from this initial trial suggest that individuals with partially weight-restored AN can safely tolerate the physical effects of REST. They may also experience improvements in anxiety and body image disturbance, but further studies involving randomized controlled designs would be required to confirm this finding.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation, to any qualified researcher.

ETHICS STATEMENT

This study involving human participants was reviewed and approved by Western Institutional Review Board. All participants provided their written informed consent to participate in this study. Written informed consent was also obtained from the individual(s) for the publication of any potentially identifiable images or data included in this article.

AUTHOR CONTRIBUTIONS

SK and JF conceived the research idea, with input into the experimental design from SM, BP, VU, and MP. VU, RP, EB, and SC collected, collated, and transcribed the data. H-WY, SK, and JF analyzed the data. SK, JF, and H-WY drafted and edited the manuscript. All authors have read and approved the final manuscript before submission.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2020.567499/full#supplementary-material

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Visual Hand Recognition in Hand Laterality and Self-Other Discrimination Tasks: Relationships to Autistic Traits and Positive Body Image

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In a study concerning visual body part recognition, a "self-advantage" effect, whereby self-related body stimuli are processed faster and more accurately than other-related body stimuli, was revealed, and the emergence of this effect is assumed to be tightly linked to implicit motor simulation, which is activated when performing a hand laterality judgment task in which hand ownership is not explicitly required. Here, we ran two visual hand recognition tasks, namely, a hand laterality judgment task and a self-other discrimination task, to investigate (i) whether the self-advantage emerged even if implicit motor imagery was assumed to be working less efficiently and (ii) how individual traits [such as autistic traits and the extent of positive self-body image, as assessed *via* the Autism Spectrum Quotient (AQ) and the Body Appreciation Scale-2 (BAS-2), respectively] modulate performance in these hand recognition tasks. Participants were presented with hand images in two orientations [i.e., upright (egocentric) and upside-down (allocentric)] and asked to judge whether it was a left or right hand (an implicit hand laterality judgment task). They were also asked to determine whether it was their own, or another person's hand (an explicit self-other discrimination task). Data collected from men and women were analyzed separately. The self-advantage effect in the hand laterality judgment task was not revealed, suggesting that only two orientation conditions are not enough to trigger this motor simulation. Furthermore, the men's group showed a significant positive correlation between AQ scores and reaction times (RTs) in the laterality judgment task, while the women's group showed a significant negative correlation between AQ scores and differences in RTs and a significant positive correlation between BAS-2 scores and dprime in the self-other discrimination task. These results suggest that men and women differentially adopt specific strategies and/or execution processes for implicit and explicit hand recognition tasks.

Keywords: visual hand recognition, hand laterality, self-other discrimination, autistic traits, body image

INTRODUCTION

Over time, hands have developed in a remarkably human-specific manner and serve as an important interface between human's external worlds (including other people) and their individual selves. In the past two decades, neuroimaging studies have revealed that a specific area of the brain [the extrastriate body area (EBA)] is selectively activated when perceiving body parts (e.g., Downing et al., 2001; Peelen and Downing, 2005; see Peelen and Downing, 2007 for a review). It is known that the right EBA responds more to allocentric view of body parts than to egocentric view and this preference in the right EBA for allocentric view is associated with social cognition (e.g., self-other discrimination; Chan et al., 2004; Saxe et al., 2006). Furthermore, Bracci et al. (2010) found a hand-preferring region in the EBA, suggesting that representations of the hand in the extrastriate visual cortex are distinct from representations of other body parts.

Many studies have investigated mental rotation tasks using hand stimuli (i.e., hand laterality judgment tasks) since the pioneering works in the field of cognitive psychology (Cooper and Shepard, 1975; Sekiyama, 1982; Parsons, 1987). These hand laterality judgment tasks developed from an object mental rotation task (Shepard and Metzler, 1971). The judgment task requires participants to determine whether a visual hand stimulus (which could be presented in several angular orientations) is a right or left hand. Reaction times (RTs) are linearly modulated by angular orientations of stimuli when performing a classic object (or letter) mental rotation task, which suggests that participants are mentally rotating the stimuli toward the familiar (i.e., the upward) position. However, the RTs in a hand laterality judgment task are not linearly modulated by the angular orientations of hand stimuli. Indeed, RTs depend on biomechanical constraints. Specifically, longer RTs were observed in this task, as it requires the biomechanically difficult mental rotation of a hand's image, in comparison with a task that is biomechanically easier, even when the necessary stimulus rotation is equal (Parsons, 1994; Parsons et al., 1998; de Lange et al., 2006). Furthermore, the hand posture adopted by participants during this task also influences their RTs (Ionta et al., 2007; Ionta and Blanke, 2009). Specifically, longer RTs for hand laterality judgments were shown when participants were holding both hands behind their back than when the same task was performed with both hands placed on their knees. The biomechanical effect is stronger when the hands were presented from palm than from back, because physically rotating palms is assumed to be more difficult than rotating backs of hands (Sekiyama, 1982; Parsons, 1987, 1994; Gentilucci et al., 1998; ter Horst et al., 2010; Bläsing et al., 2013; Zapparoli et al., 2014; Conson et al., 2020). These results indicate that hand laterality judgment tasks involve implicit motor imagery processes. However, some studies did not reveal the effect of biomechanical constraints on the RTs (e.g., Lust et al., 2006; Steenbergen et al., 2007). ter Horst et al. (2010) suggested that engagement in motor imagery when performing a hand laterality judgment task depends on the used number of axes of rotation of the stimulus set.

In the last decade, research has increasingly addressed how people distinguish between their own hands and the hands of others (e.g., Aranda et al., 2010; Rossetti et al., 2010). Frassinetti and colleagues (Frassinetti et al., 2008, 2009) found a "self-advantage" effect, whereby self-related body stimuli are processed faster and more accurately than other-related body stimuli. Ferri et al. (2011), however, reported that the self-advantage effect emerged only when performing a hand laterality judgment task in which the participant did not explicitly need to recognize the identity of the hand (i.e., an implicit hand recognition task), and noted that this effect did not emerge in an explicit self-recognition task (i.e., a self-other discrimination task). Conson et al. (2015) also ran these visual hand recognition tasks (hand laterality judgment and self-other discrimination tasks), replicating the results of Ferri et al. (2011), and suggested that implicit motor imagery processes are essential for the emergence of the self-advantage effect (see also Frassinetti et al., 2011). Furthermore, concerning self-other discrimination tasks, Conson et al. (2015) found a "self-disadvantage" effect that led to longer RTs for the self-hand image, when compared with RTs for other-hand images (see also Ferri et al., 2011).

Recently, several studies using these visual hand recognition tasks have investigated task performance in clinical populations in comparison with healthy participants. In Campione et al. (2017), women outpatients diagnosed with eating disorders [N = 15; mean (± SD) age = 18.0 ± 2.1; age range = 15–21] were recruited, and they did not show the self-advantage effect in a hand laterality judgment task (although the RTs of these outpatients were comparable to those of the control participants). Furthermore, Conson et al. (2016) found that individuals with autism spectrum disorder [ASD; 18 participants (1 woman); mean (± SD) age = 14.6 ± 4.2; age range = 10–20] showed significantly longer RTs in comparison with typically developing (TD) peers in a classical hand laterality judgment task in which self-hand images were not used (see also Conson et al., 2013).

These studies investigating clinical populations inspired a research question concerning whether and how the extent of a person's autistic traits and body appreciation affect their performance of implicit and explicit hand recognition tasks, compared to the same tasks performed by members of a population of TD participants. It is known that ASD is more common in males than females, with a male-to-female ratio of about 4 to 1 across the whole autism spectrum (Baird et al., 2006), and rising to 8 or 9 to 1 in higher-functioning samples (Mandy et al., 2011). By contrast, eating disorders are predominantly found in females, with a female-to-male ratio from about 4 to 1 during adolescence and about 10 to 1 in adulthood (Striegel-Moore and Bulik, 2007; Reijonen et al., 2016). Previous studies (e.g., Linn and Petersen, 1985; Voyer et al., 1995; Collins and Kimura, 1997) demonstrated that women exhibit inferior visuospatial performance, compared to men. The task involved in the hand laterality judgment calls for deciding whether the presented hand image is a right or left hand. Left-right discrimination is essential in everyday life, but many people report difficulties discriminating left from right in daily life, which results in left-right confusion. Sex differences in this confusion based on self-reported data have been found, indicating that women are more prone to left-right confusion than men are (e.g., Hannay et al., 1990).

With the above mind, we wondered whether and how sex difference affects the performance of implicit and explicit hand recognition tasks, even in those populations in which people have not been diagnosed. Indeed, Mochizuki et al. (2019) and Conson et al. (2020) recently investigated the effect of sex differences on the performance of a classical hand laterality judgment task, but the effect of sex differences on the performance of implicit and explicit hand recognition tasks (using self- and other-hand images) remains an open question. Answering this question will contribute to our further understanding of self-other discrimination and body part recognition.

During previous visual hand recognition tasks, the numbers of orientation conditions for the hand image were manipulated. For example, the numbers Ferri et al. (2011) and Conson et al. (2015) used were four and six, respectively (see also Ferri et al., 2012; Conson et al., 2017; De Bellis et al., 2017). It is assumed that the task would be easy and that implicit motor imagery processes would work less efficiently if the number of orientation conditions of the hand image is limited to two (i.e., upright and upside-down). Therefore, the current study aims to investigate whether the self-advantage effect emerges in the hand-laterality task and whether the self-disadvantage effect is revealed in the self-other discrimination task, even when the number of orientation conditions of the hand image in each visual hand recognition task is limited to two [egocentric (upright; 0°) and allocentric (upside-down; 180°); cf. Chan et al., 2004; Saxe et al., 2006; Conson et al., 2010].

The present study investigated how the individual traits of TD university students (who had not been diagnosed) modulated their performance in hand laterality judgment and self-other discrimination tasks using the Autism Spectrum Quotient (AQ) test (Baron-Cohen et al., 2001; Japanese version: Wakabayashi et al., 2004) and the Body Appreciation Scale-2 (BAS-2; Tylka and Wood-Barcalow, 2015; Japanese version: Namatame et al., 2017). Specifically, we focused on whether and how the differences in parameters (e.g., accuracy, reaction time, etc.) between self and other conditions, as an index of self-(dis)advantage, are modulated according to the scores of individual traits (the AQ and the BAS-2) in implicit and explicit hand recognition tasks.

MATERIALS AND METHODS

Participants

In total, 36 right-handed university students [20 men, mean age (± SD): 21.4 ± 1.4] participated in the following visual hand recognition tasks. Of these participants, six were excluded because of their outlier performances (see Results section for details), leaving 30 participants (15 men) for inclusion in the analysis. All participants were confirmed to be right-handed [the minimum score among the participants was 30, and with a mean score (± SD) of 88.0 ± 16.3], as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). They had normal or corrected-to-normal vision, and none had any motor or sensory abnormalities. This study was approved by the ethics committee of Tokyo Metropolitan University's Hino Campus, and all participants provided written informed consent according to the Declaration of Helsinki. They were naive to the purpose of the experiment and were paid for their participation.

Apparatus

Photographing Participants' Hands

A digital camera (PowerShot SX620 HS, Canon, Tokyo, Japan) installed in a box on a table (see Procedure section for details) was used, and stimuli were produced using Adobe Photoshop 2019.

Visual Hand Recognition Tasks (Laterality Judgment and Self-Other Discrimination Tasks)

A laptop PC (ZenBook Pro UX550VD-7700. AsusTek Computer Inc., Taipei, Taiwan; 15.6 inches, screen resolution = 1,920 × 1,080 pixels) was used to present the stimuli and for data acquisition. Reacting with the hand itself could influence the performance in a visual hand recognition task, so participants were required to perform the task using their preferred foot with a triple foot pedal (RI-FP3BK. Route-R Corporation, Tokyo, Japan, see **Figure 1A**).

Questionnaire

The Autism Spectrum Quotient test (Baron-Cohen et al., 2001; Japanese version: Wakabayashi et al., 2004) is one of the most well-known questionnaires for measuring autistic traits. It consists of five subscales (i.e., social skill, attention switching, attention to detail, communication, and imagination). Each subscale has 10 items, resulting in a 50-item questionnaire (i.e., the maximum

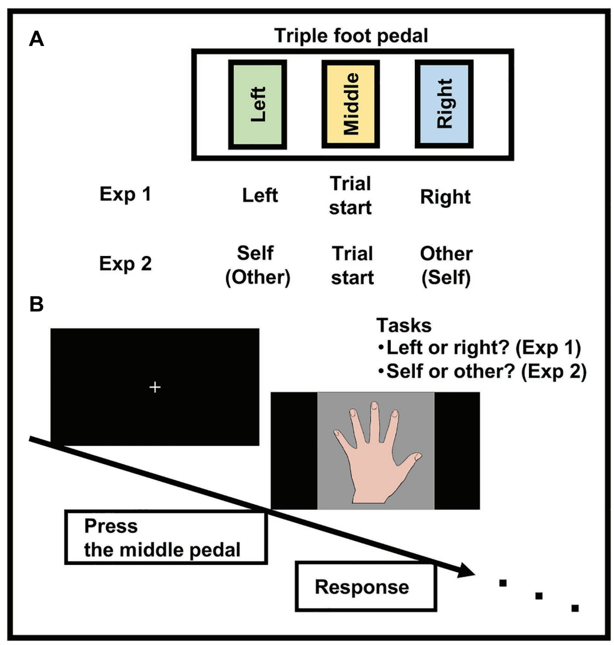

FIGURE 1 | Experimental setup. Button assignment of triple foot pedal for response. Middle button was assigned for the trial start **(A)**. A time sequence of the trial. Participants pressed the middle pedal after a white cross appeared on the screen, and then a hand image (in the experiment, a full-color photograph was used) appeared, prompting a response **(B)**.

possible score is 50). If the score is 33 (the cutoff score in the Japanese version) or higher, that participant could possibly have a clinically significant level of autistic traits.

The Body Appreciation Scale-2 (Tylka and Wood-Barcalow, 2015; Japanese version: Namatame et al., 2017) is a widely used 10-item questionnaire on positive body image. This is a revision of the original 13-item BAS (Avalos et al., 2005). The average score of the 10 items is the participant's final BAS-2 score. The maximum possible score is 5, with higher scores indicating higher levels of body appreciation.

Procedure

Photographing Participants' Hands

Participants sat comfortably on a chair and placed their hands in a box on a table. Their palms were touching the surface of the table, and the backs of the hands were photographed using a box on the ceiling of which a rail was installed for sliding the digital camera to take pictures of the right and left hands easily. Participants could not see the inside the box, and they were asked, prior to participating, to agree to have their hands photographed.

Full-color photos were made of the participants' left and right hands (i.e., backs of the hands) against a gray background (1,063 × 1,063 pixels, see **Figure 1B**). One hand image was located in the center of each stimulus. The original images of the hands (one picture per hand) in the upright orientation (0°, consistent with the perspective of the viewer, i.e., upright) were digitally manipulated to obtain the hand images at an opposite orientation (180°, i.e., upside-down). These two orientations of the hand images (0 and 180°) were used as stimuli.

Visual Hand Recognition Tasks

About 1 week after their hands were photographed, participants engaged in two visual hand recognition tasks (i.e., a laterality judgment task and a self-other discrimination task). All participants performed the laterality judgment task first, followed by the self-other discrimination task on the same day (cf. Campione et al., 2017). We adopted this order to minimize participants' attention to hand ownership when completing the laterality judgment task.

Laterality Judgment Task

Participants viewed the display on a laptop computer from a distance of approximately 60 cm while seated comfortably on a chair in front of the table on which the laptop was located. A triple foot pedal was situated beneath the participant's feet, and the center of the pedal was aligned with the participant's sagittal plane. Each participant was required to remove their shoes and to react to the stimuli using their right or left foot (**Figure 1A**). Concerning the response foot when starting the trial (i.e., pressing the middle button, **Figure 1A**), half of the participants began each trial with the right foot, while the other half started with the left foot. Once underway, the foot used could not be changed during the experiment. Participants were also required to place their hands in their lap, and their hands were concealed by a towel.

At the beginning of the trial, a white cross (i.e., a fixation point, 1.7 × 1.7°) was presented in the center of the display. When participants intended to start the trial, they pressed the middle pedal of the triple foot pedal. Immediately after pressing the pedal, a hand stimulus (18.4 × 18.4°) was presented in the center of the display. Participants were instructed to decide whether the presented hand stimulus was an image of a right or left hand and to respond as quickly and accurately as possible (**Figure 1B**). The right pedal was assigned for responding to the right hand images, and the left pedal was assigned for responding to the left hand images. For the other hand images, the hands of two sex-matched persons whom the participants did not know (i.e., the authors' colleagues and other participants) were used.

The experiment consisted of 180 trials [= 2 (hand image laterality) × 2 (visual perspective conditions) × 3 (person's hands, i.e., own and two same-sex others) × 15 trials (in each)], and participants took a 2-min break every 60 trials. Before the test trials, each participant performed 16 practice trials to ensure that they were performing the trials according to the instructions.

Self-Other Discrimination Task

The experimental procedure for the self-other discrimination task was the same as the one used in the laterality judgment task, except that the participants' reactions to the right or left hand image were replaced by a reaction to the participants' own hands or the hands of another person of the same sex.

The right pedal was assigned for responding to the self-hand images, while the left pedal was assigned for responding to the other person's hand images for half of the participants. The pedal assignment for responding was reversed for the other half of the participants.

Questionnaire

All participants completed the Japanese pencil-and-paper versions of the AQ (Wakabayashi et al., 2004) and BAS-2 (Namatame et al., 2017) tests after performing the visual hand recognition tasks. The items in the AQ (e.g., "It does not upset me when my daily routine is disturbed") are answered on a 4-point Likert scale ("definitely agree," "slightly agree," "slightly disagree," and "definitely disagree"), while the participants rated each item of the BAS-2 (e.g., "Despite its flaws, I accept my body for what it is") to indicate whether the question was true about the participant's approval and acceptance of their own body, noted on a 5-point scale (i.e., never = 1, seldom = 2, sometimes = 3, often = 4, and always = 5).

Data Processing and Analysis

Visual Hand Recognition Tasks

Accuracy and RTs were recorded in each condition. For each participant, RT outliers were removed by excluding trials with RTs that fell more than three SDs from the median of all trials. ANOVAs were conducted on accuracy and RTs, with sex (women and men) as a between-participants factor, and with hand ownership (self and other), hand image laterality (left and right), and visual perspective (upright and upside-down) as within-participant factors.

The sensitivity and response criterion for visual hand recognition were calculated as dprime and ln(β), respectively, according to the signal detection theory. The calculation of these two values was based on the formula reported by Macmillan and Creelman (1991). These values were also entered into ANOVAs, with sex (women and men) as a between-participants factor, and with two within-participant factors, namely, hand ownership (self and other) and visual perspective (upright and upside-down) in the laterality judgment task and hand laterality (left and right) and visual perspective (upright and upside-down) in the self-other discrimination task. Bonferroni-corrected *post-hoc* comparisons were performed when necessary.

Relationships Between Task Performance and Questionnaires' Scores

Two questionnaire scores (i.e., AQ and BAS-2) were calculated for each participant. To determine whether and how individual traits would be related to ability in visual hand recognition, non-parametric Kendall rank correlation coefficients between each questionnaire score (AQ and BAS-2) and each parameter of task performance [accuracy, RTs, dprime, ln(β) (these values were averaging all conditions), and the differences in accuracy and RTs between the self and other conditions] were computed by sex. When computing each correlation coefficient, two levels (i.e., men and women) were set in the experimental design, so $\alpha = 0.05/2 = 0.025$ was considered to be statistically significant, using the Bonferroni correction.

RESULTS

Data from the six participants whose accuracy or RTs did not fall within the range of the mean values ± two SDs in each visual recognition task were excluded from the data analysis. Therefore, the data of 30 participants (15 men) were included in the following results.

Accuracy

Overall accuracy was high in both tasks at 96.2% in the laterality judgment task and 98.2% in the self-other discrimination task (see **Table 1**).

Laterality Judgment Task

The main effect of laterality was significant [$F(1, 28) = 7.941$, $p = 0.009$, partial $\eta^2 = 0.221$; left hand image: 97.2 ± 4.6%; right hand image: 95.3 ± 6.7%]. The significant main effect of visual perspective [$F(1, 28) = 6.297$, $p = 0.018$, partial $\eta^2 = 0.184$] was also noted. Furthermore, a second-order interaction among sex, ownership, and visual perspective (sex × ownership × visual perspective interaction) was noted [$F(1, 28) = 4.411$, $p = 0.045$, partial $\eta^2 = 0.136$], and a *post-hoc* comparison revealed that accuracy concerning the self-image (97.3%) was higher than that concerning the other image (94.0%) on the upside-down image condition when the participant group was women, but no such significant difference was noted when the participant group was composed of men.

TABLE 1 | Mean accuracy % (standard deviation) in the laterality judgment (top) and self-other discrimination (bottom) tasks (0°: upright, 180°: upside-down).

	Self				Other			
	Left		Right		Left		Right	
	0°	180°	0°	180°	0°	180°	0°	180°
Laterality judgment task								
Men	98.7 (2.8)	96.0 (4.9)	96.0 (5.5)	92.4 (9.0)	98.0 (3.0)	96.2 (6.4)	96.0 (6.2)	92.4 (7.6)
Women	98.7 (3.7)	97.8 (4.1)	97.3 (5.5)	96.9 (5.0)	97.3 (4.4)	94.9 (6.0)	98.0 (3.7)	93.1 (7.8)
Self-other discrimination task								
Men	96.0 (8.7)	98.2 (3.1)	98.2 (4.0)	99.1 (2.3)	99.1 (2.0)	98.9 (2.4)	99.3 (1.4)	99.3 (1.9)
Women	96.4 (4.3)	99.1 (3.4)	98.7 (3.7)	96.9 (7.1)	99.1 (2.0)	98.4 (3.5)	98.0 (3.3)	96.4 (1.9)

Self-Other Discrimination Task

No significant main effects on factors and no interactions were noted ($p > 0.071$).

Reaction Times

Laterality Judgment Task

A significant main effect of visual perspective [$F(1, 28) = 53.792$, $p < 0.001$, partial $\eta^2 = 0.658$] and a significant interaction between hand image laterality and visual perspective [$F(1, 28) = 4.809$, $p = 0.037$, partial $\eta^2 = 0.147$] were noted (**Figure 2**). The results indicate that RTs for the upright image were shorter than those for the upside-down image, regardless of the hand laterality (1,037 vs. 1,273 ms, when a left hand image was presented; 985 vs. 1,288 ms, when a right hand image was presented). It is noteworthy that shorter RTs for the self-hand image, which were observed in previous studies (e.g., Ferri et al., 2011), were not revealed in the present experiment.

Self-Other Discrimination Task

We found a significant main effect of ownership [$F(1, 28) = 7.557$, $p = 0.010$, partial $\eta^2 = 0.213$], a significant interaction between sex and visual perspective [$F(1, 28) = 4.292$, $p = 0.048$, partial $\eta^2 = 0.133$] and a significant second-order interaction among sex, ownership, and visual perspective [$F(1, 28) = 7.491$, $p = 0.011$, partial $\eta^2 = 0.211$]. A *post-hoc* comparison revealed that RTs for the other hand image (876 ms) were shorter than those for the self-hand image (1,000 ms) on the upside-down image condition when the participant group was women, but no such significant difference was noted when the participant group was composed of men (**Figure 2**).

Dprime

Laterality Judgment Task

We found significant main effects of ownership [$F(1, 28) = 10.798$, $p = 0.003$, partial $\eta^2 = 0.278$], visual perspective [$F(1, 28) = 6.774$,

FIGURE 2 | Reaction times (RTs) in the laterality judgment and self-other discrimination tasks. While no significant difference between the self and other conditions was noted in the laterality judgment task, RTs for the other hand image were significantly shorter than those for the self-hand image when the upside-down image was presented in the self-other discrimination task (see the text for detailed results). A black-lined square and diamond in each condition indicate mean values for women and men, respectively.

$p = 0.015$, partial $\eta^2 = 0.195$], and a significant interaction between ownership and visual perspective [$F(1, 28) = 4.475$, $p = 0.043$, partial $\eta^2 = 0.138$]. A *post-hoc* comparison revealed that dprime for the other hand image (3.82) was greater than that for the self-hand image (3.43) when an upright hand image was presented.

Self-Other Discrimination Task

A significant interaction between sex and hand laterality was noted [$F(1, 28) = 6.164$, $p = 0.019$, partial $\eta^2 = 0.180$], but a *post-hoc* comparison revealed that no significant differences were found.

ln(β)

Laterality Judgment Task

No significant main effects on factors and no interactions were noted ($p > 0.087$).

Self-Other Discrimination Task

No significant main effects on factors and no interactions were noted ($p > 0.122$).

Questionnaires

Participants' AQ scores ranged from 6 to 34, with a mean AQ score of 19.4 (SD = 6.3), and no significant difference between the men's and women's groups was noted [$t(28) = 0.369$, $p = 0.715$]. The BAS-2 scores ranged from 1.5 to 4.3, with a mean BAS-2 score of 2.9 (SD = 0.8), and no significant difference between the men's and women's groups was noted [$t(28) = -0.824$, $p = 0.417$].

No significant correlation between AQ scores and BAS-2 was found in either the men's group ($p = 0.430$) or the women's group ($p = 0.409$).

Correlation Coefficients Involved With AQ Scores

Laterality Judgment Task

A significant correlation between total AQ scores and RTs was found in the men's group ($\tau = 0.444$, $p = 0.022$), indicating an increase in RTs in tandem with higher AQ scores (**Figure 3**, top left).

As for the women's group, the difference in RTs between the self and other conditions (i.e., RTs in the other condition – RTs in the self condition) correlated significantly and negatively with total AQ scores ($\tau = -0.586$, $p = 0.003$; **Figure 3**, bottom right). This result indicates that the lower AQ participants showed a quicker response to the self-image, in comparison with the other image, while the response pattern of the (relatively) higher AQ participants to the self-image was similar to that of the other image, or was reversed (i.e., there was a quicker response to the other image).

Self-Other Discrimination Task

No significant correlations between total AQ scores and each parameter of task performance were found in either the men's or the women's groups ($p > 0.206$).

Correlation Coefficients Involved With BAS-2 Scores

Laterality Judgment Task

Total BAS-2 scores were not significantly correlated with any parameters of task performance in either the men's or the women's groups ($p > 0.110$).

Self-Other Discrimination Task

In the men's group, the total BAS-2 scores were not significantly correlated with any parameters of task performance ($p > 0.273$).

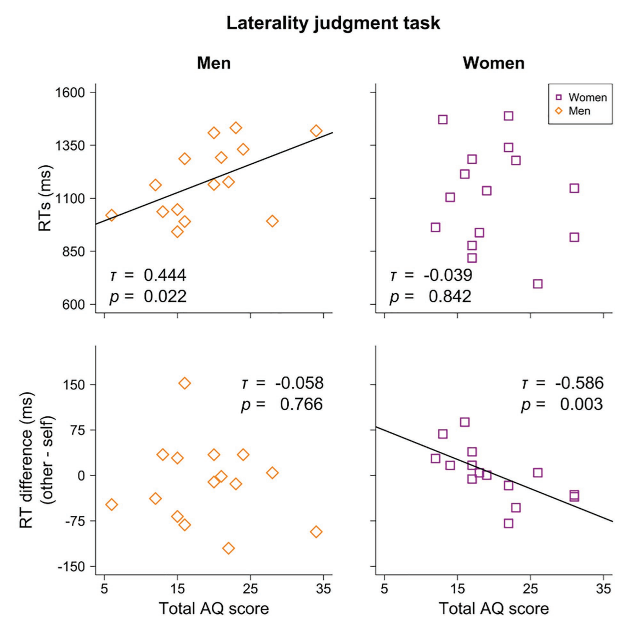

FIGURE 3 | Correlations between Autism Spectrum Quotient (AQ) scores and RTs and between AQ scores and the difference in RTs (other – self) in the laterality judgment task. A significant positive correlation between AQ scores and RTs was noted in the men's group, while a significant negative correlation between AQ scores and the difference in RTs was noted in the women's group.

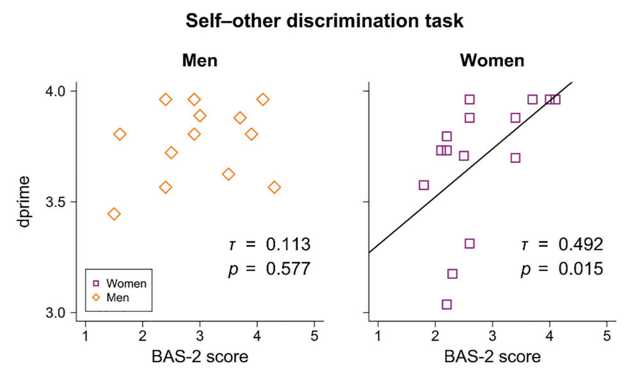

FIGURE 4 | Correlations between Body Appreciation Scale-2 (BAS-2) scores and dprime in the self-other discrimination task. A significant positive correlation between BAS-2 scores and dprime was noted only in the women's group.

In the women's group, the correlation between BAS-2 and dprime was also significant ($\tau = 0.492$, $p = 0.015$), indicating an increase in dprime according to higher BAS-2 scores (**Figure 4**).

DISCUSSION

The present study explored whether and how the extent of participants' autistic traits and body appreciation affect the performance of implicit and explicit hand recognition tasks in a TD population, divided by sex (cf. Mochizuki et al., 2019; Conson et al., 2020). In addition, we investigated whether the results of visual recognition tasks (i.e., laterality judgment and self-other discrimination tasks) in previous studies (e.g., Ferri et al., 2011; Conson et al., 2015) would be replicated, even if the number of orientation conditions of the hand image was limited to two (i.e., upright and upside-down).

Concerning the self-advantage in the laterality judgment task, previous studies (Ferri et al., 2011; Frassinetti et al., 2011; Conson et al., 2015) suggested that this task requires motor simulation based on implicit sensorimotor knowledge about the body's parts (in this case, the hands), including a combined visuo-sensorimotor strategy (cf. Brady et al., 2011; Ní Choisdealbha et al., 2011). The present task, in which the orientation had just two conditions (i.e., 0 and 180°), did not show this self-advantage. This result suggests that having only two orientation conditions is not enough to trigger this motor simulation (cf. ter Horst et al., 2010). This is consistent with the argument made by Conson et al. (2015), that implicit self-advantage is enhanced by a high "sensorimotor load."

Concerning the results of the self-other discrimination (explicit) task, we found shorter RTs in the other condition than in the self-condition, findings that are in agreement with previous studies (e.g., Ferri et al., 2011; Conson et al., 2015). Conson et al. (2010) performed a highly similar task in a sample of right-handed men and showed an interaction among hand ownership, hand image laterality, and visual perspective, such as significantly faster RTs in recognizing others' left hands than in recognizing others' right hands, from an allocentric perspective (for right-handed male participants). Our results did not replicate those of Conson et al. (2010), which showed a tight association between self-other discrimination and egocentric/allocentric views. Regarding the women's group, we found significantly shorter RTs for the other hand image (876 ms), compared to the self-hand image (999 ms) when the upside-down image was presented (i.e., the image was presented in an allocentric manner), resulting from the lengthened RTs for the upside-down self-image. The explicit task requires a mere visual representation of one's own body (Frassinetti et al., 2011; Conson et al., 2015); therefore, this result was caused by women's inferior performance in visual mental rotation (Linn and Petersen, 1985; Voyer et al., 1995; Collins and Kimura, 1997), in addition to visual unfamiliarity with self-image from an allocentric view. Concerning the women's strategy in the hand laterality judgment task, Conson et al. (2020) recently investigated these using images of the backs and palms of hands. It is said that hand images viewed from the back often induce a visual strategy, while images viewed from the palm induce a motor strategy in the classical hand laterality task (Sekiyama, 1982; Parsons, 1987, 1994; Gentilucci et al., 1998; ter Horst et al., 2010; Bläsing et al., 2013; Zapparoli et al., 2014; Conson et al., 2020). Based on this assumption, Conson et al. (2020) argued that women would best represent an image viewed from the back as a self-hand and mainly adopt this visual strategy, while men best represented an image viewed from the palm as their own hand and mainly adopted the motor strategy.

We further investigated how individual traits (such as autistic traits and the extent of positive body image) would relate to performance in the laterality judgment (implicit) and self-other discrimination (explicit) task in the men's and women's groups. A significant relationship to the AQ score was revealed only in the laterality judgment task (not in the self-other discrimination task). Specifically, longer RTs aligned with a higher AQ score were shown in the men's group but not in the women's group. Although, to our knowledge, there have been no previous studies investigating the variation in RTs according to AQ scores in the laterality judgment task, some studies investigating the task performance of individuals with ASD, in comparison with TD peers, have been conducted. Conson et al. (2016) found that, in a hand laterality judgment task when presenting hand photographs of the backs and palms in four different orientations (i.e., 0, 90, 180, and 270°), individuals with ASD [18 participants (1 woman); mean (± SD) age = 14.6 ± 4.2; age range = 10–20] showed significantly longer RTs in comparison with TD peers, although Conson et al. (2013) showed that the RTs of individuals with Asperger syndrome [24 participants (3 women); mean (± SD) age = 13.4 ± 1.3; age range = 12–16] did not significantly differ from those of TD peers in the task using line-drawn 2D hand images. Furthermore, Chen et al. (2018) found that individuals with ASD [22 participants (2 women); mean (± SD) age = 13.47 ± 1.24; age range = 11–15] demonstrated significantly longer RTs in comparison with TD peers when performing the hand laterality judgment task while manipulating the angle combination (of 3D hand-arm image) within the frontal, sagittal, and transverse planes. The ratio of men in the samples of each of the above-mentioned ASD studies is greater than 87.5%, so the results of these studies reflect men's task properties in hand laterality judgment. Of course, we must be cautious of the qualitative difference between an ASD diagnosis itself and a higher AQ score over the cutoff value; the current results, showing that longer RTs align with higher AQ scores in the men's group, are not inconsistent with the results of these ASD studies.

Furthermore, the present study revealed in the laterality judgment task that the difference in RTs between the self and other conditions (other – self) are related to the AQ score only in the women's group, indicating that women participants with (relatively) lower AQ scores react faster to a self-image than to the other's image in the laterality judgment task, while women participants with (relatively) higher AQ scores show a reverse pattern. This result implies that, even in the present experiment with only two orientation conditions, and where it is assumed that a high sensorimotor load is not necessary for performance, the self-advantage could emerge in women who have (relatively) lower AQ scores. According to the "absent-self" hypothesis in ASD (Frith and Happé, 1999; Baron-Cohen, 2005; Frith and de Vignemont, 2005; Lombardo and Baron-Cohen, 2010; Lombardo et al., 2010), atypical self-awareness (for example, reduced distinction between the self and others) was observed in ASD. Such tendencies might (at least, partially) support the reverse pattern (i.e., self-disadvantage) in the women participants who show higher AQ scores. Why only the women's group exhibited this relationship between the extent of self-(dis)advantage and autistic traits remains unclear. It could be influenced by the difference of the AQ distribution between men and women (for nonclinical populations; Ruzich et al., 2015), but this is unproven. Therefore, how visuospatial and motor abilities in each sex are modulated by autistic traits will need to be clarified in future studies.

Concerning the relationship to the BAS-2 score, an increase in dprime according to a higher BAS-2 score was found in the women's group, but not in the men's group, when performing the self-other discrimination task. This indicates that women who have greater body appreciation (i.e., higher BAS-2 scores) could better discriminate between themselves and others, suggesting that, for women, a more positive attitude toward their own body would lead to a better sensitivity to the body parts (in this case, the hands) when explicitly discriminating a self-image from an other's image. Although the BAS-2 is applicable to both men and women, the significant relationship between RTs and BAS-2 scores only emerged in the women's group. This implies that BAS-2 scores for each sex could reflect different contents. Indeed, BAS-2 scores could be related to eating disorder symptomatology for women, while the incremental variance in eating disorder symptomatology by BAS-2 scores did not reach significance for men (Tylka and Wood-Barcalow, 2015). In the future, these visual hand recognition tasks must be investigated in persons suffering from eating disorders. In fact, Campione et al. (2017) have already applied these visual hand tasks to eating disorder outpatient, but they did not report the results of the relationship between task performance and body image in the self-other discrimination task.

In summary, the men's group showed a significant positive correlation between AQ scores and RTs in the laterality judgment task, while the women's group showed a significant negative correlation between AQ scores and differences in RTs and a significant positive correlation between BAS-2 scores and dprime in the self-other discrimination task. These results suggest that men and women differentially adopt specific strategies (visual or motor simulation) and/or execution processes for implicit and explicit self-other discrimination of the hand, according to the different influences of autistic traits and the body appreciation on the visual recognition of body parts. The relatively small sample size of the current study is a limitation, therefore, a larger sample size is needed to clarify the detailed properties of hand recognition in a future study. The present finding of implicit and explicit self-other discrimination modulated by individual traits shaped by their cognitive and sensory-motor abilities provide deeper insight into how the self is shaped over the life-time.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Tokyo Metropolitan University Hino Campus. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

MK and TF conceived and designed the experiments, analyzed the data, and wrote the manuscript. MK performed the experiment. TF contributed reagents, materials and analysis tools. All authors contributed to the article and approved the submitted version.

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Interoceptive Awareness Is Negatively Related to the Exteroceptive Manipulation of Bodily Self-Location

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The perception of being located within one's body (i.e., bodily self-location) is an essential feature of everyday self-experience. However, by manipulating exteroceptive input, healthy participants can easily be induced to perceive themselves as being spatially dislocated from their physical bodies. It has previously been suggested that interoception, i.e., the processing of inner physiological signals, contributes to the stability of body representations; however, this relationship has not previously been tested for different dimensions of interoception and bodily self-location. In the present study, using an advanced automatized setup, we systematically manipulated participants' perspective of their own body (first- vs third-person perspective) as well as the synchrony of visuotactile stimulation (synchronous vs asynchronous). The malleability of bodily self-location was assessed using a questionnaire targeting in-body and out-of-body experiences. Participants also performed a heartbeat discrimination task to assess their interoceptive accuracy (behavioral performance), interoceptive sensibility (confidence in their interoceptive abilities), and interoceptive awareness (meta-cognitive representation of interoceptive signals). Bodily self-location was significantly influenced by perspective, with third-person perspective being associated with stronger out-of-body experiences compared to first-person perspective. Furthermore, there was a significant perspective × stimulation interaction, with subsequent analyses showing that participants reported out-of-body experiences particularly under third-person perspective combined with synchronous visuotactile stimulation. Correlation and regression analyses revealed that meta-cognitive interoceptive awareness was specifically and negatively related to the exteroceptively mediated malleability of body experiences. These results indicate that the perception of the self being located within one's body relies on the interaction of exteroceptive input and higher-order interoceptive abilities. This has implications for theoretical considerations about the bodily self in health as well as for the understanding of disturbed bodily self-processing in clinical contexts.

Keywords: dissociation, heartbeat, illusion, interoception, multimodal stimulation, out-of-body experience

INTRODUCTION

The perception of being located within one's body, i.e., bodily self-location, is an essential feature of bodily self-consciousness (Blanke and Metzinger, 2009), describing the perception of oneself as an embodied agent with a first-person perspective. The processes that underlie bodily self-location are anything but trivial. At any given time, a variety of sensory signals have to be processed simultaneously and integrated into a corresponding percept, resulting in the experience of the self being located within the borders of the body. These processes appear to be abnormal under certain clinical and non-clinical conditions. For example, mental pathologies such as dissociative disorders, post-traumatic stress disorder, or borderline personality disorder are accompanied by strong dissociative experiences (Lyssenko et al., 2018), which can involve aberrant bodily self-location (e.g., Stiglmayr et al., 2003). Interestingly, 5% of the general population also report having such experiences at least once in their lifetimes (Ohayon, 2000), indicating that this unusual mode of locating the self in respect to the body is somehow part of the common repertoire of human perception.

Remarkably, the perceptual processes underlying bodily self-location can be easily manipulated by the application of unusual multimodal exteroceptive input (Ehrsson, 2007). In this kind of experiment, the participant wears a head-mounted display transmitting a streaming video signal recorded by a camera placed behind the subject. Thus, this setup creates the visual impression that the subject is directly watching his or her own back, from a third-person's perspective. If the subject's real chest and the space under the camera (i.e., the "chest" of the illusory body) are now touched synchronously in a sweeping motion, participants report the sensation of being spatially dislocated from their own body (Ehrsson, 2007). Since this unusual visuotactile condition is sufficient to elicit so-called out-of-body experiences, bodily self-location has been proposed to be fully mediated by exteroceptive input.

However, interoception, defined as the processing of inner physiological signals, represents another important source for an individual's body representation. Interoception has been linked to a variety of psychological functions, such as emotion processing (e.g., Craig, 2004), social cognition (e.g., Ferri et al., 2013), or self-awareness (e.g., Ainley et al., 2012). In experimental setups, interoception is generally assessed by accuracy in identifying one's own cardiac activity, be it by a task to mentally track one's heartbeats (Schandry, 1981) or to discriminate whether a train of acoustic stimuli is synchronous or asynchronous with respect to one's true heartbeats (Whitehead et al., 1977). Trait interoceptive accuracy, measured by individual performance in a heartbeat-tracking task, has been inversely linked to proneness to the rubber hand illusion (Tsakiris et al., 2011; see also Suzuki et al., 2013), which is a setup for the induction of illusory body-part ownership, by the application of synchronous visuotactile stimulation to one's own hidden hand and a visible rubber hand (Botvinick and Cohen, 1998). This finding has been interpreted as indicating that the stability of one's body representation is—at least partly—interoceptively mediated, such that good interoceptive abilities are associated with less proneness of body experience to be influenced by unusual exteroceptive input. Since the experimental induction of both the rubber hand illusion and out-of-body experiences appears to rely on similar capabilities for sensory integration (Olivé and Berthoz, 2012), a relationship between interoceptive abilities and more global bodily self-location is likely.

Recent studies have identified several distinct interoceptive dimensions (Garfinkel and Critchley, 2013), each characterized by different mental processes. While *interoceptive accuracy* refers to objective performance in tests of interoception, *interoceptive sensibility* describes a dispositional tendency for subjective beliefs about one's own interoceptive abilities, and *interoceptive awareness* characterizes the metacognitive representation of one's own interoceptive abilities, which can be assessed by applying signal detection theory using both interoceptive accuracy and sensibility measures. The validity of these measures has been recently demonstrated empirically (Garfinkel et al., 2015; Forkmann et al., 2016), indicating that they reflect relatively distinct dimensions of interoception. For example, there is evidence that the higher-order dimension of interoceptive awareness is a particular indicator of interoceptive abilities across organ-specific axes, such as cardiac and respiratory modalities (Garfinkel et al., 2016a). Thus, it is likely that relating these different measures of interoception to bodily self-location might reveal new insights into the underlying mechanisms.

In the present study, we implemented an advanced setup for the experimental manipulation of bodily self-location as well as a heartbeat discrimination task in a sample of healthy participants. In addition to the induction of out-of-body experiences by third-person perspective (3PP) that have been previously explored (Ehrsson, 2007), we introduced a novel condition in which participants were induced to perceive the scene from a first-person perspective (1PP), eliciting "normal" but still illusory in-body experiences that do not affect the location of the self in respect to the body. Our main hypotheses were that (a) synchronous visuotactile stimulation in 3PP compared to 1PP would induce distortions of bodily self-location and that (b) lower interoceptive abilities, in particular lower metacognitive interoceptive awareness, would be associated with more malleable bodily self-location.

MATERIALS AND METHODS

Participants

There were 54 participants (42 females). Since it has been shown that accuracy in heartbeat discrimination is inversely linked to age (Khalsa et al., 2009), we checked our sample for extreme values (>3 times the interquartile range) and removed three subjects from the analysis. Body mass index (BMI) has also been found to be negatively related to interoceptive abilities (Herbert and Pollatos, 2014); however, taking into account five missing values for this measure (based on participants' self-reports), no extreme values were observed. The final sample (n = 51; 40 females) had an age of M = 20.18 years (SD = 1.60) and a BMI of M = 22.94 (SD = 4.13). All except two participants declared themselves right-handed. No participant reported a history of psychiatric or neurological disorders, cardiovascular problems, chronic somatic or mental disorders, or chronic pain. All participants had normal or corrected-to-normal vision. Since the head-mounted display used in the present study (see below) was not compatible with conventional glasses, we only included contact lens users or participants whose uncorrected eyesight fell into the range for which the head-mounted display could adapt (i.e., −5 to +2 dpt). All participants gave written informed consent before participating. The study was approved by the ethics review board of Royal Holloway, London University, and adhered to the Helsinki Declaration of 1975, as revised in 2008.

Setup for the Experiment Manipulating Bodily Self-Location

The setup for illusion induction was adapted from earlier work (Ehrsson, 2007). In our study, the participant was seated in a chair in the middle of a sparsely equipped room (about 3.5 × 4 m), wearing a head-mounted display (Cinemizer OLED 3D Multimedia Glasses, Carl Zeiss AG, Oberkochen, Germany). The head-mounted display received output from a video camera (Full HD Camcorder HC-X810, Panasonic Corporation, Kadoma, Japan), equipped with a 3D additional lens (VW-CLT2, Panasonic Corporation, Kadoma, Japan), which was mounted on a tripod at the eye level of the seated participant. The tripod was located 120 cm behind the participant so that—when in the active mode—the participant could see his or her own upper back, shoulders, and back of the head. The second tripod equipped with a stepper motor and brush (i.e., the visual brush) was placed in front of the camera, at a distance of 20 cm from the 3D lens. The level of the tripod was adjusted until one third of the brush's bristles was in view of the camera. The whole setup was placed such that the walls in front of, and behind, the participants were at a distance of 120 cm (with reference to the participant's chair and the video camera, respectively). We attached a fixation cross to the front wall at eye level. The first tripod (with the tactile brush) was placed in such a way that the brush was able to apply tactile stimulation to the participant's upper chest. The angle and position of the tactile brush was individualized for each participant, and the use of soft bristle brushes minimized friction. In order to ensure a similar surface of stimulation across individuals, we applied a skin-compatible, adhesive, thin film (Suprasorb F, Lohmann & Rauscher, Rengsdorf, Austria) to the area of stimulation. Piloting showed that the tactile sensation was not affected by this film.

In contrast to the original setup (Ehrsson, 2007) in which tactile stimulation was applied manually, tactile stimulation in the present study was applied using two stepper motors, each equipped with a soft brush, thus minimizing social interaction between the participant and the experimenter and maximizing standardization. Both stepper motors were attached to a swivel arm, each of which was in turn attached to a tripod. A control unit equipped with Arduino micro-controllers controlled both motors independently, enabling us to implement two conditions of the factor stimulation: (a) both stepper motors moved synchronously (sync condition), performing a back-and-forth movement by about 45°, or (b) both stepper motors moved asynchronously (async condition), i.e., such that as one brush moved, the other was inactive. In both modes, the brushes moved with a frequency of about 0.5 Hz. The setup is shown in **Figure 1A**, with the participant's view illustrated in **Figure 1B**.

By using this setup, we were able to implement two conditions of the factor perspective, operationalizing either the condition 3PP (as used by Ehrsson, 2007, and described above) or 1PP, during which the setup differed in the single but important point that we placed a white screen between the participant's chair and the visual brush, at a distance of 55 cm from the 3D objective and thus behind the participant (**Figure 1C**). In the two 1PP conditions (sync and async), we attached a fixation cross to the screen, whose size was adjusted to resemble the size of the fixation cross that is visible on the wall in the 3PP conditions. In other words, the visual scene in the two 1PP conditions was identical to that observable by the seated participants in the two 3PP conditions, before they put on the head-mounted display (**Figure 1D**). Thus, we implemented a full-factorial 2 (perspective, 1PP vs 3PP) × 2 (stimulation, sync vs async) experimental design, with the four conditions $1PP_{sync}$, $1PP_{async}$, $3PP_{sync}$, and $3PP_{async}$ presented in a randomized order.

Procedure

The participants were briefly given an overview of the experimental procedure before they were asked to sign the consent form. They were then seated in the chair and equipped with the adhesive film and the head-mounted display. The participants were asked to sit in a relaxed and still position during the experiment. They were told to keep their eyes closed until the experimenter verbally requested them to open their eyes.

The sequence of events for each of the four stimulation blocks (i.e., the four experimental conditions, see above) was identical. First, the experimenter switched on the stepper motors and adjusted the brushes. Then he switched on the head-mounted display and asked the participant to open their eyes. During stimulation with the brushes, the participant was asked to observe the back of their head (in 3PP conditions) or the fixation cross at an identical position (in 1PP conditions; see **Figure 1**). After 90 s, the experimenter asked the participants to close their eyes, after which he switched off the stepper motors and removed the head-mounted display.

The participant then completed a questionnaire, starting with control items asking whether the participant had seen their body or a white wall during the last stimulation block and whether the stimulation applied had been synchronous or asynchronous. Participants were 100% correct in stating whether they had observed themselves or the "wall" (i.e., the screen). In all but four trials, participants correctly identified the stimulation as having been synchronous or asynchronous (i.e., 98.04% correct). Other items of the questionnaire were presented in randomized order and asked for "normal" (i.e., locating the self within the body) and aberrant (i.e., locating the self outside the body) body experiences during the trial, in terms of in-body and out-of-body experiences, respectively. Out-of-body experiences were assessed with two items, i.e., item #1 "I felt as if I was located outside my physical body" and item #2 "It felt as if I was sitting behind myself." In-body experiences were assessed with two other items, i.e., item #3

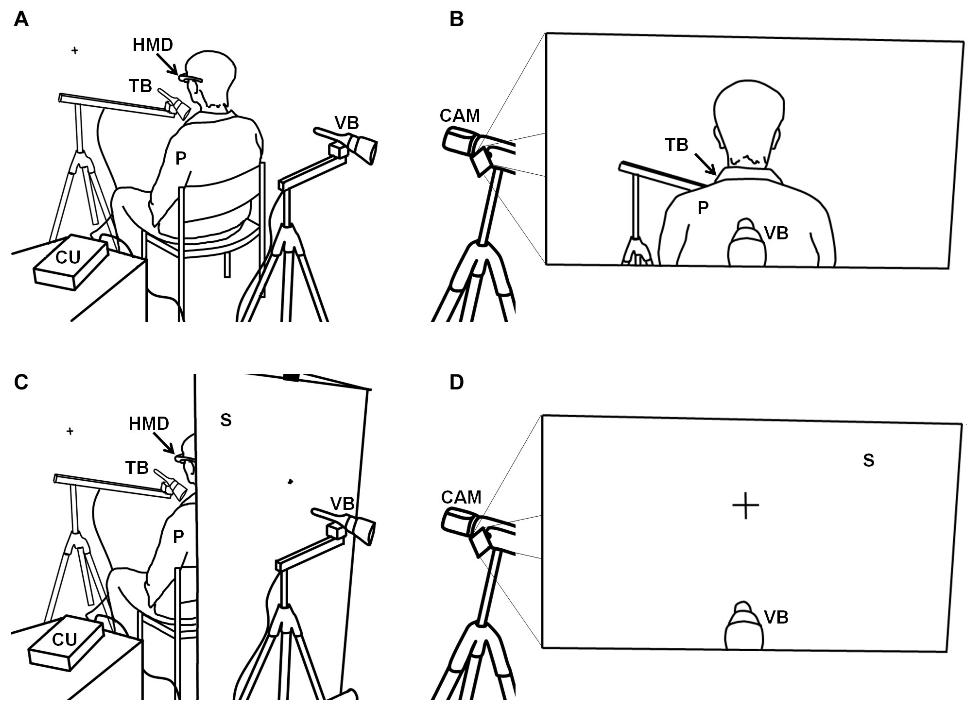

FIGURE 1 | Illustration of the setup for the bodily self-location experiment. **(A)** The setup for the third-person perspective conditions with **(B)** the visual output received by the head-mounted display and perceived by the participant. **(C)** Setup for the first-person perspective conditions with **(D)** the visual output received by the head-mounted display and seen by the participant. P, participant; HMD, head-mounted display; TB, tactile brush; VB, visual brush; CAM, video camera; CU, control unit; S, screen.

"I felt as if my body belonged to me" and item #4 "I felt as if I was connected to my body." Finally, in order to obtain a measure of the general vividness of the induced illusionary experiences, we included two further items, i.e., item #5 "I felt as if the scene I observed was directly in front of me" and item #6 "It seemed as if the touch I felt was caused by the brush I saw." All items were designed to obtain valid responses in both the 3PP and the 1PP conditions and were tested in a pilot study (unpublished data). Responses were measured with a visual analog scale, ranging from 0 (*not at all*) to 100 (*very strong*). After the four randomly presented stimulation blocks, the interoceptive discrimination task was administered, as described below.

Interoceptive Discrimination Task

Participants were equipped with three electrocardiography electrodes (ADInstruments PowerLab 8/35 and Bio Amp 132)[1] placed in a modified lead II chest configuration: two electrodes were positioned underneath the left and right collarbones and another one on the participant's lower back on the left side. The signal was recorded with a sampling rate of 1,000 Hz, and a hardware band-pass filter between 0.3 and 1,000 Hz was applied. Participants then performed the interoceptive discrimination task (Whitehead et al., 1977): on each trial, the subjects heard 10 sounds, each set of which was either synchronous with their own heartbeat (200 ms after the R-peak) or asynchronous (500 ms after the R-peak; Kleckner et al., 2015). There were 20 synchronous and 20 asynchronous trials, in randomized order. Subjects had to indicate on each trial whether the external sounds were synchronous or asynchronous with their own heartbeat. They also had to rate the confidence in their decision on each trial using a visual analog scale ranging from 0 (*not confident*) to 100 (*confident*). Participants were asked to sit relaxed with their hands on their thighs and their legs uncrossed. They could freely choose whether they preferred to do the task with their eyes open or closed. Due to artifacts (visual inspection), we removed a total of 21 trials (i.e., 1.03% of all trials).

Data Analysis

Ratings of Body Experiences and Its Malleability by Exteroceptive Input (Exteroception Index)

Ratings of In-Body and Out-of-Body Experiences

Intensity of out-of-body experiences (i.e., locating the self outside the body) was calculated as the mean of questionnaire items #1 and #2, and intensity of in-body experiences (i.e., locating the self within the body) was defined as the mean of items #3 and #4. In-body and out-of-body experiences were separately analyzed with analyses of variance (ANOVAs) for repeated measures, with the two factors *perspective* (1PP vs 3PP) and *stimulation* (sync vs async). For all ANOVAs, we report test statistics, *p*-values, and effect size (partial η^2). Whenever an interaction effect was significant, we further applied *post hoc* paired-sample *t*-tests for which we also report effect sizes (Cohen's *d*). In these, as well as

[1] http://www.adinstruments.com/

all other analyses reported below, the tests were performed two-tailed. The two types of body experiences were also checked for intercorrelation using Spearman correlations. These, and all the analyses described below, were performed with IBM SPSS v26.

Exteroception Index

For each condition, we subtracted the ratings of out-of-body experiences (the mean of items #1 and #2) from the ratings of in-body experiences (mean of items #3 and #4), such that positive values indicate net co-location of the body and the self and negative values indicate net dislocation of the body and the self (see **Table 1**). This procedure is based on a pilot study revealing a significant negative relationship between both measures (unpublished data), suggesting content validity. The resulting scores—representing bodily self-location for each condition on the continuum *self located outside the body* and *self located inside the body*—were used in the following formula, to create an *exteroception index* (potential range: −100 to +100), representing the extent to which bodily self-location is malleable by the manipulation of exteroceptive input:

$$\frac{1}{4}\left[\left(1PP_{sync} - 1PP_{async}\right) - \left(3PP_{sync} - 3PP_{async}\right)\right]$$

The advantage of this index is that it uses all four of our conditions to represent a measure of the extent to which an individual is using both *perspective* and *stimulation* as sources of information with which to establish/maintain bodily self-location. The operative word here is "both," since high values can only be achieved if both the type of perspective and the type of stimulation influence the location of the self in respect to the body. Hypothetically, an exteroception index of +100 would indicate maximum malleable bodily self-location by consistent exteroceptive input, in terms of strong in-body experiences when in $1PP_{sync}$ and strong out-of-body experiences when in $3PP_{sync}$. Asynchronous visuotactile input, on the other hand, would reverse this response. Such a hypothetical participant's body experience would thus adjust completely to consistent exteroceptive input. By contrast, an exteroception index of 0 would indicate that exteroceptive input has no effects on bodily self-location or that this hypothetical participant's body experience is relying solely on one exteroceptive source (either *perspective* or *stimulation*). An exteroception index of −100 would not only indicate that the participant's bodily self-location does not comply at all with consistent exteroceptive input but that there is some kind of psychological resistance to conflicting exteroceptive input, resulting in strong co-location of the body and the self under $1PP_{async}$ and strong dislocation of the body and the self under $3PP_{async}$ conditions.

The exteroception index was tested against 0 using a one-sample t-test to check whether, on average, bodily self-location was experimentally manipulated by exteroceptive input.

Vividness of Body Experiences

Vividness of body experiences has generally been included in previous calculations of illusion scores in experiments on body perception (e.g., Botvinick and Cohen, 1998; Ehrsson, 2007). Calculating this as the mean of questionnaire items #5 and #6, we entered this measure in an ANOVA, similarly as for the body experience scores. The purpose was a manipulation check for whether the vividness of induced illusory experiences would differ as a result of visuotactile stimulation (i.e., with expected higher vividness in the sync compared to the async conditions), but not as a function of perspective alone (i.e., 1PP vs 3PP).

Interoceptive Measures

For analyzing the three different dimensions of interoception, i.e., interoceptive accuracy, interoceptive sensibility, and interoceptive awareness, we followed the procedure described by Garfinkel et al. (2015). First, we calculated the relative number of correct heartbeat discrimination trials, i.e., interoceptive accuracy, resulting in an individual value potentially ranging from 0 (*no correct responses*) to 1 (*all responses were correct*). Second, interoceptive sensibility was defined as mean confidence in one's own interoceptive performance, which was divided by 100 in order to make this measure comparable to the others [i.e., 0 (*very unconfident*) to 1 (*very confident*)]. Third, for determining interoceptive awareness, we again performed analyses in accordance with Garfinkel et al. (2015): we applied receiver operating characteristic (ROC) curve analysis (Green and Swets, 1966), quantifying the extent to which confidence in interoception predicts interoceptive accuracy. The area under the ROC curve thus gives a measure for the association between confidence and performance, by plotting the hit rate (performance is correct *and* the participant is highly confident in his or her performance) against the false alarm rate (performance is *in*correct while the participant's confidence is still high). Since this method accounts for the individual bias in reporting high or low confidence, this measure represents a valid indicator of metacognitive awareness for interoceptive processes (Garfinkel and Critchley, 2013; Garfinkel et al., 2015).

For each of these measures, we applied a one-sample t-test with the test value 0.5 to test the hypothesis that the group as

TABLE 1 | Mean (*M*) values and standard deviations (*SD*) for in-body experiences, out-of-body experiences, and net body experiences, the net body experience, and the latter of which represent the in-body minus out-of-body experiences, per condition.

Condition	In-body experiences *M* (*SD*)	Out-of-body experiences *M* (*SD*)	Net body experience *M* (*SD*)
$1PP_{sync}$	83.05 (15.63)	12.31 (13.63)	70.74 (26.30)
$1PP_{async}$	77.64 (20.93)	16.36 (20.68)	61.27 (37.12)
$3PP_{sync}$	59.85 (22.74)	65.20 (24.81)	–5.34 (42.64)
$3PP_{async}$	59.76 (24.35)	56.12 (26.37)	3.65 (44.36)

1PP, first-person perspective; 3PP, third-person perspective; sync, synchronous visuotactile stimulation; async, asynchronous visuotactile stimulation.

a whole performed above chance (interoceptive accuracy and awareness) or had above 50% confidence in their interoceptive abilities (interoceptive sensibility), respectively.

Association Between Bodily Self-Location and Interoceptive Dimensions

Across the total sample, we correlated the exteroception index with the interoceptive measures by applying two-tailed Pearson correlations. Furthermore, we used multiple linear regression to better evaluate our results. Interoceptive measures, i.e., interoceptive accuracy, interoceptive sensibility, and interoceptive awareness, were entered (simultaneous entry). The ANOVA testing for significance of explained variance (R^2) is reported, as well as the adjusted R^2. For each regressor, the unstandardized coefficient *B* and its standard error *SE* are reported, along with the standardized regression coefficient β and the respective *p*-value.

Since out-of-body experiences were particularly affected by perspective and stimulation (see section "Body Experience Ratings and the Exteroception Index" below), the analyses described above were repeated for the effect between $3PP_{sync}$ and $3PP_{async}$ conditions.

RESULTS

Body Experience Ratings and the Exteroception Index

Descriptive statistics for the in-body and out-of-body experiences are provided in **Table 1** (mean values for each item are further shown in **Supplementary Figures 1A,B** in the **Supplementary Material**). We performed a 2 × 2 ANOVA for repeated measurements, entering the two factors *perspective* (1PP vs 3PP) and *stimulation* (sync vs async). For in-body experiences, we found a significant main effect of the factor *perspective* ($F_{1,50}$ = 38.95, $p < 0.001$, and $\eta^2 = 0.44$), but not for the factor *stimulation* ($F_{1,50}$ = 1.35, $p = 0.25$, and $\eta^2 = 0.03$). There was no interaction ($F_{1,50}$ = 2.39, $p = 0.13$, and $\eta^2 = 0.05$). For out-of-body experiences, there was a significant main effect for the factor *perspective* ($F_{1,50}$ = 172.41, $p < 0.001$, and $\eta^2 = 0.78$), but not for *stimulation* ($F_{1,50}$ = 1.17, $p = 0.28$, and $\eta^2 = 0.02$). However, there was a significant interaction ($F_{1,50}$ = 9.02, $p = 0.004$, and $\eta^2 = 0.15$), which was caused by significantly stronger out-of-body experiences in the $3PP_{sync}$ condition compared to the $3PP_{async}$ condition ($t_{50} = 2.53$, $p = 0.01$, and $d = 0.35$); there were no significant differences in the $1PP_{sync}$ condition compared to the $1PP_{async}$ condition ($t_{50} = -1.48$, $p = 0.14$, and $d = 0.23$).

There were highly significant, negative correlations between in-body and out-of-body experiences (r_{49} between −0.53 and −0.64, all $p < 0.001$ for each condition; $r_{49} = -0.63$, $p < 0.001$ across conditions). This indicates that the ratings for in-body experiences represent at least partly the opposite to the ratings for out-of-body experiences and *vice versa*, suggesting valid assessments.

The mean value of the exteroception index (M = 4.61, SD = 12.21) differed significantly from 0 ($t_{50} = 2.70$, $p = 0.01$, and $d = 0.38$), indicating that, on average, bodily self-location was successfully manipulated by exteroceptive input in the experiment (**Figure 2**).

Vividness of Body Experiences

Mean vividness was higher for synchronous conditions (M = 76.91, SD = 19.87 for $1PP_{sync}$; M = 69.02, SD = 20.96 for $3PP_{sync}$) than for asynchronous conditions (M = 39.81, SD = 18.86 for $1PP_{async}$; M = 40.93, SD = 21.11 for $3PP_{async}$; see **Figure 3**).

We performed a 2 × 2 ANOVA for repeated measurements, again entering the two factors *perspective* and *stimulation*. We found a significant main effect on vividness of the factor *stimulation* ($F_{1,50}$ = 146.42, $p < 0.001$, and $\eta^2 = 0.75$), but no main effect of the factor *perspective* ($F_{1,50}$ = 1.80, $p = 0.19$, and $\eta^2 = 0.03$). There was a significant *perspective* × *stimulation* interaction ($F_{1,50}$ = 5.91, $p = 0.02$, and $\eta^2 = 0.11$); subsequent *post hoc* paired-samples *t*-tests revealed that the interaction was caused by a significant difference between $1PP_{sync}$ and $3PP_{sync}$ ($t_{50} = -2.41$, $p = 0.02$, and $d = 0.39$), which was not present when comparing $1PP_{async}$ and $3PP_{async}$ ($t_{50} = 0.38$, $p = 0.71$, and $d = 0.06$).

Mean values for individual vividness items per condition are shown in **Supplementary Figure 1C** in the **Supplementary Material.**

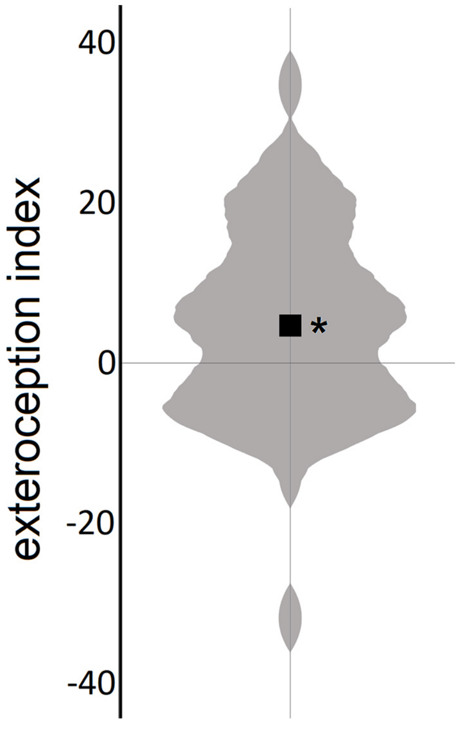

FIGURE 2 | Experimental manipulation of body self-location. Violin plot of the exteroception index (the black square represents the mean); positive values indicate malleable bodily self-location by exteroceptive input. *$p < 0.05$.

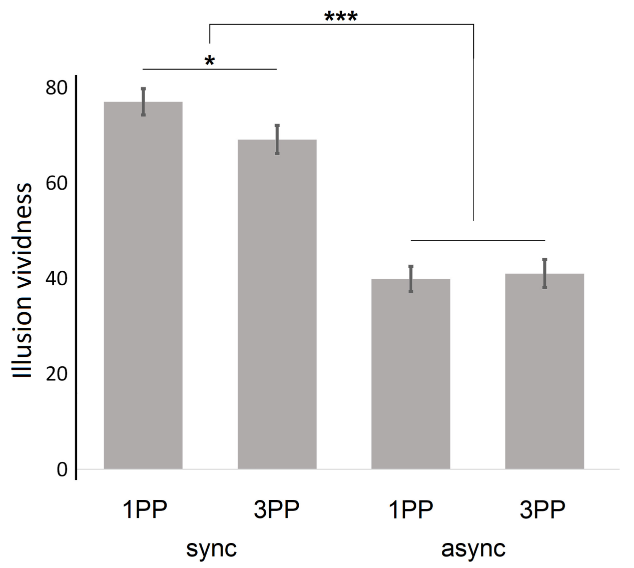

FIGURE 3 | General vividness of illusory sensations; given are the means; error bars indicate the standard error of the mean. 1PP, first-person perspective; 3PP, third-person perspective; sync, synchronous visuotactile stimulation; async, asynchronous visuotactile stimulation; *$p < 0.05$; ***$p < 0.001$.

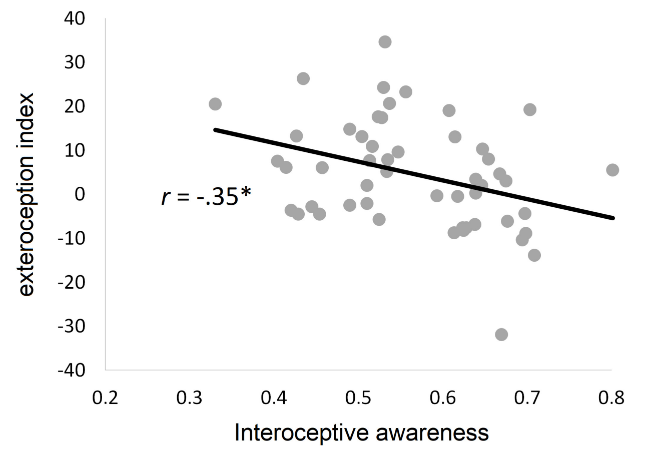

FIGURE 4 | Relationship between interoceptive dimensions and bodily self-location. Scatter plot and regression line for the relationship between malleability of bodily self-location by exteroceptive input (exteroception index) and interoceptive awareness (r = Pearson correlation coefficient). *$p < 0.05$.

Dimensions of Interoception

Regarding interoceptive accuracy, the total group performed above chance in correctly distinguishing between synchronous and asynchronous trains of sounds and their own heartbeats ($M = 0.55$, $SD = 0.13$; $t_{50} = 2.89$, $p = 0.006$, and $d = 0.38$). Confidence in their own interoceptive abilities (i.e., interoceptive sensibility) was significantly above 0.5 ($M = 0.61$, $SD = 0.12$; $t_{50} = 6.83$, $p < 0.001$, and $d = 0.92$). Metacognitive interoceptive awareness, measured using ROC curve analysis of accuracy and confidence in heartbeat discrimination task data, reached above-chance significance across the whole group ($M = 0.56$, $SD = 0.10$; $t_{50} = 4.25$, $p < 0.001$, and $d = 0.60$).

Relationship Between Interoceptive Dimensions and the Exteroception Index

While the exteroception index was not significantly correlated with interoceptive accuracy ($r_{49} = -0.04$, $p = 0.77$) or interoceptive sensibility ($r_{49} = -0.22$, $p = 0.11$), there was a significantly negative correlation with interoceptive awareness ($r_{49} = -0.35$, $p = 0.01$), indicating that the higher the interoceptive awareness, the less a participant's bodily self-location is malleable by exteroceptive input. This relationship is shown in **Figure 4**.

The ANOVA for the regression analysis including all three interoceptive measures was significant, $F_{3,47} = 3.56$, $p = 0.02$, with an adjusted R^2 of 13.3%. Only interoceptive awareness showed a significant association with the exteroception index (for statistical details, see **Table 2**).

Since the analysis of body experience ratings (see section "Body Experience Ratings and the Exteroception Index" above) revealed a significant *perspective* × *stimulation* interaction only for out-of-body experiences, the validity of the exteroception index has been challenged during the revision process. Thus, we repeated the correlation and regression analyses for the score representing this significant interaction effect (i.e., subtracting the out-of-body experience ratings from the $3PP_{async}$ condition from those obtained in the $3PP_{sync}$ condition; see **Table 1**). The pattern of correlations remained stable ($r_{49} = -0.03$, $p = 0.83$ for interoceptive accuracy; $r_{49} = -0.26$, $p = 0.07$ for interoceptive sensibility; $r_{49} = -0.32$, $p = 0.02$ for interoceptive awareness), and also the regression analysis results were comparable ($F_{3,47} = 3.53$, $p = 0.02$; adjusted $R^2 = 13.2\%$; for details, see **Table 2**), particularly regarding the specific association with interoceptive awareness, suggesting that exteroceptive manipulation predominantly affected perceived dislocation, rather than co-location, of the body and the self, which itself is specifically negatively associated with interoceptive awareness.

DISCUSSION

Bodily self-consciousness is composed of three key components, perceptually reflected by the sensation of having a body that (a) belongs to one's self (self-identification), (b) is the locus from where an individual is experiencing the world (first-person perspective), and (c) is experienced as occupying a specific location in space (self-location; Blanke, 2012). These dimensions of bodily self-consciousness are tightly interlinked (Huang et al., 2017) and can be mediated by exteroception and/or interoception (e.g., Aspell et al., 2012, 2013). The experience of one's self being located within one's body, as assessed in the present study, represents the "normal" perceptual consequence of these processes. Both exteroceptive (Ehrsson, 2007; Lenggenhager et al., 2007) and interoceptive (Adler et al., 2014) processes have been identified as specifically contributing to the co-location of the body and the self.

TABLE 2 | Results of regression analyses.

Criterion	Regressors	*B*	*SE*	β	*P*	R^2	adjusted R^2
Exteroceptive index	(constant)	35.82	11.70		0.004	0.19	0.13
	Interoceptive accuracy	20.17	14.83	0.21	0.18		
	Interoceptive sensitivity	−22.58	14.04	−0.22	0.11		
	Interoceptive awareness	−50.92	18.30	−0.41	0.008		
Out-of-body experiences ($3PP_{snyc}$ minus $3PP_{async}$)	(constant)	74.67	24.60		0.004	0.18	0.13
	Interoceptive accuracy	44.21	31.19	0.22	0.16		
	Interoceptive sensitivity	−56.83	29.53	−0.26	0.06		
	Interoceptive awareness	−98.50	38.48	−0.38	0.01		

3PP, third-person perspective; sync, synchronous visuotactile stimulation; async, asynchronous visuotactile stimulation; R^2, explained variance; B, unstandardized coefficient; SE, standard error; β*, standardized regression coefficient.*

In the present study, we further investigated the interrelationship between exteroception and interoception underlying the feeling that the self is located within the borders of one's own body. Healthy subjects participated in an experiment composed of four conditions that systematically manipulated exteroceptive multimodal input in terms of *perspective* (1PP vs 3PP) and visuotactile *stimulation* (sync vs async), using an advanced setup based on the work of Ehrsson (2007). Participants were asked to complete a questionnaire that measured their level of perceived co-location (i.e., in-body experiences) or dislocation of their body and their self (i.e., out-of-body experiences). We found that *perspective* had a significant main effect on bodily self-location, with 1PP being associated with higher levels of co-location of the body and the self, while 3PP being associated with perceived dislocation. Particularly, for the unusual experience to be separated from one's physical body, inconsistent multimodal exteroceptive input might play a crucial role: the out-of-body-specific significant *perspective* × *stimulation* interaction suggests that $3PP_{snyc}$ induced significantly stronger feelings of dislocation of the body and the self than $3PP_{async}$, indicating that visuotactile stimulation is particularly capable of modulating bodily self-location under unusual perspectival conditions.

We also calculated an "exteroception index" that reflects the degree to which a participant's individual body experience adjusted to exteroceptive input. Correlating this index with our three dimensions of interoceptive abilities, assessed with a heartbeat discrimination task, showed that interoceptive awareness, i.e., the metacognitive representation of interoceptive abilities, was significantly negatively related to the exteroception index. This relationship was specific to interoceptive awareness, since interoceptive accuracy (in terms of behavioral accuracy in performance) and interoceptive sensibility (in terms of being confident in one's own interoceptive abilities) did not show any similar correlation. Regression analyses further emphasized that interoceptive awareness was specifically associated with the malleability of bodily self-location by exteroceptive input. This indicates that better metacognitive interoceptive awareness is accompanied by a body percept that is less prone to being malleable by exteroceptive input. In other words, such participants' perceptual systems rely more on higher-order interoceptive processes rather than on exteroception, resulting in a more stable body representation. The results also remained significant if we focused on the significant *perspective* × *stimulation* effect on out-of-body experiences, suggesting that dislocation, rather than co-location, is particularly relying on metacognitive interoceptive capabilities. These results are of importance for theoretical conceptions about bodily self-consciousness, as well as for the understanding of psychopathologies characterized by aberrant connections between the body and the self.

Our novel setup induced significantly higher levels of perceived co-location between the body and the self in 1PP conditions compared to 3PP conditions, emphasizing its exteroceptive basis. Braithwaite et al. (2017) recently showed that participants who report that they have out-of-body experiences, i.e., an extreme form of aberrant bodily self-location in their normal life, also display (not necessarily pathological) aberrations in the integration of exteroceptive sensory input. This is supported by our results. In our study, visuotactile stimulation interacted with perspective (1PP vs 3PP), albeit the effect sizes were rather small compared to other studies (e.g., Ehrsson, 2007). This might result from our exclusion of the vividness component—which has previously been included as an illusion marker in other studies on body experience (e.g., Botvinick and Cohen, 1998; Ehrsson, 2007)—and could have reduced the apparent effect of stimulation in the present study, given that vividness has been shown to be particularly associated with synchronous visuotactile stimulation. Furthermore, the small to absent effects of the factor *stimulation* on in-body experiences could reflect that this particular feature of everyday bodily self-consciousness is binary rather than continuous (cf. De Vignemont, 2011): if someone feels already being in his or her body, this perception cannot be easily increased by exteroceptive stimulation. Prospective studies have to further explore the dimensionality of in-body and out-of-body experiences.

This study adds to the existing empirical evidence that links the malleability of bodily self-consciousness to interoceptive abilities (e.g., Tsakiris et al., 2011; Adler et al., 2014). While the integration of sensory information across exteroceptive and interoceptive domains has previously been shown to modulate bodily self-consciousness (Suzuki et al., 2013), this has mainly been probed by using the rubber hand illusion paradigm. However, the rubber hand illusion and its derivatives (for a review, see Riemer et al., 2019) transfer the sense of self to an artificial body-part, while in the present study, we manipulated the perceived location of the self in respect to one's *own* body, which might represent a distinct phenomenon relying on different neurocognitive mechanisms [see the discussion linked to the articles by Ehrsson (2007) and Lenggenhager et al. (2007)]. A further difference here to the rubber hand illusion might be that general bodily self-location represents a rather implicit level of bodily awareness. One previous study asked participants to localize their self in their body (Alsmith and Longo, 2014) and found participants pointing predominantly to the core of the body (the torso or the head) and not to the body's periphery. Thus, there is reason to assume that co-location of the body and the self might be a more fundamental aspect of bodily self-consciousness than body-part ownership as tested by the rubber hand illusion.

Most importantly, our results indicate that higher-order, metacognitive interoceptive awareness, rather than behavioral performance on interoceptive accuracy or interoceptive sensibility, predicts the malleability of the bodily self-location. Interoceptive awareness, compared to the other interoceptive dimensions, seems to be a particularly reliable indicator of one's own bodily states, since previous findings revealed that interoceptive awareness—in contrast to interoceptive accuracy—represents a relatively stable trait across physiological modalities (Garfinkel et al., 2016a). Thus, this particular interoceptive dimension might also play a role in the stability (or malleability) of body representations: the more reliable the information is from my body and the more I am aware of this reliability, the less dependent my perceptual system is on exteroceptive information. Accordingly, high cardiac interoceptive awareness could be a protective factor against aberrant bodily experiences. Whether other forms of interoceptive awareness (e.g., for respiratory signals; Garfinkel et al., 2016a) will show the same relationship remains open. However, one has to keep in mind that the amount of explained variance in the current regression and correlation analyses is rather small, which might emphasize the multifactorial origin of bodily self-consciousness. Prospective studies have to further elucidate the complex interplay of perceptual and cognitive factors.

Previous studies have investigated the neurophysiological mechanisms underlying the importance of interoception for body representations. Park et al. (2016) found that neural responses to heartbeats covary with changes in self-location. In accordance with those results, lesions of the right insula, which represent a key area for interoceptive processing (Critchley et al., 2004), decrease heartbeat awareness and alter self-location (Ronchi et al., 2015). In addition to the insula, higher-order brain areas such as the parietal cortex or the Rolandic operculum seem to integrate both interoceptive and exteroceptive signals in order to maintain bodily self-consciousness (Blefari et al., 2017; Park and Blanke, 2019; Salvato et al., 2020). Other results highlight the relevance of interoceptive information for the visual processing of the body (Ronchi et al., 2017), and this processes' impact on brain areas involved in processing cognitive aspects of body representation. If replicated, the present results might further point to the frontal cortex: as Molenberghs et al. (2016) reported, the anterior medial prefrontal cortex seems to be specifically involved in metacognitive awareness, while this region has also been associated with switching between 1PP and 3PP taking (Ruby and Decety, 2003). Whether or not this region also mediates a trait-like coupling between exteroceptive and interoceptive sensory information by means of a malleable sense of bodily self-location, however, remains open.

Although we only included participants who did not report a history of psychopathology, our results might have implications for disorders associated with abnormalities in interoception and bodily self-consciousness. There is growing evidence that disturbed interoception may be important for dysfunctions in several conditions of disordered mental health (Khalsa et al., 2018). For example, borderline personality disorder patients, who frequently report dissociative body perceptions (Löffler et al., 2020), have been characterized by both abnormal integration of multimodal sensory input (Bekrater-Bodmann et al., 2016) and disturbed neural representation of interoceptive signals (Müller et al., 2015). Accordingly, interoceptive abilities, particularly interoceptive awareness, have been proposed to play an etiological role in the development of this disorder (Löffler et al., 2018), probably via repeated invalidation experiences in early life. Further, recent studies suggest that discrepancies between interoceptive processing and beliefs about, or interpretation of, interoceptive signals might reflect body awareness and affective deficits in individuals with autism spectrum disorder (Garfinkel et al., 2016b; Shah et al., 2016). In this group, aberrant interoception has also been linked to proneness to the rubber hand illusion (Schauder et al., 2015), suggesting that an impaired interplay between exteroception, interoception, and the malleability of the body percept plays a role for certain psychopathologies characterized by disturbed self-representation. We propose that disturbed integration of interoceptive and exteroceptive inputs is potentially linked to higher cognitive functions, which may be the basis of abnormal (bodily) self-processing. Thus, therapeutic treatments for these disorders could consider techniques, such as mindfulness-based interventions, that focus not only on the ability to correctly attend to body signals but also on the change of metacognitive representations and related cognitions (Khalsa et al., 2018). Prospective studies could investigate whether interoceptive awareness might be trained in such settings and whether improvement would be accompanied by reductions in the frequency or intensity of aberrant body experiences.

Limitations of the present study include that in-body and out-of-body experiences exclusively rely on self-reports. It is possible that the setup itself induced response biases in the participants, which might reduce the validity of results. Previous studies have used behavioral (e.g., Lenggenhager et al., 2007), peripheral physiological (e.g., Ehrsson, 2007), or central neurophysiological measures (e.g., Ionta et al., 2011) as correlates of uncommon body experiences, which should also be included in future studies. Since we initially assumed that $1PP_{sync}$ mimics the "normal" experience of bodily self-location, we omitted to operationalize a further control condition in which participants' body experiences would be assessed in the absence of any tactile stimulation (be it in 1PP or 3PP). Thus, it remains an open question how similar the experimentally manipulated processes, and the perceptions they give rise to, are to real-life embodied experiences. This missing external validation is of particular relevance, since the nature of the experiment (i.e., seeing a body in 3PP conditions, while seeing no body in 1PP conditions) could itself have affected the results. The fact that perspective, rather than stimulation, influenced the findings of in-body experience in the present study might point to such a confounding effect. Future studies should explore the validity of the present findings by including behavioral or physiological measures, such as skin temperature (Salomon et al., 2013), reaction times (Adler et al., 2014), or behavioral measures of sensory interference (Maselli and Slater, 2014).

Conclusion

Our results suggest that exteroceptive input and higher-order interoceptive abilities both contribute to the stability or malleability of perceived co-location of the body and the self. The implications of these findings are of relevance for theoretical considerations as well as for treatment of disorders characterized by abnormal self-processing. The neurobiological underpinnings should be investigated in future studies.

DATA AVAILABILITY STATEMENT

The dataset analyzed for the current study is available from the corresponding author on reasonable request.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Ethics review board of Royal Holloway, London University. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

RB-B and MT conceived and planned the experiments. RB-B and RA developed the technical setup. RB-B carried out the experiments and performed the data analysis. RA, VA, and MT contributed to the interpretation of the results. RB-B wrote the first draft of the manuscript, and RA, VA, and MT provided critical feedback. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2020.562016/full#supplementary-material

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Peripersonal Space and Bodily Self-Consciousness: Implications for Psychological Trauma-Related Disorders

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Peripersonal space (PPS) is defined as the space surrounding the body where we can reach or be reached by external entities, including objects or other individuals. PPS is an essential component of bodily self-consciousness that allows us to perform actions in the world (e.g., grasping and manipulating objects) and protect our body while interacting with the surrounding environment. Multisensory processing plays a critical role in PPS representation, facilitating not only to situate ourselves in space but also assisting in the localization of external entities at a close distance from our bodies. Such abilities appear especially crucial when an external entity (a sound, an object, or a person) is approaching us, thereby allowing the assessment of the salience of a potential incoming threat. Accordingly, PPS represents a key aspect of social cognitive processes operational when we interact with other people (for example, in a dynamic dyad). The underpinnings of PPS have been investigated largely in human models and in animals and include the operation of dedicated multimodal neurons (neurons that respond specifically to co-occurring stimuli from different perceptive modalities, e.g., auditory and tactile stimuli) within brain regions involved in sensorimotor processing (ventral intraparietal sulcus, ventral premotor cortex), interoception (insula), and visual recognition (lateral occipital cortex). Although the defensive role of the PPS has been observed in psychopathology (e.g., in phobias) the relation between PPS and altered states of bodily consciousness remains largely unexplored. Specifically, PPS representation in trauma-related disorders, where altered states of consciousness can involve dissociation from the body and its surroundings, have not been investigated. Accordingly, we review here: (1) the behavioral and neurobiological literature surrounding trauma-related disorders and its relevance to PPS; and (2) outline future research directions aimed at examining altered states of bodily self-consciousness in trauma related-disorders.

Keywords: peripersonal space, bodily self-consciousness, trauma-related disorders, neurobiology, defense response, multisensory processing, PTSD, dissociation

INTRODUCTION

Peripersonal space (PPS) refers to the space surrounding the body where we can reach or be reached by external entities, including objects or other individuals (Rizzolatti et al., 1997; Brozzoli et al., 2012b). It is a fundamental characteristic of our everyday life, where we move through space to reach our goals, interact with other individuals, avoid colliding with objects or other people, and act in a way that protects our bodies from potential incoming threats (de Haan et al., 2016). In order to engage in such a complex task, we need to integrate visual, auditory, tactile, interoceptive, and proprioceptive stimuli from our own body and from the environment, thereby not only constantly monitoring our body location in space but also scrutinizing changes occurring in the surrounding space (Salomon et al., 2017). PPS thus represents an aspect of bodily self-consciousness that emerges and changes with the flow of experience (Noel et al., 2015b, 2018b). Interestingly, PPS can also be viewed as a "defensive zone," activating bodily alarm reactions when PPS boundaries are surpassed or violated (Holmes and Spence, 2004; Graziano and Cooke, 2006; Sambo et al., 2012; de Haan et al., 2016). Accordingly, the investigation of PPS is critical to the study of psychopathology, in particular anxiety disorders such as phobias and trauma-related disorders, where fear responses and/or altered states of bodily self-consciousness play a crucial role. A substantial number of studies provides further evidence of the crucial role played by PPS in everyday experience. Taken together, these studies have identified a neural network in both animal models and humans that is dedicated specifically to bodily self-consciousness and PPS representation (Rizzolatti et al., 1997; Fogassi et al., 1999; Gallivan et al., 2011; Brozzoli et al., 2012a; Blanke et al., 2015; Cléry et al., 2015; di Pellegrino and Làdavas, 2015; Limanowski and Blankenburg, 2015).

In this review, we discuss PPS and its relation to bodily self-consciousness in psychopathology using a multidisciplinary perspective that includes cognitive science, neuroscience, psychiatry, and clinical psychology. We present first a definition of PPS and illustrate its characteristics and functions. We then identify the cortical and subcortical structures underlying PPS representation in animal models and in humans. Furthermore, we explore the scant literature describing the relation between psychopathology and PPS, with a focus on trauma-related disorders, where out-of-body experiences can be an important component of the underlying psychopathology. Finally, we describe the importance of studying PPS in trauma-related disorders in an effort to not only enhance our understanding of the critical role of bodily self-consciousness in these disorders but also to deepen our insight regarding the characteristics of PPS that are influenced by psychological traits and states.

PERIPERSONAL SPACE AND BODILY SELF-CONSCIOUSNESS

Bodily self-consciousness has been described as the conscious experience of owning a body (self-identification), occupying a specific location in space (self-location), and having a specific perspective from where to perceive the world that coincides with one's body (first-person perspective; Blanke, 2012). While all these aspect of bodily self-consciousness are interconnected to create a sense of self that is embodied, they are also related to the representation of the space surrounding the body (PPS). Here, body ownership has been largely studied using experimental paradigms that aim to create the illusion of owning external body-parts or alter bodies that are located within the PPS, suggesting the PPS as a spatial constraint for the body ownership illusion to occur (Botvinick and Cohen, 1998; Makin et al., 2008; Ehrsson, 2012; Serino, 2019). In addition, self-location is an essential reference to build the PPS representation (since the PPS surrounds the body) and has been found to depend strongly on the first-person perspective (Blanke, 2012). Neuroimaging studies have corroborated the interaction of these different aspects of bodily self-consciousness, where overlap has been identified among the neural correlates of body ownership, self-location, first-person perspective, and PPS (see paragraph "Neural Correlates of Peripersonal Space in Humans" on neuroimaging studies in humans).

Multisensory integration of information represents a crucial mechanism underlying all aspects of bodily self-consciousness. Park and Blanke (2019) have recently proposed interoceptive-exteroceptive bodily self-consciousness (xBSC) as a conceptualization that aims to include both exteroceptive bodily self-consciousness (gathering information within the PPS) and interoceptive bodily self-consciousness (gathering information from the inner body) into a unique integrated neural system (for details please see Park and Blanke, 2019). In this manuscript, we focus our attention on PPS specifically, while considering the dynamic interplay of PPS with other aspects of the conscious experience that build a fluid embodied sense of self (body ownership, interoception, self-location, and first-person perspective).

Peripersonal and Extrapersonal Space

Peripersonal space (PPS) is defined as the space surrounding the body where we can not only reach and manipulate objects by movement but we can also be reached by external elements, including other individuals. By contrast, extra-personal space constitutes an area further from the body, where objects cannot be reached, and the environment is explored primarily through visual means (Bartolo et al., 2014; di Pellegrino and Làdavas, 2015). Interestingly, this dichotomous (in-or-out) conceptualization of PPS has been debated recently by Bufacchi and Iannetti (2018). They suggest, instead, that the PPS unfolds as a set of graded fields, similar to magnetic fields, where the representation of the PPS depends on its relevance within a specific context and the measures used to define it. Taken together, these notions suggest that PPS representation depends heavily on the relevance of possible actions aimed at creating or avoiding contact between the body and external elements. Further studies are needed to unravel this complexity.

The concept of PPS stems from electrophysiological research on monkey models (Hyvärinen and Poranen, 1974; Mountcastle, 1976; Leinonen and Nyman, 1979; Rizzolatti et al., 1981b). Here, researchers identified a specific population of neurons in the fronto-parietal cortex—dedicated to sensorimotor processing—that were specifically activated by stimuli presented in the space surrounding the animal; these neurons were bimodal (visuo-tactile) and responded selectively to somatosensory stimuli. These neurons may underlie bodily self-consciousness in that they are dedicated specifically to the integration of somatosensory bodily signals and stimuli originating in a limited space surrounding the body.

Peripersonal Space and Body Schema

Movement of the body in space while monitoring its surroundings is critical to the notion of PPS (Holmes and Spence, 2004). As PPS facilitates guidance of the body through space, it requires integration of an individual's internal bodily representation and body schema with the surrounding space (Holmes and Spence, 2004; Cardinali et al., 2009). Body schema has been defined as the active and operative non-conscious performance of the body in relation to the environment and is thought to integrate multisensory information derived from proprioceptive, interoceptive, somatosensory, visual, and auditory input from the body and the environment (Gallagher, 1986). For example, it reflects and determines the posture of the body in the environment. Critically, the integration of body schema and PPS allows bodily self-consciousness to emerge with reference to a physical body that is perceived as one's own body in a specific location in space (self-identification and self-location) (Blanke, 2012; Noel et al., 2015b, 2018b). The relationship among plasticity, multisensory integration in PPS, and body schema representations has given rise to the question whether the two representations correspond in fact to the same concept (Cardinali et al., 2009). While a definitive conclusion has not been achieved yet, Cardinali et al. (2009) have argued that the two representations should be considered dissociable in principle (one can change without modifying the other), both in terms of spatial continuity (body schema is constrained within the body limits) and time (different latency in plastic changes). Further studies have also supported the notion of two separate mechanisms underlying the two constructs (Bassolino et al., 2014; D'Angelo et al., 2018).

Peripersonal Space Extension

To identify and investigate PPS, researchers have focused on the mechanisms underlying multisensory integration. Multimodal neurons involved in the representation of PPS activate when tactile, visual, and auditory stimuli are presented close to the body but not when far away from the body, thus allowing for the identification of PPS boundaries around the body. Critically, researchers have recognized approaching stimuli as most relevant to identify PPS boundaries, likely because they might represent a potential incoming threat (Graziano and Cooke, 2006). Here, a research study found that an approaching auditory stimulus increased the processing of a concomitant tactile stimulus on the body surface when the auditory stimulus was perceived at a limited distance from the hand, thus setting the boundaries of PPS (measured through reaction time to a tactile stimulus to the hand delivered at different temporal delays from the sound onset, where the sound was delivered in a way that created a looming effect via volume modulation; Canzoneri et al., 2012). It is also important to note that this effect was stronger for an approaching auditory stimulus as compared to a receding one. Similarly, Noel et al. (2015b) identified PPS boundaries through reaction times in response to vibro-tactile stimuli administered to the participant's chest while task-irrelevant sounds, administered through loud speakers disposed at gradually closer distances, loomed toward the subject's body. Reaction times increased when the boundaries of PPS were surpassed by the auditory stimuli. Taken together, these results demonstrate that during multisensory processing we assign unique relevance to external stimuli that are closer to the body and dynamically looming toward the body.

Peripersonal Space Is Body-Part Centered

Research in humans and animal models have shown that PPS can vary depending on what part of the body is examined. Indeed, a specific representation of PPS has been identified for the hand, the arm, the face, and the trunk (Serino, 2019). This unique characteristic accounts for the dynamic reshaping of PPS representations when body parts move in space while the rest of the body remains still. For example, when researchers investigated PPS in relation to the hand, they found that when the subject moved her/his hand, the PPS would update to follow the movement, thus maintaining PPS map coordinates centered on the hand (Brozzoli et al., 2012a; di Pellegrino and Làdavas, 2015; Dijkerman and Farnè, 2015; Serino et al., 2015b). This characteristic is maintained through integration between the visual/auditory receptive fields and the somatosensory receptive fields within bimodal neurons in the fronto-parietal regions (Graziano et al., 1997b). In a seminal series of seven studies, Serino et al. (2015b) investigated PPS in healthy humans, concluding that PPS appears to involve at least three differentiated representations centered in the hands, the face, and the trunk. Moreover, these representations appear to be unified by a common reference frame of the trunk. For example, when an individual moves one of her/his hands, the relative PPS also modifies according to the new location of the hand in space. However, the extent of PPS boundaries relative to the hand depends on the proximity to the trunk, appearing larger when the hand is closer to the trunk. Serino and colleagues suggest this effect to stem from the trunk-centered PPS taking over the hand-centered PPS when the hand is very close to the trunk. Moreover, the extent of PPS among individuals tested appeared increasingly larger for the hands (average 45 ± 7 cm), the face (average 59 ± 6 cm) and the trunk (average 72 ± 7 cm), respectively. Accordingly, peri-trunk personal space is assumed to best represent a whole-body reference frame for the egocentric representation of self (Serino et al., 2015b). Finally, these studies revealed that whereas receding stimuli modulate the PPS for the hands, no such effect was observed for the face and trunk.

In summary, the PPS representation is characterized by: (a) being specifically dedicated to a limited space surrounding the body; (b) being hyper-sensitive to stimuli that are moving toward the body; (c) being anchored to body parts (hand-centered, face-centered, arm-centered, and trunk-centered PPS have been identified so far). Collectively, these findings assist in shaping our understanding of PPS as an essential feature for bodily self-consciousness, where either distinct and/or unified flexible representations of our own body in space guide our actions through the external environment.

PLASTICITY OF PERIPERSONAL SPACE

A key feature of PPS is its plastic and dynamic representation. Whereas plastic changes refer to the flexibility elicited through training or learning, dynamic changes occur in response to modifications in the environment or in response to the internal state changes of an individual, including emotional state changes (Cléry et al., 2015). Extensive animal and human research has demonstrated flexibility of the PPS (Holmes and Spence, 2004; di Pellegrino and Làdavas, 2015; Dijkerman and Farnè, 2015). For example, plastic changes have been demonstrated in studies where repeated use of tools (e.g., a stick) resulted in remapping of PPS representation, where the tool was perceived as an extension of the body (e.g., the hand) and was incorporated within the hand-centered PPS (Berti and Frassinetti, 2000; Bonifazi et al., 2007; Làdavas and Serino, 2008). Berti and Frassinetti (2000) seminal study showed remapping of PPS in an individual with left visual neglect following right hemisphere stroke. Here, the patient's neglect involved a dissociation between near and far space, where neglect was apparent in the "near space" only. The use of a tool (a stick in one hand) was able to change the neglect manifestation, as the "far space" was remapped as "near space" in the patient's brain, and neglect now appeared in what was previously coded as "far space." In another recent study, plastic changes were associated with the body modifications occurring in the third trimester of pregnancy: the PPS of the expectant mothers became enlarged over time, incorporating more gradual boundaries between near and far space as measured by an audio-tactile integration task (tactile stimulation to the abdomen concurrent with looming sounds delivered via loudspeakers, which were positioned in the far space — 1 m away from the participant's hand — and the near space — close to the hand — in order to give the perception of a sound traveling toward the participant's body; Cardini et al., 2019).

This gradual expansion of the boundaries between near and far space is of critical importance in psychological disorders involving altered perception of self-other distinction and has indeed been observed in schizophrenia and autism spectrum disorders (Noel et al., 2017). Here, Noel and colleagues (Noel et al., 2017) proposed that whereas shallow PPS boundaries (as revealed by a larger space indexing the transition from extrapersonal to peripersonal space) reflect a weaker self-other distinction, steep PPS boundaries (smaller space indexing the transition from extrapersonal to peripersonal space) point toward a rigid self-other differentiation (Noel et al., 2017). Taken together, these studies suggest a gradual passage from PPS to extrapersonal space (and vice versa), where PPS boundaries are conceptualized in terms of gradients instead of a dichotomous in-out transition. Interestingly, these studies demonstrate further how psychological characteristics may affect PPS size, as well as the graduality of PPS boundaries.

Body illusion experiments have also shown dynamic changes in PPS as revealed through illusions experienced by subjects. For example, when a virtual body was placed *in front* of subjects and was stroked in synchrony with the real body, Noel et al. (2015b) reported a self-location drift toward the virtual body. Accordingly, the boundaries of PPS extended in the front space toward the virtual body and shrunk in the back. This outcome was interpreted as a shift in PPS representation from being centered on the physical body to being centered on a new subjectively experienced location of the self (Noel et al., 2015b).

The use of a mirror has also been shown to produce dynamic changes in PPS in humans. For example, Maravita et al. (2000, 2003) investigated cross-modal extinction in a patient with a right-hemisphere lesion, where a visual stimulus delivered to the right side of the visual field impaired the perception of a simultaneous tactile stimulus on the left side of the body. This extinction of touch to the left hand occurred in particular when a simultaneous visual stimulus (flashlight) was delivered close to the right hand (thus within PPS). Interestingly, the same outcome resulted (touch extinction to the left hand) when the patient saw the visual stimulus close to his right hand as a reflection in a mirror placed directly in front of him/her. Importantly, the same result was not obtained when the mirror was removed and both the visual stimulus and the hand (a fake hand reproducing the patient's hand) were distant in space (thus in extrapersonal space). These results demonstrated that the space surrounding one's body reflection in a mirror is perceived as PPS.

Similar results were obtained among healthy participants in a study investigating event-related potential (ERP) correlates of crossmodal interactions between tactile (delivered via a tactile stimulator) and mirror-reflected visual stimuli (LED light) (Sambo and Forster, 2011). Here, multimodal stimuli (in this case, tactile, and visual) produced enhanced ERPs within the somatosensory cortex when the stimuli were spatially congruent (on the same side with respect to the body) and close to the body (the visual stimulus was delivered within the PPS) as compared to when the stimuli were spatially incongruent. These results using mirror-reflected visual stimuli replicate findings observed when a visual stimulus was delivered near the actual hand of the study participant (thus within the PPS). Taken together, these studies indicate that when our body is reflected in a mirror, images appearing close to our reflected body are perceived as pertaining our PPS, with the PPS representation dynamically remapping to include a space that would otherwise be considered to be in the extrapersonal space. Even body shadows have been found to initiate a similar remapping of PPS. When the body shadow becomes part of the body schema, the representation of PPS is reorganized accordingly (Pavani and Castiello, 2004).

Another impressive finding by Noel et al. (2015a) revealed remapping of the PPS during walking as compared to a standing position. Here, the researchers tested PPS boundaries relative to the trunk through audio-tactile stimulation (tactile stimulation of the chest during approaching sound stimuli) and showed that PPS extension, measured via response times to the tactile stimulation, clearly increased in the walking (around 166cm

PPS extension) as compared to the standing condition (65 to 100 cm PPS extension). This outcome confirms further the dynamic nature of PPS, reshaping continuously in relation to body movements and to the relevance of its surroundings. This integration of body location and objects in the environment, essential to bodily self-consciousness, appears to require an extended PPS when moving through space. Moreover, the relevance of the body's surroundings appears to increase during walking, finding that could stem, in part, from increased attention to potential new encounters or new obstacles in the space while we move.

Interestingly, recent studies have utilized biologically plausible network modeling to simulate and investigate the neural networks underlying the PPS representation (Serino et al., 2015a; Noel et al., 2020). Here, Hebbian learning strengthening and weakening of feedback and feedforward synapses have been used to unravel plasticity of PPS. For example, the neural network model used in the work presented by Serino et al. (2015a) was able to predict the extension of the PPS representation without tool-use and was subsequently confirmed by behavioral measurements. A similar computational approach led the authors to suggest that neural adaptation could account for dynamic aspects of PPS, such as PPS resizing at the speed of looming stimuli (Noel et al., 2018a).

Notably, equally dynamic social cognitive processes and interactions with other people may affect the extent of PPS. In a study investigating PPS and social interactions, face-centered PPS appeared to shrink in the presence of another person as compared to a mannequin placed at a distance of 1m from the participant (Teneggi et al., 2013). Specifically, when the study participant was in the presence of another person, PPS boundaries moved closer to the participant (thus the PPS size shrank) as compared to when the study participant was in the presence of a mannequin and no such effect occurred. Interestingly, however, a larger PPS was observed in the presence of another person considered cooperative (previously showed to be cooperative with the subject during an economic game) as compared to the presence of a non-cooperative other individual (Teneggi et al., 2013). Taken together, these findings suggest that PPS functions serve not only as an interface between internal sensorimotor information and the spatial environment needed to grasp or manipulate objects, but also play a critical role in higher-order social cognitive processes and in interpersonal relationships.

FUNCTIONS OF PERIPERSONAL SPACE

Motor Function

As Holmes and Spence (Holmes and Spence, 2004) pointed out, PPS guides us through space, integrating different perceptive modalities (visual, tactile, auditory, interoception, and proprioception) to allow us to locate ourselves in space and to move through it safely. Indeed, PPS has been defined by the motor function of reaching, grasping, and manipulating objects in our surroundings (Brozzoli et al., 2012b). This view is supported further by observations of the plasticity characterizing the PPS, as exemplified by remapping of the PPS during body movement. Here, the PPS updates its representation while motor action occurs (Brozzoli et al., 2012b), an observation exemplified in studies investigating PPS during walking or during limb movement (di Pellegrino and Làdavas, 2015; Noel et al., 2015a). For example, Brozzoli and colleagues (Brozzoli et al., 2011) reported that visuo-tactile interference occurs during voluntary action performed by grasping a target object, thus providing evidence for a remapping of PPS during movement of the hand[1].

More recently, a series of studies (Dijkerman and Farnè, 2015) examined the bidirectional association between PPS and motor action, where PPS is modulated by motor action and influence activity within the motor system. Here, one study revealed that keeping one arm at forced rest for a prolonged time (10 h) resulted in a decreased PPS around that same arm (Bassolino et al., 2014). Furthermore, using transcranial magnetic stimulation while recording motor evoked potentials, Finisguerra et al. (2015) found that auditory stimuli within the PPS (within 60 cm from the subjects' hand) can modulate neural activity within the motor system (motor excitability; Finisguerra et al., 2015), thus providing further evidence for the important relation between motor action and PPS.

Defense Zone

Central to work surrounding PPS is the notion that this space represents not only a zone where an individual can have an effect on objects, but also the space where we can be reached by external entities (objects, animals or people) and potentially be harmed. As PPS surrounds one's body, it represents a vital space for any contact with the external environment. This perspective has been adopted by researchers investigating PPS as a defense zone. For example, de Haan et al. (2016) found that PPS was modulated by visuo-tactile predictions of an incoming threat: when subjects saw the image of a spider approaching their hand, their response time to a contingent tactile stimulus to the hand (time employed to press a foot pedal after perceiving a tap on the hand) was significantly faster. Critically, this outcome was apparent only for participants afraid of spiders. In a similar experiment, participants with a fear of dogs showed larger PPS boundaries (audio-tactile integration task) when in the presence of a rear-approaching sound that resembled a growling dog as compared to non-fearful participants (Taffou and Viaud-Delmon, 2014). Interestingly, studies on monkeys have shown that when neurons in the fronto-parietal cortex involved in the PPS representation (polysensory zone) are stimulated, a defensive arm movement is triggered, thus supporting the defensive purpose of the PPS at the neural level (Cooke and Graziano, 2003).

The hand-blink reflex has also served as a key experimental procedure to study the concept of PPS as a defense zone. This reflex consists of involuntary blinking of the eye that is generated by stimulation of the median nerve in the wrist and is mediated by the reticular formation in the brainstem (Miwa et al., 1998).

[1]The visuo-tactile interference (VTI) paradigm requires study participants to discriminate between tactile stimuli delivered at different locations (up or down) on the participant's finger while task-irrelevant visual stimuli are displayed on a target object. When investigating VTI during movement, study participants were asked to perform the task (discriminating the location of a tactile stimulus) while grasping the target object (Brozzoli et al., 2011).

In a groundbreaking experiment using the hand-generated blink reflex, Sambo et al. (2012) demonstrated that the amplitude of the blink reflex is mediated by the distance between the hand itself and the face, thus supporting the notion of the PPS as a defensive zone. Specifically, the blink reflex occurred only when the stimulated hand was located within the face-centered PPS, that is, the PPS representing the space surrounding the face. In a further study, Fossataro et al. (2016) investigated the influence of social interactions on the hand-blink reflex, showing that interpersonal interaction can affect subcortical defensive responses as measured by the hand-blink reflex (increased blink reflex during stimulation of the median nerve in the wrist in the study participant when someone else's hand enters the individual's PPS). Notably, this effect was dependent on the level of empathy endorsed by study participants, with an increased defensive blink reflex observed in persons with higher empathy scores as measured through the Interpersonal Reactivity Index – IRI; (Davis, 1983). Critically, these findings suggest that brainstem circuits involved in the hand-blink reflex are modulated in a top-down fashion by neocortical brain areas involved in not only proprioceptive location of body parts in space but also in social cognition.

Additional work suggests that the defensive function of PPS depends on attention selection (de Haan et al., 2016), where a visually detected threat appears to bias our attention toward the imminent potential harm, particularly when the threat is approaching the body and thus has the potential to enhance response to any following stimulus in that particular zone (Poliakoff et al., 2007; Carretié et al., 2009; Ferri et al., 2015). This putative defensive mechanism appears conserved and further amplified in psychological disorders that involve attention bias and threat responding, such as trauma-related and anxiety disorders. For example, a study investigating freeze-like response (characterized by tonic immobility of the body and tested as a slowing of reaction times) to approaching stimuli (thus impinging on PPS) in humans showed that reaction times were significantly slower during exposure to a threatening as compared to a non-threatening stimulus and that this response correlated with state-anxiety scores endorsed by participants (Sagliano et al., 2014).

Dual Model

de Vignemont and Iannetti (2015) have proposed a dual model of PPS, where a goal-oriented PPS can be differentiated from a defensive PPS by their purpose and sensorimotor features. Here, goal-oriented PPS serves the purpose of intentionally moving body parts (primarily arms and hands) to reach a goal such as grasping and manipulating objects. At the sensory level, the motor-oriented PPS would be focused primarily on fine-grained features of objects in order to better execute reaching and grasping actions. By contrast, a defensive PPS would be characterized by automatic protective actions, such as avoiding contact with objects, or by no actions at all (e.g., freezing/tonic immobility states). Moreover, it is postulated that this defensive PPS encompasses the entire body and would be influenced by the salience of an incoming stimulus, where a potential threat would represent the most salient information in the surrounding environment that needs to be rapidly detected for survival. This defensive PPS is also expected to be characterized by sharp boundaries. Here, studies using the hand-blink reflex as a measure of the defensive response found a sharp change in the defensive response when a hand entered the PPS, thus providing support for sharp boundaries characterizing the defensive PPS (Sambo and Iannetti, 2013). Although compelling, the dual model hypothesis has yet to be supported by empirical studies.

In summary, two main functions of the PPS have been identified: (1) a goal-oriented representation of space where bodily self-consciousness subserves motor intentions and action planning; and (2) a defense zone where bodily self-consciousness is oriented to protect the body from incoming potential threats.

NEURAL CORRELATES OF PERIPERSONAL SPACE

Neural Correlates of Peripersonal Space in Animal Models

The initial definition of PPS derived from neurophysiological studies performed in primates in the 1980s examining bimodal neurons in the periarcuate (premotor) cortex (Rizzolatti et al., 1981a,b). Multisensory neurons are able to respond to different combinations of sensory inputs—visual, tactile, proprioceptive, vestibular, auditory—when these inputs are perceived simultaneously, for example when a visual input (e.g., a looming cue) is perceived at the same time as a tactile stimulus (e.g., a tap on the hand). The functioning of these multimodal neurons is comparable to the multisensory integration occurring within the superior colliculus, where convergent visual, auditory, and somatosensory stimuli elicit maximal neuronal activity (Meredith and Stein, 1986; Cardinali et al., 2009). Furthermore, the evoked response in multimodal neurons is mediated by the distance between the visual object and the tactile receptive field (RF), such that the appraisal of visual information is dependent on how close this visual input is to the body part containing the tactile receptive field (Brozzoli et al., 2012b). Multisensory neurons, dedicated to the representation of PPS, have been identified in different brain regions of macaque monkeys, and specifically within the premotor and parietal cortex, and the putamen (Rizzolatti et al., 1997; Fogassi et al., 1999; Graziano, 2001; Graziano and Cooke, 2006).

The ventral-caudal premotor cortex (also called area F4), adjacent to the ventral-rostral premotor cortex (area F5) and to the primary motor cortex, contains multisensory neurons that respond to both visual and tactile stimuli, and a somatotopic map of arms, hands, and face (Holmes and Spence, 2004). Interestingly, electrical stimulation of area F4 in monkeys (labeled as a polysensory zone due to the neuronal response to multisensory stimuli; Graziano and Cooke, 2006) results in a defensive movement aimed at protecting the body (withdrawing and blocking movements). Within the posterior parietal cortex, the ventral intraparietal sulcus, Brodmann area 7, and Brodmann area 5 contain multimodal neurons that have been associated with PPS in monkeys (Holmes and Spence, 2004; Brozzoli et al., 2012b). Here, neurons shape a gross somatotopic representation (reproducing the same arrangement as the body surface such that neighborhood relation are preserved), with tactile RFs dedicated to the face, arm, and head. Of note, the ventral intraparietal sulcus is in close proximity to the medial intraparietal sulcus, also called the parietal reach region due to its role in reaching action representation (Koob et al., 2010). While the ventral and medial intraparietal areas are known to be interconnected and functionally intertwined (Grefkes and Fink, 2005), they are considered as pertaining two distinct neural networks (one for PPS and one for reaching representations, respectively). Other brain areas involved in PPS representation in monkeys include the parietal occipital junction (Brozzoli et al., 2012b) and the putamen (Graziano and Gross, 1994). Whereas the parietal occipital junction is thought to carry a face- and hand-centered representation of visual space, the putamen appears relevant to visuo-tactile processing of the space around the body and contains visuo-tactile neurons with tactile RFs on the arm, hand, and face that are somatotopically organized.

Another notable characteristic observed through neurophysiological studies of PPS in monkeys is the observation that neurons in the premotor cortex activated by the presence of an object in the space surrounding the body continue firing in the absence of the visual stimulus if the monkey believes the stimulus is still there, thus suggesting that PPS is maintained internally on the basis of previous experience (Graziano et al., 1997a).

Neural Correlates of Peripersonal Space in Humans

Studies examining the neural correlates of PPS in humans reproduce largely findings in monkeys. Emerging work using electroencephalography to record electrical brain activity in humans (Sambo and Forster, 2011; Bernasconi et al., 2018; Noel et al., 2019) showed electrodes corresponding to somatosensory-motor regions in the parietal cortex to be associated with PPS representation. In particular, the study conducted by Bernasconi et al. (2018), using intracranial electroencephalography, was able to identify specific cortical and subcortical regions involved in multisensory integration and PPS representation. Here, they demonstrated that the postcentral gyrus, insula, and parahippocampal gyrus are central to the encoding of spatio-temporal aspects of PPS. While the postcentral gyrus has been well established as brain region underlying PPS, the insula and parahippocampal gyrus appear to be novel in the conceptualization of PPS representation.

A wealth of functional neuroimaging studies have further established a PPS neural network that encompasses the ventral intraparietal sulcus, the lateral occipital cortex, and the ventral premotor cortex (see **Figure 1**; Makin et al., 2007; di Pellegrino and Làdavas, 2015). The ventral intraparietal (VIP) sulcus has been associated with the visual guidance of head movements, as well as hand, eye, and mouth coordination, further eliciting complex defensive movements (eye closure, facial grimacing, and protective movement of the hand were elicited via electrical stimulation of the VIP in monkeys; Cooke and Graziano, 2003) under perceived threat. Most VIP neurons integrate visual and tactile afferent information, with a matching representation of body surface appearing present within this area (Squire, 2009). Similarly to the primate brain, the VIP in humans is specifically associated with PPS representation, despite its proximity and interconnections with other distinct intraparietal areas associated with visual-motor coordination for reaching and grasping (e.g., anterior and medial intraparietal areas; Grefkes and Fink, 2005). The lateral occipital complex (extra-striate regions in the human visual cortex) is also involved in shape perception and object recognition (Grill-Spector et al., 2001) and is essential to representation of the surroundings of the body.

Conversely, the ventral premotor cortex is involved in hand movements, recognition of other individuals' hand movements, motor aspect of speech, associative sensorimotor learning and sensorimotor integration (Binkofski and Buccino, 2006). For example, one study revealed a close resemblance between monkey and human brains relative to multimodal processing of moving stimuli in the intraparietal sulcus (equivalent to the ventral intraparietal area in monkeys), the ventral premotor, and the lateral postcentral cortex—the site of the primary somatosensory cortex (Bremmer et al., 2001). More recent studies investigating the integration of visuo-tactile stimuli in the human brain find that the intraparietal sulcus, supramarginal gyrus, parietal operculum (second somatosensory area), insula, dorsal premotor cortex, cerebellum (lobule VII), and putamen emerge as key areas containing multimodal neurons that integrate visuo-tactile stimuli in the near-hand space (Gentile et al., 2011, 2013). Critically, all these brain regions have shown activation during visuo-tactile stimulation of the hand in humans (where the tactile stimulus was delivered on the hand and the visual stimulus was displayed at ∼2 cm above the hand; Gentile et al., 2011) and are involved in visuo-spatial and visuo-motor functions essential to the multisensory representation of the space surrounding the body (Gentile et al., 2011). Interestingly, a study by the same research group found the ventral premotor area to serve as the focus of whole body-centered multimodal processing (Gentile et al., 2015). In addition, the superior parietal occipital junction appears to play a critical role in representing a hand- and face-centered visual space surrounding the body (Gallivan et al., 2011). Finally, recent research reveals the role of the vestibular system in modulating PPS boundaries. Here, as compared to no rotation, vestibular stimulation (whole-body rotation) that was congruent with the direction of external inputs (leftward or rightward approaching auditory stimuli) was found to speed tactile detection and expand PPS boundaries around the body (as measured by tactile response time; Pfeiffer et al., 2018).

Crucially, the neural correlates underlying PPS representation appear to overlap with brain areas associated with other aspects of bodily self-consciousness. For example, fronto-parietal regions that process multisensory information are linked to both PPS and body ownership (Blanke, 2012; Serino, 2019). In addition, the insula and the putamen have been linked to both PPS and body ownership tasks (Blanke, 2012). Of note, a conjunction analysis by Grivaz et al. (2017) identified only two small activation clusters within the left parietal cortex during tasks involving PPS and body ownership (Grivaz et al., 2017; Serino, 2019). Furthermore, the posterior parietal cortex and vestibular regions associated

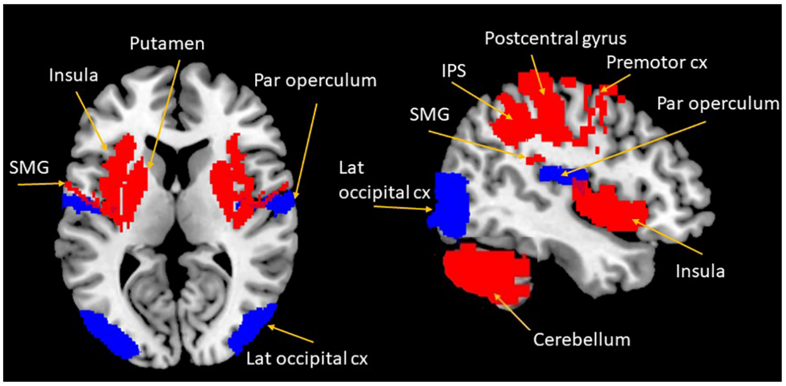

FIGURE 1 | Overview of cortical and subcortical regions involved in the PPS representation and in PTSD. Blue areas show regions primarily involved in the PPS representation; red areas show regions associated with both PPS representation and PTSD. Cx, cortex; IPS, intraparietal sulcus; lat, lateral; SMG, supra marginal gyrus; par, parietal.

with PPS representation have also been found to be involved in processing self-location and first-person perspective (Blanke, 2012). Taken together, neuroimaging data support the hypothesis of interconnection and functional interaction among different aspects of bodily self-consciousness necessary to create a coherent conscious experience; however, further studies are warranted to better understand the neural correlates underlying different aspects of bodily self-consciousness.

PERIPERSONAL SPACE AND PSYCHOLOGICAL TRAITS AND DISORDERS

As illustrated in **Table 1**, consistent with ongoing conceptualizations of the PPS as a protective zone surrounding one's body (a so-called defensive peripersonal space), specific personality traits and psychopathologies have been found to affect the PPS representation and its plasticity. We conducted a literature review using PubMed and the following search keywords: "personal space" in addition to "anxiety," "autism," "schizophrenia," "PTSD," "disorder," respectively. The rationale behind the keywords stemmed from previous PPS research reporting specific PPS characteristics in anxiety, autism, and schizophrenia (Noel et al., 2015b, 2018b), and from our interest in PTSD in particular. The keyword 'disorder' was used to explore potential additional research in psychopathology. The studies included used evidence-based methodology to measure PPS boundaries, a valid standardized psychological measure for assessment, and involved adults. The present literature search was intended to provide a background of the research on PPS in psychopathology, and did not intend to cover the entire literature on psychological traits and PPS in a systematic fashion. Taken together, the studies presented point toward a significant correlation between PPS representation and specific psychological characteristics. Further studies are warranted to clarify whether specific characteristics of the PPS underlie the etiology of psychological disorders and how psychological states and traits can affect the representation of an individual's surrounding space (see **Table 1** for a summary).

Trait Anxiety

As described above, the hand-blink reflex has been used to measure the defensive response within the PPS. This brainstem-driven reflex is modulated by the sensorimotor cortices responsible for representation of PPS (Sambo et al., 2012). Here, Sambo and colleagues investigated the correlation between the hand-blink reflex and trait anxiety in a student sample. They found a significant positive correlation between the size of the PPS and trait anxiety, suggesting that the higher the level of anxiety experienced by an individual, the larger the PPS as indexed by the magnitude of the hand-blink reflex (Sambo and Iannetti, 2013). Interestingly, however, no such correlation emerged from claustrophobic traits in this study (see below). A following experiment showed similar results, where trait anxiety was found to be positively correlated with a larger peripersonal space in a healthy sample (Iachini et al., 2015).

Phobias

Using a line bisection task in far and near space (where a leftward versus rightward bias is usually employed to differentiate between the near versus far space, respectively), Lourenco and colleagues (Lourenco et al., 2011) found that individuals reporting higher claustrophobic scores had a larger PPS (i.e., they showed a leftward bias within a larger space around the body). These authors suggested that a larger PPS may be critical to the etiology of claustrophobia. Critically, similar results were reported in a more recent study where subjects endorsing high levels of claustrophobic fear had a larger PPS when compared to those with low claustrophobic fear while using a laser point to perform the line-bisection task (Hunley et al., 2017). These researchers also found that people with high claustrophobia scores have a decreased ability to expand the PPS when using a tool (a stick) to perform the line bisection task, thus showing decreased flexibility of the PPS. Another study examining cynophobia (unreasonable fear for dogs) (Taffou and Viaud-Delmon, 2014),

TABLE 1 | List of studies investigating PPS in psychopathology.

References	PPS measure	Sample	Psychological characteristics	Psychological assessment	Results
Bogovic et al., 2014	The variable measured is Personal Space (PS), through a stop-distance paradigm, where participants self-judge PS boundaries and communicate them verbally with respect to a person approaching them	83 male veterans with PTSD, 68 male veterans without PTSD	PTSD	PTSD prior diagnosis according to DSM IV, Mississippi Scale for Combat-Related Posttraumatic Stress Disorder (M-PTSD)	Participants with PTSD showed a significant preference for greater interpersonal distances as compared to the control group. The PTSD group also showed a preference for greatest interpersonal distance when approached from behind. By contrast, the control group preferred the greatest distance when approached frontally.
Delevoye-Turrell et al., 2011	The variable measured is Personal Space (PS), through a stop-distance paradigm, where participants self-judge PS boundaries and communicate them verbally with respect to either an object or a person.	20 individuals with schizophrenia (SCZ), 20 paired-matched healthy controls (HC)	Schizophrenia	Positive and Negative Syndrome Scale-PANSS for individuals with Schizophrenia	Either in the object condition and the person condition, SCZ participants revealed increased judgment variability of PS boundaries, as compared to HC.
Di Cosmo et al., 2018	Time reaction to a tactile stimulus administered on the hand, while task-irrelevant approaching sounds are presented	Study 1: 20 adults with Schizophrenia (SCZ), 20 healthy participants (HC). Study 2: out of 36 healthy participants, 18 were included in the low-schizotypy group and 18 in the high-schizotypy group	Study (1) Schizophrenia Study (2) Schizotypal traits	Positive and Negative Syndrome Scale-PANSS for individuals with Schizophrenia, Schizotypal Personality Questionnaire-SPQ for healthy controls	Study 1: SCZ showed significantly narrower and sharper PPS boundaries as compared to HC, as measured through independent sample t-test on the reaction time to tactile hand stimulation during approaching sounds. Study 2: independent sample t-test showed high-schizotypy group had significantly narrower PPS boundaries than the low-schizotypy group
Hunley et al., 2017	Line bisection bias in the far and near space with a laser point or a stick	70 healthy participants	Claustrophobic fear	CLQ Claustrophobia Questionnaire	In the laser point condition, the suffocation subscale scores of the CLQ were found to be significant independent predictors of the size of near space (PPS), using multiple least-squares regression, where higher scores corresponded to larger PPS. In the stick condition, individuals with higher claustrophobic fear did not show expansion of PPS when bisecting lines at farther distances.
Iachini et al., 2015	variable measured is Personal Space (PS), through a stop-distance paradigm, where participants self-judge PS boundaries and communicate them verbally with respect to a person approaching them	70 healthy participants	Trait anxiety	STAI State-Trait Anxiety Inventory	The correlation analyses showed that reachability space and comfort-distance judgments were positively correlated to both trait and state anxiety scores.

(Continued)

TABLE 1 | Continued

References	PPS measure	Sample	Psychological characteristics	Psychological assessment	Results
Lourenco et al., 2011	Line bisection bias in the far and near space	35 healthy participants	Claustrophobic fear	CLQ Claustrophobia Questionnaire	CLQ scores were found to be significant independent predictors of the size of near space (PPS), using multiple least-squares regression, where higher scores corresponded to larger PPS.
Mul et al., 2019	Time reaction to a tactile stimulus administered on the hand, while task-irrelevant approaching sounds are presented	22 adults with autism spectrum disorders and 29 healthy participants	Autism Spectrum Disorder	Autism Diagnostic Observation Schedule diagnostic interview (ADOS)	ASD participants exhibited a smaller PPS size as compared to healthy controls, and showed to have sharper PPS boundaries, as measured by the slope in their RTs as a function of the temporal delay of the tap, when they were approached by sound.
Sambo and Iannetti, 2013	Hand-blink reflex	15 healthy participants	Trait anxiety	STAI State-Trait Anxiety Inventory	Using multiple least-squares regression, trait anxiety resulted to be a significant predictor of PPS size, where higher anxiety scores corresponded to a larger PPS size.
Taffou and Viaud-Delmon, 2014	Audio-tactile interaction task: time reaction to vibration stimulation of a finger, during presentation of threatening vs. non-threatening approaching sounds.	30 healthy participants: 15 with low cynophobia scores, 15 with high cynophobia scores	cynophobia-unreasonable fear of dogs	Questionnaires from the authors exploring fear of dogs	Participants with high cynophobic scores showed larger PPS boundaries as compared to participants with low cynophobic scores during the threatening sound condition (growling dog).

using an audio-tactile interaction task, found that a group of dog-fearful participants showed a larger PPS as compared to a group of non-dog-fearful participants when exposed to a threatening growling dog sound.

Autism

A recent study found that adults with autism spectrum disorder had a PPS that was smaller and with sharper boundaries (steeper slope in reaction times between extrapersonal and peripersonal space) than those observed in healthy controls (Mul et al., 2019). Here, the researchers employed a standard audiotactile task (tactile stimulation on a finger while an irrelevant looming sound was delivered) and used reaction times as an indirect measure of PPS.

Schizophrenia

A recent study investigated PPS in schizophrenic adults (Di Cosmo et al., 2018) using a standard audio-tactile task (where reaction times to a tactile stimulus to the hand were used as a proxy of PPS boundaries, while irrelevant looming sounds were administered to the participant). Here, a smaller PPS seemed to characterize individuals with schizophrenia as compared to healthy controls. Additionally, individuals with higher scores on the schizotypal traits, as measured through the Schizotypal Personality Questionnaire (Raine, 1991), showed smaller PPS as compared to individuals with lower schizotypal traits. This result was interpreted as evidence of the abnormal representation of the space surrounding the body in schizophrenia. In line with this conclusion, a study using self-judgment as a measure of PPS boundaries (participants indicated verbally when they thought a target—person vs. object—reached the boundaries of their PPS) found that as compared to healthy controls, participants with schizophrenia showed high variability in defining their PPS through self-judgment (Delevoye-Turrell et al., 2011). This result is in keeping with the conceptualization that schizophrenia is a disorder of the self, where PPS boundaries are not clearly defined and/or a high variability characterizes them, depending on the symptomatology present moment by moment (Noel et al., 2017).

HOW TRAUMA MAY AFFECT PERIPERSONAL SPACE

Peripersonal Space in Trauma-Related Disorders

Experiencing trauma has the potential to strongly impact the individual's life, with associated biological, social, and psychological repercussions. In trauma-related disorders (PTSD, Acute Stress Disorder, Adjustment Disorder) hyper-arousal, re-experiencing, avoidance, negative mood and cognition, as well as dissociative symptoms may occur, with affected individuals enduring significant impairment in their lives (APA, 2013). This array of symptoms can alter the representation of the self at multiple levels, including at the cognitive, bodily, and social levels, thus leading to significant effects on how an individual interacts with her/his environment. Here, we explore alterations of bodily self-consciousness as they relate to symptoms of depersonalization and of derealization, where an individual feels detached from his/her entire body or parts of the body, or when surroundings are perceived as unreal or dream-like, respectively (Lanius et al., 2010; APA, 2013; Stein et al., 2013).

Critically, altered neural activity and connectivity associated with PTSD symptomatology shows significant overlap with cortical and subcortical regions that have been found to be involved in the PPS representation (e.g., Lanius et al., 2006, 2016; Shaw et al., 2009; Shin and Liberzon, 2010; Daniels et al., 2012; Whalley et al., 2013; Teicher et al., 2016; Wang et al., 2016; Naegeli et al., 2018).

Accordingly, we propose that trauma-related symptoms may affect the representation of PPS, especially when considering its defensive purpose. As previous research demonstrates, psychological traits can influence PPS boundaries: whereas, for example, trait anxiety and claustrophobia have been correlated with larger PPS boundaries (Lourenco et al., 2011; Sambo and Iannetti, 2013; Hunley et al., 2017), schizotypal traits and autism have been linked to smaller and sharper PPS boundaries (Di Cosmo et al., 2018; Mul et al., 2019). To date, however, no research has explored specifically the influence of trauma exposure on the PPS representation. Considering that hyper-arousal symptoms involve a heightened alertness and hyper-vigilance (APA, 2013), we hypothesize that individuals diagnosed with PTSD and Acute Stress Disorder will exhibit a larger PPS as compared to controls as a self-protective function, thus ensuring a bigger safety zone surrounding their body. In addition, avoidance symptoms—the tendency to fleeing from trauma reminders in the form of places, interactions, emotions (APA, 2013)—are likely to require larger PPS boundaries in order to avoid interpersonal contact. Consistent with this hypothesis, one study investigating interpersonal space representation in a population of male veterans (Bogovic et al., 2014) found that when asked to state their preferred interpersonal distances, participants with combat-related PTSD preferred significantly larger interpersonal distance as compared to controls. Interestingly, greater interpersonal distance was also preferred by PTSD participants when the other person was approaching the back of the participant as compared to the front. Finally, in a previous study using the Rubber Hand Illusion experimental paradigm, as compared to healthy controls, we observed a more rigid representation of the body among individuals with PTSD (Rabellino et al., 2018a). As pointed out by previous literature reviews (Ehrsson, 2012; Serino, 2019), the interdependence among different aspects of bodily self-consciousness allows us to unravel characteristics of the PPS representation while observing the expression of self-identification (e.g., body ownership). Here, individuals with PTSD were significantly less affected by the illusion effect of owning a fake hand instead of their own (as revealed by a smaller perception drift), thus showing a less malleable representation of the bodily self. Taken together, these observations suggest that in PTSD the PPS is likely to be characterized by a larger size (for defensive purposes) and limited plasticity and dynamics (less susceptibility to modify the body schema in adaptation to changes in multisensory inputs, which would in turn lead to a rigid PPS; see **Figure 2**). In addition, we would expect to observe sharp PPS boundaries in PTSD—including a sharp contrast in response to stimuli in the near versus far space—, similar to a previous study that investigated PPS in association with trait anxiety (Sambo and Iannetti, 2013).

By contrast, the dissociative subtype of PTSD, characterized by depersonalization and derealization (APA, 2013) is likely to have the effect of preventing the individual from creating a stable space as a defensive zone around the body. During states of depersonalization involving detachment from one's own body, the individual lacks the ability to maintain a coherent representation of the body (Lanius et al., 2012; Spiegel et al., 2013; Ataria et al., 2015). When this is lost, one may speculate that the PPS might become highly variable in size, depending on the psychological state of the individual (for example, changing from an embodied state to a state of depersonalization). Indeed, in our own study of sense of ownership in PTSD and its dissociative subtype (Rabellino et al., 2016b, 2018a), we observed high variance in the rubber hand illusion effect among individuals within the dissociative subtype group. Here, some of participants switched from a very rigid representation of the body (very small illusion effect, as measured by the proprioceptive drift) to a high susceptibility to the illusion during the experiment (as measured by an increased proprioceptive drift and an endorsement of the subjective illusion effect). We suspect that significant disruption of multisensory integration processes, among individuals with dissociative symptoms, manifested as either a hyper-rigid (as in non-dissociative PTSD) or extremely weak representation of the body during characterization of the flow of experience (as experienced in out-of-body experiences, where the individual perceives him/herself as out of the body; Ataria, 2016). We thus expect the emergence of extremely variable, state-dependent PPS boundaries among individuals with the dissociative subtype of PTSD, where the boundaries of the PPS representation would vary depending on the psychological state of the individual (for example, transitioning in and out of a state of depersonalization; see **Figure 2**).

Similarly, a review of studies on peripersonal space in schizophrenia and in autism spectrum disorder (see also above paragraph "Peripersonal Space and Psychological Traits and Disorders;" Noel et al., 2017) indicated that individuals diagnosed with schizophrenia experience shallow and highly variable boundaries between the peri- and extrapersonal space (as measured via various body-illusion experiments). Shallow and highly variable PPS boundaries were thus interpreted as an impairment in distinguishing between the self and others, a difficulty in keeping with the aforementioned conceptualization of schizophrenia as a disorder of the self (Noel et al., 2017). Accordingly, we hypothesize that disorders of consciousness,

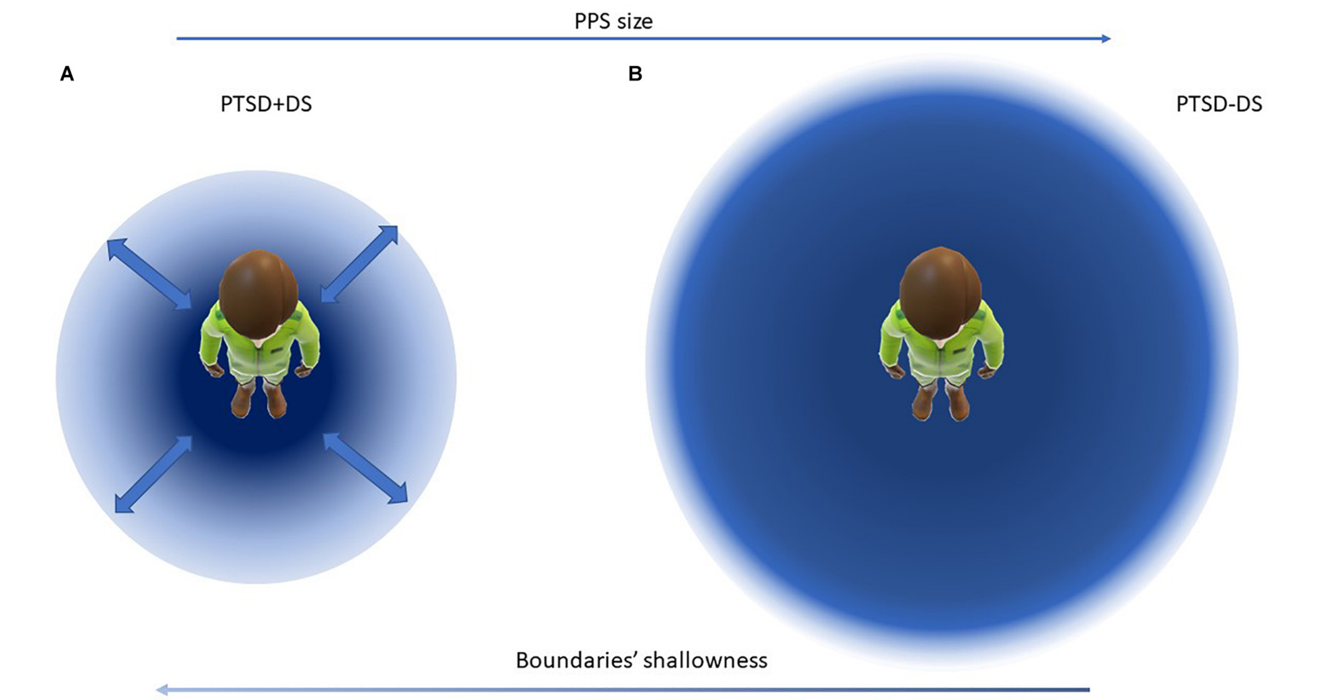

FIGURE 2 | Visualization of the proposed model of PPS representation in individuals with the dissociative subtype of PTSD **(A)** and with PTSD **(B)**. In panel **(A)** the PPS is smaller and with shallow boundaries, in panel **(B)** the PPS is larger and with sharper boundaries. Arrows indicate progressive increase of sharp shift peri-extra-personal space toward the right, and increase of shallowness of PPS boundaries toward the left. Bold arrows indicate high variability in the PPS size in panel **(A)**.

including depersonalization disorders, are likely to involve similar shallow boundaries surrounding PPS representation, with high variability characterizing the delimitation of the PPS. This high variability in PPS boundaries could correspond to an unstable self-other distinction in the moment-to-moment flow of bodily self-consciousness. In fact, the dissociative subtype of PTSD often presents a comorbidity with other dissociative disorders (e.g., dissociative amnesia, dissociative identity disorder; APA, 2013; Wabnitz et al., 2013; Swart et al., 2020) and with associated instability of the sense of self.

Sense of agency — the sense of controlling one's own body actions (De Vignemont and Fourneret, 2004; Haggard and Chambon, 2012) is another intriguing aspect of self-consciousness. In a recent study on the relation between sense of agency, body schema, and PPS (D'Angelo et al., 2018), sense of agency was found to shape body schema and PPS, where an increased sense of agency appeared to extend the boundaries of the PPS. Experiencing trauma also profoundly affects the sense of agency (Ataria, 2015) as the traumatic event itself can produce a loss in the sense of agency, at least temporarily. For example, during a traumatic event, an individual may experience the body as not responsive to one's intentions, an experience defined as a freezing/tonic immobility state, where the body feels frozen and unable to move (Kozlowska et al., 2015; Volchan et al., 2017) or, alternatively, may experience extreme helplessness when the event itself involves the impossibility of action (e.g., when no physical escape is viable; Schauer and Elbert, 2010). Indeed, our study using the rubber hand illusion paradigm to investigate sense of ownership and agency in PTSD revealed a negative correlation between the illusion effect and sense of agency in individuals with PTSD, where a higher illusion effect corresponded to a decreased sense of agency (Rabellino et al., 2018a). Taken together, these studies suggest that individuals with PTSD who report a decreased sense of agency, especially the dissociative subtype of PTSD, would show unique PPS representations.

Neural Correlates of Peripersonal Space in Trauma-Related Disorders

In this section, we aim to present the interesting overlap between the neural substrates underlying PTSD and the neural correlates involved in the PPS representation. A range of neuroimaging studies involving individuals with PTSD provides strong evidence for altered neural activity and connectivity in cortical and subcortical brain structures that are also implicated in key processes underlying the representation of PPS, including multisensory processing, bodily perception, and self-consciousness (see **Figure 1**). The following section explores how altered neural activity in PTSD in key brain regions involved in PPS may influence PPS in this disorder.

Premotor Cortex

As compared to healthy controls, victims of urban violence with PTSD show reduced volume in the ventral portion of the premotor cortex (Rocha-Rego et al., 2012), a region central to sensorimotor integration, hand movements, and the motor aspect of speech (Binkofski and Buccino, 2006). By contrast, the dorsal part of the premotor cortex, associated with the multisensory representation of the PPS, shows increased activity during reliving symptoms in PTSD (Whalley et al., 2013) and hyper-responsiveness to alerting sounds in PTSD as compared to trauma-exposed controls (Naegeli et al., 2018). Functional connectivity studies in PTSD reveal further increased connectivity of the premotor cortex with the dorsolateral periacqueductal gray, a brainstem structure involved in active defensive responses (such as fight/flight responses), thereby suggesting increased active defense responses in PTSD at rest (Harricharan et al., 2016). In addition, weakened connectivity between the premotor cortex and middle frontal gyrus has been shown in individuals with PTSD during implicit threat processing, a finding in keeping with the widespread documentation of disruption in executive functioning among individuals with PTSD (Cisler et al., 2013). Taken together, these studies point toward altered neural activity and connectivity of the premotor cortex in PTSD, suggesting a trauma-related differential functionality of the sensorimotor integration in this disorder, likely affecting the representation of PPS.

Intraparietal Sulcus

The intraparietal sulcus, a region fundamental to PPS representation and also containing multimodal neurons for multisensory processing, appears hyper-responsive to exposure to loud sounds among individuals with PTSD as compared to trauma-exposed controls (Naegeli et al., 2018). This result suggests atypical noradrenergic influences stemming from the locus coeruleus, an effect likely to trigger attention and motor preparation processes associated with an alerting state, thus affecting sensorimotor processing and PPS representation in PTSD.

Putamen

In addition to its well-known role in motor planning and in executive functioning (Gentile et al., 2011), the putamen is also involved in visuo-tactile integration. For example, one study examining PTSD in relation to interpersonal trauma reported increased functional connectivity of the locus coeruleus with the putamen in PTSD (Steuwe et al., 2015). The putamen has also shown to be hyper-active among individuals with PTSD in association with reliving symptoms (Osuch et al., 2001), and at rest (Wang et al., 2016) and has shown to be positively correlated with PTSD symptom severity during trauma processing (Mickleborough et al., 2011) and autobiographical memory retrieval (Thome et al., 2020). Taken together, these findings point toward the important role played by the putamen in the planning of motor actions in the surrounding environment, thus likely affecting the goal-oriented function of PPS.

Supramarginal Gyrus

The supramarginal gyrus is a crucial area for bodily self-consciousness and for maintaining a stable representation of one's body in space (self-location; Serino et al., 2013; Blanke et al., 2015). One study investigating neural activity in PTSD found increased activity of the supramarginal gyrus during flashbacks — a common symptoms in PTSD where the individual re-experiences a traumatic event as if reoccurring in the present moment — (Whalley et al., 2013), a time when bodily self-consciousness and self-location are likely disrupted. By contrast, a metanalysis of neuroimaging studies of PTSD reported that the supramarginal gyrus is among those neural areas showing decreased neural activity when compared to controls (Patel et al., 2012). Furthermore, in our own work examining the functional connectivity of two areas of the cerebellum involved in sensorimotor integration (the anterior cerebellum and the anterior vermis) in PTSD, we found decreased functional connectivity of these regions with the supramarginal gyrus among individuals with the dissociative subtype of PTSD as compared to PTSD and healthy controls (Rabellino et al., 2018b). These results are suggestive of an impairment in maintaining a stable sense of bodily self-consciousness in the dissociative subtype of PTSD. Similarly, a study investigating the functional connectivity of the vestibular nuclei (involved in bodily orientation in space) in PTSD at rest found that the functional connectivity of the vestibular nuclei with the supramarginal gyrus was negatively correlated with depersonalization/derealization symptoms scores (Harricharan et al., 2017). This result pointed further toward an impaired sense of bodily orientation in space among individuals experiencing depersonalization states, a finding consistent with the results of previous studies suggesting altered functioning of the supramarginal gyrus during induced out-of-body experiences (De Ridder et al., 2008; Lopez et al., 2008). Taken together, these findings suggest that altered bodily self-consciousness, associated strongly with the dissociative subtype of PTSD, may affect functionality of the PPS representation in this disorder.

Postcentral Gyrus

Notably, the postcentral gyrus, also involved in motor responses and PPS representation, shows increased neural activity, as compared to healthy controls, among individuals with PTSD during attention and working memory tasks (Brown and Morey, 2012). By contrast, decreased activation of the bilateral postcentral gyri was reported in a meta-analysis investigating neural activity during symptom provocation (trauma-related stimuli) among individuals with PTSD as compared to controls (Sartory et al., 2013). Moreover, decreased functional connectivity of the postcentral gyrus with the anterior cerebellum (lobule IV-V) and the anterior vermis (cerebellar regions involved in sensorimotor processing and integration) has been reported in the dissociative subtype of PTSD when compared to PTSD and healthy controls (Rabellino et al., 2018b), thus supporting our hypothesis of impaired functionality of sensorimotor processing and integration in the dissociative subtype of PTSD. Finally, decreased functional connectivity between the insula and postcentral gyrus has been reported in PTSD and its dissociative subtype as compared to controls, pointing toward impairment in the monitoring and emotional appraisal of the surrounding environment

(Harricharan et al., 2020). On balance, these results support further the presence of alterations of sensorimotor processing and multisensory integration in PTSD, an effect particularly pronounced in the dissociative subtype of PTSD, which may be associated with altered representation of PPS.

Cerebellum

Different regions of the cerebellum (especially anterior cerebellum and anterior vermis that are of interest for bodily self-consciousness and PPS representation) have shown altered neural activity and functional connectivity in PTSD and its dissociative subtype either during trauma processing and at rest (Bonne et al., 2003; Yin et al., 2011; Wang et al., 2016; Carletto and Borsato, 2017). In particular, neural activity within the anterior cerebellum (lobules IV-V) was found to correlate positively with flashback intensity in PTSD (Osuch et al., 2001). In addition, increased regional cerebral blood flow (rCBF) has been reported within the anterior vermis among individuals with combat-related PTSD during exposure to combat sounds as compared to neutral sounds (Pissiota et al., 2002). At rest, increased resting-state functional connectivity of the anterior vermis with the amygdala – involved in emotional response – and periaqueductal gray – a key region for the fight-or-flight response under threat – (Thome et al., 2016) was demonstrated in PTSD as compared to healthy controls. Furthermore, decreased functional connectivity of the anterior cerebellum and anterior vermis with temporo-parietal regions and somatosensory cortices (postcentral and supramarginal gyrus), brain regions essential to multisensory integration and bodily self-consciousness, has been reported in the dissociative subtype of PTSD as compared to PTSD and healthy controls at rest (Rabellino et al., 2018b). By contrast, in the same report, increased functional connectivity of the posterior cerebellum (Crus I, involved in cognitive functioning) with multisensory processing cortices (temporal pole) was observed in the dissociative subtype of PTSD as compared to PTSD at rest (Rabellino et al., 2018b). Finally, reduced cerebellar volume has been reported in PTSD (De Bellis and Kuchibhatla, 2006; Carrion et al., 2009; Baldaçara et al., 2011), a finding suggestive of decreased functioning of bodily self-consciousness processes. Collectively, these observations of alterations in the neural activity and functional connectivity of cerebellar regions essential to sensorimotor integration are in line with an overall pattern of impaired functioning of bodily self-consciousness in PTSD, which may in turn have consequences on the processing and integration of inputs representing the surrounding environment.

Insula

The insula serves as a fundamental structure for interoceptive awareness. Interoception plays a crucial role in bodily self-consciousness and represents an essential function for differentiating internal and external sensory inputs. Interestingly, PTSD is often characterized by hyperarousal symptoms, where interoception (internal signals such as heart rate, breathing rate, sweating) may overload the conscious experience of the bodily perception. By contrast, the dissociative subtype of PTSD is characterized by detachment from the body, including bodily signals, with a resulting impairment of interoceptive awareness (Harricharan et al., 2020). In numerous neuroimaging studies of individuals with PTSD, the insula appears hyper-responsive during various tasks involving trauma processing or presentation of emotional stimuli (Lanius et al., 2007; Simmons et al., 2008; Shin and Liberzon, 2010; Aupperle et al., 2012; Brinkmann et al., 2017) and its neural activity correlates positively with symptom severity (Osuch et al., 2001; Hopper et al., 2007). In addition, functional connectivity studies have revealed increased functional connectivity between the insula and amygdala – involved in emotional responsiveness – (Nicholson et al., 2016) in PTSD, and between insula and BNST – associated with sustained threat response – in the dissociative subtype of PTSD (Rabellino et al., 2017) as compared to healthy controls, suggesting an association between interoceptive awareness and fear response.

A more recent study examining the functional connectivity of the insula in PTSD at rest showed decreased functional connectivity of the insula with sensorimotor cortices (pre- and post-central gyri) in PTSD as compared to healthy controls, with even weaker connectivity observed in the dissociative subtype as compared to the PTSD group. These findings have been discussed in relation to the limited capacity of individuals with PTSD and its dissociative subtype to integrate afferent information from internal states and from the environment into a unified conscious experience (Harricharan et al., 2020), an ability fundamental to maintain an integrated bodily self-consciousness and create an effective representation of the PPS.

Vestibular System

Finally, the vestibular system serves as fundamental neural network involved in interoceptive awareness and multisensory information processing. This latter is essential to orient the body in space and has been considered crucial to the PPS representation. Vestibular neurons have been indicated to be involved in trimodal visuo-tactile vestibular integration to allow the processing of self-location and self-identification, two main aspects of bodily self-consciousness (Blanke, 2012). Interestingly, a recent study investigating the functional connectivity of the vestibular nuclei in the brainstem of individuals with PTSD at rest (Harricharan et al., 2017) showed decreased connectivity of the vestibular nuclei with the posterior insula in PTSD as compared to controls, and disrupted connectivity with key cortical vestibular areas (parieto-insular and dorsolateral prefrontal cortex) in the dissociative subtype of PTSD as compared to PTSD and controls. These data suggest a disturbed body orientation in space in PTSD that would affect the representation of the body and related PPS. Previous studies in neurological patients have described heautoscopic symptoms (visual illusion of seeing one's body from out of the body, often from above) as self-identification and self-location disorders, where impaired multisensory integration of bodily signals and disintegration of vestibular signals may be at the root of out-of-body experiences (Blanke and Mohr, 2005; Blanke, 2012). Here, an interesting research question arises about the nature of the PPS representation during dissociative experiences associated with psychological trauma-related disorders (dissociative subtype of

PTSD; Frewen et al., 2015). Importantly, we argue that state-dependent dissociative symptoms (affected by the psychological temporary state; Frewen and Lanius, 2014; Lanius, 2015) would facilitate the investigation of temporary dynamic distortions of the PPS, thus deepening our understanding of bodily self-consciousness as a dynamic experience that changes over time.

Taken together, the neuroimaging studies reviewed here support the hypothesis of an atypical representation of the PPS in PTSD, where neural structures related to bodily self-consciousness, self-location, motor planning, and multisensory integration show altered neural activity and/or functional connectivity in PTSD and its dissociative subtype when compared to controls. This neural pattern can be interpreted as a general reorganization of neural networks in PTSD that favors innate alarm responses to potential threats and preparation for defense responses, thus affecting the integration of multisensory afferent and efferent inputs, with the resulting representation of the bodily self and its surroundings being biased toward potential incoming threats (Rabellino et al., 2015, 2016a, 2019; Steuwe et al., 2015; Lanius et al., 2016; Frewen et al., 2017).

CONCLUSION

On balance, our review of PPS and its relation to trauma-related disorders points clearly to the need for further study within this field and, overall, aims to inspire future directions of research on PPS and bodily self-consciousness in the aftermath of trauma.

Although this work provides an extensive overview of PPS characteristics and its relationship with psychological traits and symptoms, it is not intended as a systematic review but rather as a perspective contribution to the understanding of PPS and trauma-related disorder. Investigation of the different aspects of PPS representation (function, plasticity and dynamics, neural correlates) in psychopathology can deepen our scientific and clinical understanding of bodily self-consciousness, particularly in relation to the altered states of consciousness that underlie dissociative symptoms characterizing certain psychological disorders, including trauma-related disorders. Depersonalization and derealization symptoms remain among the most difficult psychological symptoms to recognize, diagnose, and treat, despite seriously impacting the quality of life of individuals (Boyd et al., 2018). A greater understanding of the PPS representation in trauma-related disorders has the potential to lead to innovative diagnostic methods for recognizing dissociative symptoms, as well as the development of novel clinical interventions designed to specifically target these symptoms. In addition, enhanced knowledge of bodily self-consciousness in relation to the immediate surroundings of an individual may give rise to targeted treatment approaches that could improve multisensory integration in potentially stressful situations, such as social contexts, thus improving social relationships among individuals with trauma-related disorders.

Given that trauma-related disorders are also associated with impairment of bodily self-consciousness in relation to a threat response (Kozlowska et al., 2015; Lanius, 2015; Ataria, 2016), investigation of PPS in this population has the potential to elucidate further the defensive purpose of PPS, while clarifying its role in innate alarm responses under threat. Indeed, preliminary studies examining the flexibility of body schema in PTSD and its dissociative subtype (Rabellino et al., 2016b, 2018a) appear promising in pointing toward the need for further research on the plasticity and dynamics of PPS, which together have the potential to elucidate further unique gradients in PPS boundary representations, thus providing insight on the categorization and function of shallow versus sharp boundaries (Noel et al., 2017).

Finally, studying the neural correlates of PPS in diverse contexts (e.g., under threat, in social context) among healthy individuals and individuals with trauma-related disorders appears crucial to a deeper understanding of functional connectivity and integration between subcortical structures in the brainstem that are dedicated to innate alarm response, balance, and consciousness, sensorimotor cortices devoted to multisensory integration, and prefrontal and posterior cortices involved in higher-order cognition, such as social cognition and self-referential processing.

AUTHOR CONTRIBUTIONS

DR contributed to conception, literature review, and wrote the original draft of the manuscript. MM and RL contributed to funding acquisition. All authors contributed to manuscript revision, read, and approved the submitted version.

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Feeling Oneself Requires Embodiment: Insights From the Relationship Between Own-Body Transformations, Schizotypal Personality Traits, and Spontaneous Bodily Sensations

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Subtle bodily sensations such as itching or fluttering that occur in the absence of any external trigger (i.e., spontaneous sensations, or SPS) may serve to locate the spatial boundaries of the body. They may constitute the normal counterpart of extreme conditions in which body-related hallucinations and perceptual aberrations are experienced. Previous investigations have suggested that situations in which the body is spontaneously experienced as being deformed are related to the ability to perform own-body transformations, i.e., mental rotations of the body requiring disembodiment. We therefore decided to consider whether the perception of SPS might relate to embodiment as assessed through (i) the ability to perform own-body transformations (OBT task) and (ii) schizotypal traits (Schizotypal Personality Questionnaire, or SPQ), since high degrees of schizotypy in the general population have been associated with more vivid perceptions and aberrant perceptual experiences. Then participants completed a standard SPS task. Our analysis revealed that the slower the response time in the OBT task, the more frequent the perception of SPS. This suggests that difficulties in disembodying and mentally transforming one's own body facilitate *feeling* oneself. Furthermore, a greater number of correct responses in the OBT task was associated with less frequent perception of SPS. This suggests that finding it easier to disembody and perform mental own-body transformations interferes with the ability to sense oneself. The results also show that higher schizotypal traits, as assessed through the SPQ, are associated with more frequent perception of SPS. Taken together, these results provide a coherent picture and suggest that embodiment is required in order to correctly *feel* oneself, as expressed through the perception of SPS. The ability to easily experience disembodiment reduces the sense of feeling oneself, and proneness to schizotypal traits produces body misperceptions that enhance and amplify this feeling. The results are discussed in the light of current knowledge and theories about body representations, taking into account attention and interoception as factors that influence body awareness. We offer explanations for perceptual aberrations, body-related delusions, and hallucinations based on misperceived or misinterpreted SPS, and we discuss possible mechanisms that may contribute to *feeling* and misperceiving oneself.

Keywords: spontaneous sensations, embodiment, mental own-body transformations, schizotypy, schizotypal personality

INTRODUCTION

How does it feel to be you? How do you know that this is you? Subjective feelings of the sense of self, when one knows that this is one's own hand or face (Gallagher, 2000), are grounded within one's own body and representations of the body and its parts (Kinsbourne, 1998; Gallace and Spence, 2010; Sakson-Obada et al., 2018). This is what is known as embodiment, or embodied sense of self (Asai et al., 2016).

Research on embodied sense of self has garnered considerable interest during recent decades, and several experimental paradigms have been used to investigate its functional and neural aspects (Manos Tsakiris, 2010). Embodiment has primarily been investigated through its motor and behavioral aspects, such as sense of agency, i.e., subjective awareness of initiating, executing, and controlling voluntary actions (Braun et al., 2018); its sensory aspects, such as experimentally induced illusions that an external object is part of one's body (e.g., the rubber hand illusion) (M. Tsakiris et al., 2007) or the measurement of the boundaries of the peripersonal space (e.g., the estimation of the moment a stimulus will be in collision with the body) (Canzoneri et al., 2012); own-body mental transformations, such as mentally rotating one's own body in order to match a visually presented figure (Bonda et al., 1995; Blanke, 2005) and so on. All these paradigms (as well a number of others) are based primarily on responses to external triggers aimed at assessing self-related phenomena. Yet the term "sense of self" also evokes the status of one's own body, which makes bodily sensations seem unique to oneself. This is the *feeling* that this body or a part of the body belongs to me (Gallagher, 2000; Braun et al., 2018;; Manos Tsakiris, 2017). Major contributions to our understanding of this aspect of embodiment come from research that involves the perception of natural bodily signals, i.e., interoception [(Bud) Craig, 2003; (Bud) Craig, 2004; Duschek et al., 2015]. This aspect is usually investigated through the perception of visceral signals such as heartbeats (Schandry, 1981) or gastric functions (Herbert et al., 2012), which is reminiscent of the original terminology (i.e., "enteroception," meaning the perception of visceral sensations) (Vaitl, 1996). Since the above-mentioned paradigms are all meant to investigate embodiment and the sense of self, they should in theory yield consistent results overall. However, the picture is rather puzzling. For example, some researchers have found no clear relationship between heartbeat perception and the rubber hand illusion, while others have, and still others have found a relationship under certain circumstances only (Suzuki et al., 2013; Filippetti and Tsakiris, 2017; Crucianelli et al., 2018).

Imagine we try to conjure up a quick, introspective view of ourselves, sitting on a chair. Do we have to act, bump into objects, perform mental acrobatic rotations of our own body image, or feel visceral signals coming from inside to sense that we are there, having the direct and immediate experience of our own body in the first-person perspective? Sense of self does not seem to arise exclusively from the perception of stimuli delivered physically on peripheral receptors, the sense of agency, and the perception of visceral signals. Maybe a starting point to better apprehend some of the factors that contribute to the sense of self is looking at what underlies the perception of body boundaries and location in space, something that is clinical in nature (Stanghellini et al., 2014; Sakson-Obada et al., 2018).

The experience of abnormalities of consciousness and neuropsychiatric symptoms is considered by some researchers to be due to disruptions of the sense of self (Moe and Docherty, 2014) and the blur or malleability of the self-others boundaries (Thakkar et al., 2011; Noel et al., 2017; Di Cosmo et al., 2018). There is clinical evidence that abnormal functioning of some cortical areas, such as the temporoparietal junction, may result in seeing oneself from a distance (Blanke and Mohr, 2005), feeling a presence nearby (Arzy et al., 2006), or other bodily illusions (Leker et al., 1996; Persinger, 2001; Thakkar et al., 2011). In schizophrenia spectrum disorders, numerous symptoms relating to the body are observed (Chapman et al., 1978; Peled et al., 2000; Stanghellini et al., 2012), ranging from abnormal feelings of altered shape, to changes in the composition of the body and body decomposition, to blurred body boundaries (Noel et al., 2017; Di Cosmo et al., 2018; Sakson-Obada et al., 2018; Ferroni et al., 2019) up to the point that some authors suggested that schizophrenia (and related spectrum disorders) is a self-disorder in the sense that the first person perspective of the world is altered (Sass and Parnas, 2003). These disruptions in the basic sense of embodiment are viewed as key symptoms and are even used as early predictors of disease (Stanghellini et al., 2012; Ferri et al., 2014). These kinds of perceptual aberrations are also reported by individuals in the general population with high schizotypal personality traits (Chapman et al., 1978; Mohr et al., 2006; Arzy et al., 2007; Di Cosmo et al., 2018). Schizotypal personality refers to a set of traits thought to reflect the subclinical expression of the symptoms of schizophrenia spectrum disorders (Barrantes-Vidal et al., 2015) according to the theory of a psychosis continuum (Nelson et al., 2012). Individuals with high schizotypal traits are at higher risk for psychosis. Three types of factors seem to underlie behavior in schizotypy: cognitive-perceptual (ideas of reference, magical thinking, unusual perceptual experiences, and paranoid ideation), social-interpersonal (social anxiety, no close friends, constricted affect and, again, paranoid ideation), and disorganized (odd behavior and odd speech) (Raine et al., 1994). High schizotypal personality traits—especially in terms of cognitive-perceptual and social-interpersonal factors (Mohr et al., 2006; Van Doorn et al., 2018)—are associated with a higher frequency of body-related aberrant perceptual phenomena (Cicero et al., 2020), such as feelings of a presence nearby, spontaneous disembodiment and out-of-body experiences, perceptions that others fail to experience, modified perception of body parts, exaggerated self-consciousness (Sass and Parnas, 2003) and blurred body boundaries (Sass and Parnas, 2003; Ettinger et al., 2015; Di Cosmo et al., 2018; Ferroni et al., 2020). People with high schizotypal personality traits also seem to experience difficulties in perspective-taking (Langdon and Coltheart, 2001), which is also a basic feature of self-referential processes (Buckner and Carroll, 2007). These experiences suggest that schizotypal personality is associated with proneness to experience self-related disturbances (Mohr et al., 2006; Arzy et al., 2007) and, therefore, that schizotypy may be a way to investigate the sense of self and embodiment.

On the other hand, reports of body-related hallucinatory phenomena in neurologic and psychiatric populations, such as sensing a ghostly gentle touch or the feeling that insects are crawling beneath the skin (Berrios, 1982), suggest that disturbances of body awareness and the self may occur due to abnormal spontaneous activity in cortical areas related to somatosensation and disorders of multimodal integration (Blanke, 2005; Blanke and Arzy, 2005; Geoffroy et al., 2014; Eccles et al., 2015; Graziano, 2018; Bretas et al., 2020). Have you ever felt tingling, tickling, or other sensations on your skin even when there are no mosquitos around to bother you? There are situations in which awareness of touch occurs without any stimulus actually being delivered. Does this mean that you are experiencing some kind of body-related disturbance? These kinds of bodily sensations have been anecdotally reported in the scientific literature by clinical researchers working on tactile sensitivity, and are referred to as paresthesia (Schmidt et al., 1990a,b) or tactile hallucinations (Gallace and Spence, 2014). However, both these terms are highly evocative of pathological conditions (Berrios, 1982) and do not account for the fact that almost everyone experiences such sensations on an everyday basis. This is why the term "spontaneous sensations" (SPS) is preferred (Michael and Naveteur, 2011), as these are believed to constitute the normal counterpart of bodily hallucinations. The spontaneous nature of these phenomena does not allow for experimental manipulation at will. However, over the past 15 years, several researchers have used subjective reports to assess SPS under controlled conditions [e.g., (Naveteur et al., 2005; Michael and Naveteur, 2011; Bauer et al., 2014a; Tihanyi and Köteles, 2017)].

That SPS may constitute the ever-present background of bodily sensations through which body representations arise (Kinsbourne, 1998) suggests that their perception gives cues as to the position of body parts at a given moment, their spatial boundaries and limits, and that they therefore contribute to the sense of self (Michael et al., 2017; Sakson-Obada et al., 2018). The relationship between SPS and neurocognitive body-related processes has been established by means of several forms of evidence. For instance, neuroimaging findings suggest that attending to well-circumscribed and localized SPS results, as a minimum, in activation in the primary somatosensory cortex (Bauer et al., 2014a,b), which includes a precise point-by-point representation of the body (i.e., somatotopy) (Penfield and Boldrey, 1937). A recent investigation gathered evidence that default oscillatory EEG activity in both the primary and secondary somatosensory cortices relates to the perception of SPS, and probably reflects individual differences in bodily awareness. Furthermore, behavioral evidence also supports the involvement of somatosensory cortices in the perception of such sensations, since when perceived in the hands they exhibit a proximodistal gradient: SPS occur more frequently toward the fingertips. This spatial pattern strikingly resembles traces of peripheral receptor distribution in the somatosensory cortex (Schady et al., 1983). Another study found a relationship between SPS and EEG connectivity between cortical areas involved in self-awareness, such as the temporo-parietal junction and the insula (Salgues et al., 2021). Despite such cues, and despite suggestions that SPS may contribute to body awareness and the perception of the spatial limits and boundaries of the body, direct evidence of the relationship between SPS and embodiment is limited. In fact, SPS have been found to be related to interoception (Michael et al., 2015) as classically assessed through the silent heartbeat counting task (Schandry, 1981). Good heartbeat perceivers have increased perception of SPS, and this supports the idea that SPS have something to do with the sense of self and embodiment. Finally, chronic pain syndromes that modify the perception of the body through disruptions of somatosensory and interoceptive functions (Kim et al., 2017; Borg et al., 2018) also modify the perception of SPS (Borg et al., 2015; Echalier et al., 2020).

However, the picture is still incomplete. By nature and by definition, perceiving SPS is *feeling* oneself. Yet evidence of the relationship between SPS and other phenomena related to embodiment (or disembodiment) is missing. One way to establish such a relationship would be to show that SPS perception relates to performance in one of the tasks designed to assess self-referential processes, as would showing that proneness to experiencing body-related unusual phenomena changes the perception of SPS. Therefore, we set out to investigate the relationship between SPS and embodiment through a two-fold procedure. First, we used an own-body mental rotation paradigm (i.e., an own-body transformation task, or OBT task) (Blanke, 2005), in order to establish a direct relationship between SPS and the ability to change perspective by mentally rotating own-body image. The ease with which this mental transformation is achieved naturally relates to loose embodiment. If SPS were linked to embodiment, then increased performance in the OBT task would negatively correlate with SPS perception. Second, we used a popular self-completed schizotypal personality questionnaire (SPQ; Raine, 1991). As described above, individuals from the general population with high schizotypal traits have difficulties controlling perspective-taking (Langdon and Coltheart, 2001) and are more prone to experience sensations that others do not usually experience, or experience usual experiences more vividly (Chapman et al., 1978; Raine et al., 1994; Van Doorn et al., 2018). Therefore, if SPS were linked to embodiment, then schizotypal (especially cognitive-perceptual and social-interpersonal) traits would correlate with SPS perception, signaling either diminished self-perception or, on the contrary, exaggerated, enhanced and more vivid self-perception. In order to achieve our aim, all participants completed the SPQ, a validated SPS task, and a computerized OBT task.

MATERIALS AND METHODS

General Procedure

The study was completed in two stages, separated by one to two weeks. During the first stage, participants completed the Edinburgh Handedness Inventory (Oldfield, 1971), the Schizotypal Personality Questionnaire (Raine, 1991), and a form containing questions on age, gender, height, weight, use of psychotropic medications (antidepressants, anxiolytics, neuroleptics, anticonvulsants, hypnotics, tranquilizers, etc.) and reason for use (if applicable), regular use of other psychoactive substances (alcohol, marijuana, etc.), and history of cardiovascular disease or diabetes. During the second stage, participants completed the SPS task, followed by the OBT task.

Participants

The study was carried out in accordance with the Declaration of Helsinki and was approved by the local ethics committee (reference number IRB 00009118). Participants were undergraduate students at Lyon 2 University, France. Exclusion criteria were as follows: history of neurological or psychiatric disease, history of psychoactive substance abuse, history of diabetes or cardiovascular disease, a laterality quotient of less than 50%, reported body mass index (BMI) of less than 18 and greater than 31 kg/m^2 (previous research showed that BMI influences interoceptive processes and SPS, this is why it is necessary to control for such a confounding factor; (Cameron, 2002; Michael and Naveteur, 2011; Michael et al., 2015)], incomplete responses to the SPQ, or more than 50% errors in the OBT task. Of the 78 individuals that initially volunteered to participate, 23 were excluded on the basis of the above-mentioned criteria or did not show up to complete the second stage of the research. The sample therefore included 55 participants (44 female and 11 male), all right-handers (mean laterality quotient 88.7, SD = 13.7), with a mean age of 21.3 years (SD = 2.03; range: 18 to 27) and a mean BMI of 21.4 kg/m^2 (SD = 1.94; range: 18.1 to 27 kg/m^2). Power analyses were conducted on the effect size of the proximo-distal gradient in frequency of SPS, which is their standard characteristic. Based on 8 published studies (Michael and Naveteur, 2011; Michael et al., 2012, 2015, 2017; Beaudoin and Michael, 2014; Borg et al., 2015; Echalier et al., 2020; Salgues et al., 2021) carried out on 367 participants (10 experiments and 1206 hand maps), the weighted mean affect size expressed as Cohen's w is 0.38 (i.e., medium to large) and expressed as Cramér's V is 0.20 (i.e., medium to large). Provided a power of 90% to detect a medium effect size, the number of hand maps needed is 99. Given that two hand maps per participants are collected (one per hand) in the present study, the sample size needed is 50 participants. With a sample of 55 participants (i.e., 110 hand maps) the power is good (92%) and the probability that Type II errors occur is considerably reduced. All participants gave their written informed consent to participate prior to the test.

SPQ

The Schizotypal Personality Questionnaire (Raine, 1991) is a commonly used self-report measure of schizotypy in healthy community samples. It is a simple and quick evaluation involving 74 quoted items with a "yes/no" response, exploring the DSM-IV criteria for schizotypal personality disorder. Its structure reveals a three-factor model of schizotypy reflecting positive/cognitive-perceptual symptoms, negative/social-interpersonal symptoms, and disorganization. The French version of the SPQ (Dumas et al., 2000) has the same factorial structure as the original, a high internal reliability, and good internal consistency.

SPS Task

Participants completed the task at a desk in a quiet, normally lit room with an ambient temperature of 20–23°C. Once they were ready, SPS were introduced as normal phenomena, and to give the participants some idea of what they could expect SPS to feel like, they were given a list of 11 sensations most likely to be felt (beat/pulse, itch, tickle, numbness, skin stretch, tingling, warming, cooling, muscular stiffness, flutter, and vibration). The list used in the SPS protocol was based on the one used originally by Ochoa and Torebjörk (1983), Macefield et al. (1990), Naveteur et al. (2005). Participants were asked to remove any jewelry from their hands and wrists, and to roll up their sleeves to ensure the wrist was not covered. They then had to wash their hands with an antiseptic gel for 15 seconds (Aniosgel® 85 NPC, ≈3 ml per participant), in order to remove any external surface agents that could interfere with the task, and to ensure a homogenous glabrous skin surface across all participants. The test began 15 seconds after the participants finished washing their hands. A protocol was given to each participant. It contained the standardized reduced maps of each hand shown palm up (with a distance of 11.2 cm between the tip of the middle finger and the palm/wrist border). Below each map, the list of 11 SPS was provided, along with two visual analogue scales (i.e., two 10-cm continuous horizontal lines without markers at each ends) for the purposes of confidence rating. A pencil and a 25 × 25 cm piece of smooth white fabric were also given to each participant. Once participants had familiarized themselves with the materials, the task began. The protocol and the pencil were placed away from the participants on the desk to prevent any interference from visual stimuli. Each hand was tested once in a balanced order across the participants. The participants had to sit with their back supported by the backrest of their chair. The leg ipsilateral to the tested hand was turned outwards by about 60 degrees from the midline. Participants placed the white cotton fabric on their thigh, with the tested hand resting on it, palm up, with fingers spaced slightly apart. Only the dorsal part of the hand was in contact with the fabric. The hand not being tested was allowed to hang down on the outer side of the chair. A "start" signal was given verbally by the experimenter, marking the beginning of each test. Participants were asked to gaze at the tested hand for 10 seconds, focusing their attention on the whole hand so that they could detect any sensations that might occur. They were informed beforehand that there was a possibility they would not perceive any sensations, and this is also normal. A "stop" signal given by the experimenter marked the end of the focusing period. Participants were immediately asked to use the protocol to report whether they had detected any sensations on the tested hand, and if they had, to (a) map the extent and location of the sensations by shading on the map of the tested hands the areas where they perceived sensations, (b) estimate the perceived intensity of each sensation according to a 10-point scale (1 = just perceptible; 10 = very intense but not painful), (c) identify the sensations using the list of descriptors. They were allowed to choose more than one descriptor and to add descriptors to the list based on what they detected, and (d) indicate their degree of confidence in the location and extent of the perceived sensations on the two visual analogue scales (ranging from "not confident" to "very confident"). The task lasted approximately 10 minutes, and depicted in **Figure 1A**.

OBT Task

The stimuli and the procedure were taken from a previous study on own-body transformations (Arzy et al., 2007). Participants were presented with a human figurine subtending a visual space of 5.0° × 6.1° angles. The figurine could be front-facing or back-facing, and had either the left or the right hand marked, such that it appeared to be wearing a gray glove with a black ring at the wrist (**Figure 1B**). Stimuli appeared for 200 ms in the center of the computer screen with an inter-stimulus interval of 2000 ms. Participants were asked to make right/left judgments while imagining themselves in the body position of the figure, taking its spatial perspective. This requires mental own-body positioning that can be achieved through mental transformations (O.Blanke, 2005). Responses were given by pressing two predefined buttons on the computer keyboard using the index finger of each hand. Participants were asked to respond as quickly and accurately as possible but always to perform the requested mental transformation before giving the response. A total of 120 trials were presented (60 per facing condition), and the session was preceded by a 10-trial training session. The facing (front vs. back) condition and the gray hand location (left vs. right) were presented randomly and equiprobably. Response times and correct responses were recorded by the computer.

RESULTS

SPQ

The mean scores for each of the three factors of the SPQ were 7.1 (SD = 5.7) for cognitive-perceptual, 7.9 (SD = 5.7) for social-interpersonal, and 5.1 (SD = 3.6) for disorganized. The mean score for the full SPQ scale was 20.1 (SD = 12.1). Internal consistency of each subscale for the present sample was good: cognitive-perceptual $\alpha = 0.87$, social-interpersonal $\alpha = 0.82$, disorganized $\alpha = 0.91$. The internal consistency of the total score was excellent, with $\alpha = 0.93$.

OBT Task

Response times (RT) below 150 ms and over 2000 ms were dismissed as reflecting anticipation and inattention, respectively. Discarded trials accounted for less than 2% of the total number of trials. Response times for correct trials and the number of correct trials were submitted to *t*-tests with the facing condition (front

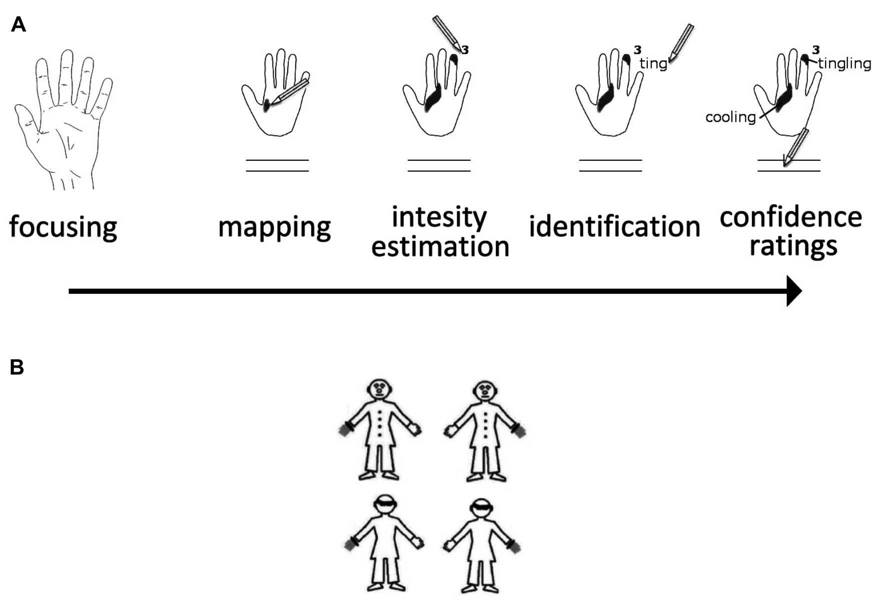

FIGURE 1 | (A) Illustration of the SPS Paradigm. **(B)** The four stimuli used in the OBT task are shown here.

vs. back) as the within factor. As in previous investigations, RTs were faster in the back-facing condition (mean RT = 790 ms, SD = 205 ms) than in the front-facing condition (mean RT = 917 ms, SD = 265 ms; $t(54) = 7.23$, $p < 0.001$, Cohen's $d = 0.96$). And as in previous investigations, no differences were found between the two facing conditions as far as the number of correct responses was concerned (front-facing mean = 56.6, SD = 7.7; back-facing mean = 57.4, SD = 2.7; $t(54) = 0.75$, $p > 0.45$, Cohen's $d = 0.1$). Since both facing conditions evaluate own-body mental transformations in a similar way, the mean RT and the mean number of correct responses were used for subsequent analyses, as in previous papers (O.Blanke, 2005; Mohr et al., 2006).

Topography of SPS Frequency

Maps filled by participants with shaded areas were projected onto a 140 × 140 mm grid, with a 1 mm × 1 mm resolution, and converted into binary code (0 = nil, 1 = shaded cell). This generated two binary maps per participant (i.e., right and left hand), with a total number of 110 maps. By superimposing these maps, a frequency map was obtained, in which each cell value represented the percentage of participants who had shaded it. The presence of a distal-to-proximal gradient in frequency was observed (**Figure 2**, top left), with the surface of the reported SPS relative to the surface of each anatomical segment of the hand being, respectively, 14.3% for the distal phalanx, 10.0% for the intermediate phalanx, 8.8% for the proximal phalanx, and 10.4% for the palm. This suggests that the SPS task was successful.

SPS Frequency and Spatial Correlations

This analysis was carried out to detect any significant effects in the spatial distribution of SPS as a function of the SPQ scores and OBT task performance. In order to achieve a cell-by-cell analysis, SPQ score, RT, and number of correct responses obtained in the OBT task were used to fill two maps (right and left hand) for each participant. A point-biserial cell-wise correlation between the presence of SPS and the SPQ and OBT measures was performed, with $N = 110$ maps, degrees of freedom = 108, and the probability threshold set at 0.05, one-tailed due to the oriented hypotheses. The point-biserial correlation is a special case of the Pearson product-moment correlation that follows the t-distribution and in which one variable is dichotomous (here, 0 = non-shaded cell; 1 = shaded cell) and the other variable is continuous. Afterwards, the correlation maps obtained were converted into binary maps (0 = non-significant cell, 1 = significant cell), for the application of a spatial scan procedure for binary data (Kulldorff, 1997). This consists of a circular window that scans, detects, and localizes significant clusters in a step-wise manner. Based on previous studies, a radius of 6 cells was chosen, containing 113 cells and corresponding to a surface area of 1 cm^2 on a real hand (Michael et al., 2012). After 999 runs of the Bernoulli (binomial) model, all detected and localized clusters were significant to at least the $p < 0.001$ level bicaudal. Finally, the 95% two-sided asymmetrical confidence interval was also computed (Altman et al., 2000) for the significance of the overall percentage area of the hand covered by previously detected reliable clusters.

SPS Frequency and OBT Task

Only positive correlations were found between SPS frequency and mean RT obtained in the OBT task. The r-values ranged from 0.20 to 0.30, and the corresponding p-values from 0.02 to 0.0007 one-tailed. Significant clusters detected by the spatial scan statistic were distributed over the fingers and the palm (both thenar and hypothenar eminences) and covered 22.8% (95% confidence interval: 21.6% to 24.1%) of the total surface area of the hand. Conversely, only negative correlations were found between SPS frequency and the mean number of correct responses obtained in the OBT task (r-values range = −0.19 to −0.28; p-values range = 0.025 to 0.001 one-tailed). Significant clusters detected by the spatial scan statistic were located in the fingers and the palm and covered 4.2% (95% confidence interval: 3.7% to 4.9%) of the total surface area of the hand. The correlations between SPS frequency and the OBT task are presented in **Figure 2**.

SPS Frequency and SPQ Scores

Only positive correlations were observed between SPS frequency and total SPQ score (r-values range = 0.21 to 0.28; p-values range = 0.015 to 0.0015 one-tailed), as well as between SPS frequency and each of the SPQ subscales (cognitive-perceptual r-values range = 0.20 to 0.26; p-values range = 0.02 to 0.0025 one-tailed; social-interpersonal r-values range = 0.16 to 0.285; p-values range = 0.05 to 0.001 one-tailed; disorganized r-values range = 0.16 to 0.30; p-values range = 0.05 to 0.0007 one-tailed). Significant clusters of correlations with total SPQ score subtended an overall area of as much as 13.5% of the hand (95% confidence interval: 12.5% to 14.6%) and were all located in the palm. Significant clusters of correlations with the cognitive-perceptual SPQ subscale score subtended an area of 7.3% of the hand (95% confidence interval: 6.6% to 8.1%) and were located in the fingers and the palm. Significant clusters of correlations with the social-interpersonal SPQ subscale score subtended an area of 11.1% of the hand (95% confidence interval: 10.1% to 12.1%) and were located in the palm. Finally, significant clusters of correlations with the disorganized SPQ subscale score subtended an area of 18.2% of the hand (95% confidence interval: 17.1% to 19.4%) and were located in the palm and the thumb.

Other Parameters

Other SPS parameters, i.e., mean perceived intensity, confidence in location and extent, total number of disjoined areas, spatial extent per area, and variety of SPS, were submitted to multiple linear regression analyses with OBT task performance (mean RT and number of correct responses) and SPQ scores (cognitive-perceptual, social-interpersonal, disorganized) as predictors. Age, gender, and BMI were also used as predictors, since previous research has shown that they may influence the perception of SPS (Michael and Naveteur, 2011; Michael et al., 2015; Naveteur et al., 2015). No significant effects were found (**Table 1**). A second, independent analysis was conducted in order to assess whether schizotypy interacted with performance in the OBT task. This moderation relationship was assessed through a regression analysis where the total SPQ score * RT in the OBT task, and

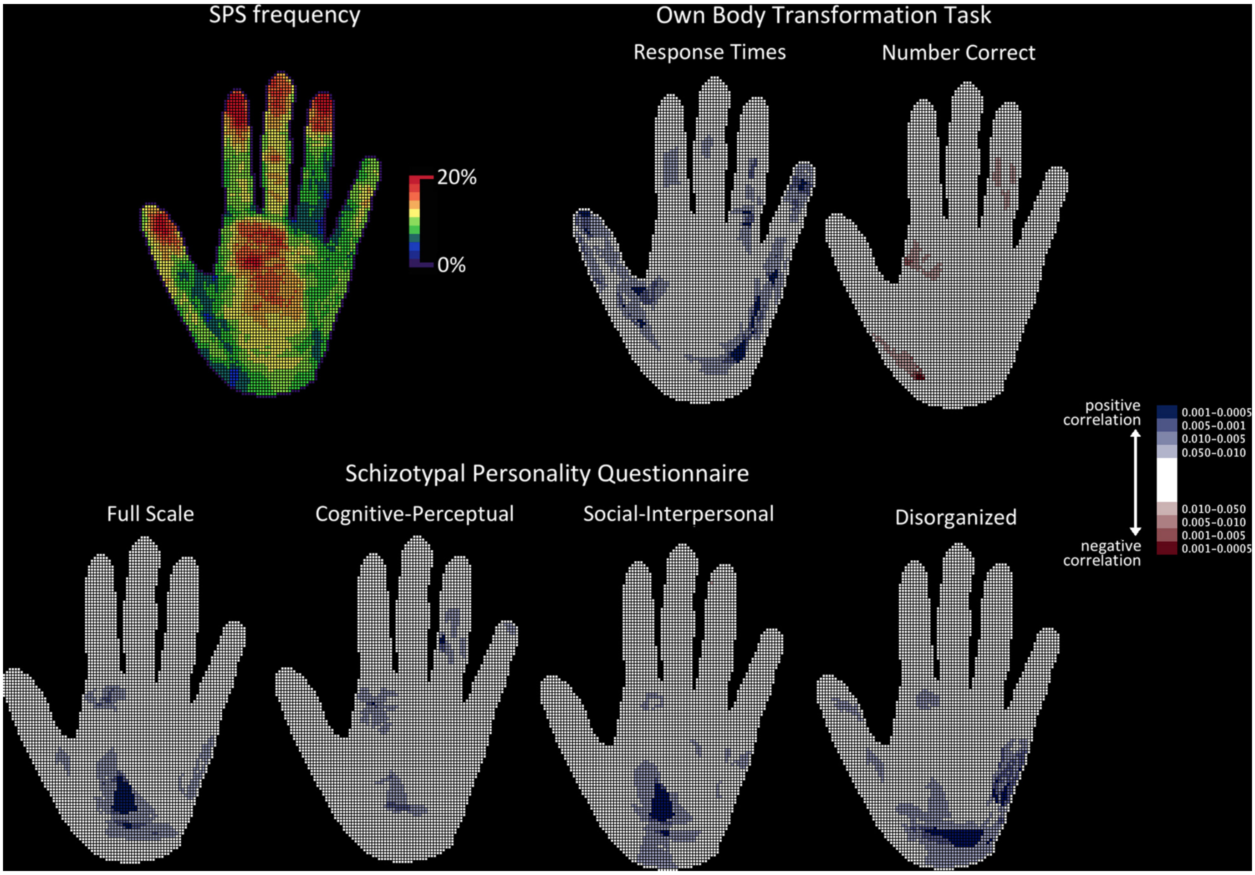

FIGURE 2 | Topographical analyses of SPS frequency. The hand is shown palm up. **Top left:** Raw frequency of SPS showing the proximo-distal gradient. **Top right:** Probability maps of the topographical cell-wise point-biserial correlation analysis carried out between response times and number of correct responses obtained in the OBT task and the presence of SPS. **Bottom:** Probability maps of the topographical cell-wise point-biserial correlation analysis carried out between individual scores in the SPQ (total scale and each of the three individual SPQ factors). For all probability maps, only significant clusters are presented. Bluish cells denote significant positive correlations, while reddish cells denote significant negative correlations. Color shading on the probability map represents different probabilities.

the total SPQ score * number of correct responses in the OBT task were used as predictors, and each of the abovementioned SPS parameters was used as dependent variable. The total SPQ score * number of correct responses in the OBT task significantly and negatively predicted confidence in location ($\beta = -38.05$, SEM = 17.68, $t = 2.15$, $p < 0.037$) meaning that the higher the degree of schizotypy and the better the performance in the OBT task, the lower the confidence in the location of SPS.

Types of Sensations

All SPS types were reported at least once and some participants even reported other types of sensations, such as pins and needles, weightiness, and compression. The reported SPS types were sorted into five categories based on previous studies (Beaudoin and Michael, 2014): thermal (warming and cooling), deep (beat/pulse and muscle tension), paresis-like (numbness and weightiness), surface (tickle, stretch, tingling, flutter, vibration, and compression) and pain-like (pins and needles, and itch). SPS types were not distributed uniformly across these five categories ($\chi^2(4) = 218.4$, $p < 0.001$). Surface-type SPS were most likely to be perceived and reported (55.2%), followed by deep (20.8%), thermal (13.2%), paresis-like (9.6%), and pain-like sensations (1.2%). Each of the five categories of sensations, as well as the total number of reported SPS, were submitted to multiple linear regression analyses with OBT task performance, SPQ scores, age, gender, and BMI as predictors (**Table 1**). The SPQ cognitive-perceptual scale positively predicted the number of thermal sensations ($\beta = 0.37$, SEM = 0.17, $t = 2.18$, $p < 0.035$), and the social-interpersonal scale positively predicted the number of paresis-like sensations ($\beta = 0.39$, SEM = 0.18, $t = 2.13$, $p < 0.039$). Finally, mean RT from the OBT task positively predicted pain-like sensations ($\beta = 0.32$, SEM = 0.16, $t = 2.04$, $p < 0.049$). The same moderation analysis as before was conducted on the types pf sensations. No significant effect was found.

Correlation Between the SPQ and the OBT Task

Pearson correlations were carried out between the SPQ scores and OBT task performance, with $N = 55$ and degrees of

TABLE 1 | Results of the regression analyses (β and SEM) carried out with the parameters and categories of spontaneous sensations as dependent variables.

	SPS parameters						SPS categories				
	Intensity	Confidence in location	Confidence in extent	Number of disjoined areas	Spatial extent per area	Variety	Thermal	Deep	Surface	Paresis-Like	Pain-Like
Demographics											
Age	−0,005 (0,15)	−0,103 (0,15)	−0,052 (0,15)	0,105 (0,15)	−0,097 (0,16)	0,041 (0,15)	−0,087 (0,14)	0,147 (0,16)	0,037 (0,16)	0,112 (0,15)	0,181 (0,15)
Gender	−0,198 (0,18)	−0,101 (0,18)	0,033 (0,17)	−0,059 (0,18)	0,161 (0,19)	−0,205 (0,17)	0,078 (0,17)	−0,098 (0,18)	0,02 (0,18)	0,055 (0,18)	0,004 (0,2)
BMI	−0,179 (0,15)	−0,216 (0,15)	−0,296 (0,15)	−0,13 (0,15)	0,048 (0,15)	−0,241 (0,14)	−0,14 (0,14)	−0,021 (0,16)	−0,096 (0,15)	−0,157 (0,15)	−0,142 (0,14)
SPQ											
Cognitive-perceptual	0,052 (0,18)	0,085 (0,18)	0,111 (0,17)	0,145 (0,18)	−0,089 (0,19)	0,044 (0,17)	0,372 (0,17) *	0,126 (0,18)	−0,043 (0,18)	−0,162 (0,17)	−0,09 (0,17)
Social-interpersonal	0,045 (0,18)	−0,074 (0,18)	0,066 (0,18)	−0,005 (0,19)	0,073 (0,19)	0,02 (0,17)	0,225 (0,17)	−0,01 (0,18)	0,058 (0,19)	0,391 (0,18) *	−0,123 (0,18)
Disorganization	0,103 (0,18)	0,179 (0,18)	0,081 (0,18)	0,145 (0,19)	0,033 (0,19)	0,131 (0,17)	−0,293 (0,17)	−0,101 (0,19)	0,205 (0,19)	−0,176 (0,18)	0,284 (0,18)
OBT task											
Response Times	−0,156 (0,16)	−0,018 (0,16)	0,082 (0,15)	0,004 (0,17)	0,109 (0,16)	−0,019 (0,15)	−0,151 (0,15)	−0,037 (0,16)	0,038 (0,16)	0,022 (0,15)	0,322 (0,15) *
Number correct	0,038 (0,15)	−0,005 (0,15)	−0,071 (0,15)	0,08 (0,16)	0,008 (0,16)	−0,159 (0,15)	−0,095 (0,14)	−0,06 (0,16)	0,071 (0,16)	−0,158 (0,15)	0,041 (0,15)

SPS, Spontaneous Sensations; BMI, Body MassIndex; SPQ, Schizotypal Personality Questionnaire; OBT task, Own Body Transformation task.
**Significant prediction.*

freedom = 53. No significant correlations were found (all $r < 0.18$, all $p > 0.20$).

DISCUSSION

To our knowledge, along with interoception, the perception of SPS is a domain that seems related to that aspect of embodiment that is the direct and immediate experience of our own body in the first-person perspective. The difference between interoception and SPS perception is that the former targets the monitoring of internal bodily signals (Vaitl, 1996) while the latter expands to *feeling* one's own body and its boundaries (Naveteur et al., 2015; Michael et al., 2017). However, both are encompassed by the broader definition of interoception [(Bud) Craig, 2003] and are seemingly related phenomena (Michael et al., 2015). The aim of this study was to investigate the relationship between the perception of SPS and embodiment, since the literature provides mostly indirect evidence of this (Michael and Naveteur, 2011; Bauer et al., 2014b; Michael et al., 2017). This was achieved by combining an SPS perception task, an experimental own-body mental transformation task (OBT task), and a questionnaire assessing schizotypal personality traits.

Embodiment, Disembodiment, and SPS

Since embodiment is related to the experience of one's own body in the first-person perspective, changing perspective by mentally rotating the body image in order to judge whether it matches a visually presented figurine is challenging. Indeed, complex body-related mechanisms are required (Blanke, 2005; Kaltner et al., 2014; van Elk and Blanke, 2014), such as flexible control of self-perspective-taking and disembodiment (Arzy et al., 2007), and alignment of somatosensory and vestibular information (Zacks et al., 1999; van Elk and Blanke, 2014; Gardner et al., 2017). Therefore, better performance in the OBT task (i.e., shorter RT and higher accuracy) suggests that changing self-perspective and disembodying is achieved more easily. The ease with which this task is completed thus relates to loose embodiment: a proneness to experiencing out-of-body experiences (Blanke, 2005), in which the sense of spatial unity between self and body is abnormal since the self is not experienced as residing within the limits of one's body (Blanke et al., 2004; Blanke and Arzy, 2005). The results paint a quite coherent picture. The frequency with which SPS were perceived correlated positively with RT in the OBT task. Since performing the OBT task quickly requires flexible control of disembodying and self-perspective-taking, and since a higher RT in the OBT task suggests greater difficulty in completing the task, this correlation suggests that difficulties in disembodying voluntarily and mentally transforming one's own body facilitates *feeling* oneself. Similarly, the frequency with which SPS were perceived correlated negatively with accuracy in the OBT task. Since performing the OBT task correctly requires flexible control of disembodying and self-perspective-taking, and since greater accuracy in the OBT task suggests less difficulty in completing the task, this correlation suggests that the ability to easily disembody and mentally transform one's own body decreases the sense of *feeling* oneself. Taken together, these results suggest that the perception of untriggered bodily sensations is related to embodiment and that embodiment is required in order to correctly *feel* oneself. The ability to disembody easily reduces this *feeling*. Since the correlation between OBT task performance and SPS perception was not perfect, the present experiment does not allow us to draw conclusions as to which of the processes involved in the OBT task determine the perception of SPS, or even to what degree. For instance, processes of spatial mental manipulation, attention, and simulation of sensory and vestibular information have been advanced as determinants of the ability to align one's own body orientation to that of a third party and to perspective-taking (Gardner et al., 2017, 2018; Pesimena et al., 2019).

Schizotypy and SPS

Our investigation into the way in which SPS contribute to embodiment also involved a self-completed schizotypal personality questionnaire, the SPQ (Raine, 1991). Schizotypal personality is considered to be a model for the study of schizophrenia spectrum disorders (Sass and Parnas, 2003; Nelson et al., 2012; Barrantes-Vidal et al., 2015), in which disruptions to the basic sense of embodiment are viewed as key symptoms (Stanghellini et al., 2012; Ferri et al., 2014). Therefore, assessing the relationship between schizotypal personality and the perception of SPS can provide insights not only into sense of self and embodiment, but into their disturbances too. Schizotypal personality is associated with a proneness to experiencing self-related disturbances (Mohr et al., 2006; Arzy et al., 2007), altered self-other boundaries (Di Cosmo et al., 2018; Ferroni et al., 2020), difficulties in controlling perspective-taking (Langdon and Coltheart, 2001), and unusual, exaggerated and vivid perceptual experiences involving the body (McCreery and Claridge, 2002; Sass and Parnas, 2003; Ettinger et al., 2015; Van Doorn et al., 2018). It was thus expected that higher schizotypal traits would correlate with the perception of SPS, signaling altered body boundaries (Di Cosmo et al., 2018) and difficulties in controlling and changing self-perspective (Mohr et al., 2006). The results showed that proneness to the cognitive-perceptual, social-interpersonal, and disorganized factors of schizotypy is sufficient to produce enhanced perception of SPS, as expected. The literature mostly points to the cognitive-perceptual factor as being associated with body-related unusual phenomena (Raine, 1991; Raine et al., 1994; Mohr et al., 2006; Arzy et al., 2007; Barrantes-Vidal et al., 2015; Ettinger et al., 2015). However, our findings are corroborated by some studies, which have shown that other factors may also relate to body-related experiences (Van Doorn et al., 2018), suggesting that altered sense of self is probably a hallmark of schizotypal personality as a whole. This is backed up by the interacting effect found between the total SPQ score and performance in the OBT task which suggests that despite more vivid perception of SPS due to both higher risk for psychosis and to the ease with which one disembodies and mentally transforms own body (as shown separately through the frequency of SPS), localizing SPS is less certain. This strengthens the idea of blurred bodily boundaries in schizotypy and also tallies well with the idea that abnormal bodily experiences may be a presenting symptom of schizophrenia spectrum disorders (Sass and Parnas, 2003; Quinones, 2009; Stanghellini et al., 2012).

At this point it is also possible to hypothesize that, as compared to a control sample, patients with schizophrenia would report larger sensitive zones of SPS as a reminiscence of the relationship found between SPS perception and the degree of schizotypy. Also, lower degrees of confidence in their location and extent are to be expected as a result of altered perceptual experiences and malleable body frontiers (Sass and Parnas, 2003; Di Cosmo et al., 2018; Ferroni et al., 2019).

The overall similar topography of correlations between SPS frequency and each of the factors subtending schizotypal personality, as well as the fact that the total SPQ score seems to combine these patterns, backs the idea that SPS perception captures subtle aspects of body-related unusual experiences, as has already been shown with different kinds of syndromes (Borg et al., 2015; Echalier et al., 2020), making it possible to relate schizotypal personality as a whole to alterations in *feeling* oneself. The exact origins of aberrant bodily perception in schizotypal personality are not known, but there is evidence suggesting that somatosensory cortical processing is modified (Lenzenweger, 2000; Chang and Lenzenweger, 2005), that the remapping of environmental stimuli in the body space is altered (Ferri et al., 2016), and that multisensory integration necessary to the perception of the self and distinction from others may be involved (Burrack and Brugger, 2005; Asai, 2016; Di Cosmo et al., 2018; Ferroni et al., 2020). All these aspects are essential for embodiment (Gallace and Spence, 2010; Sakson-Obada et al., 2018; Manos Tsakiris, 2010, 2017), since they allow us to establish the nature and location of perceived sensations, as well as the boundaries between the self and the external world (Bretas et al., 2020). We believe this is where embodiment meets the perception of SPS, one function of which is to provide information on the spatial boundaries of the body. Indeed, perceiving the boundaries of the body is central to distinguishing it from the world and others, an aspect that is altered in schizotypy and, generally, on the schizophrenia spectrum (van der Weiden et al., 2015; Asai, 2016).

Origins of Feeling Oneself

From a phenomenological perspective, there is no doubt that perceiving SPS is *feeling* oneself as a bodily entity that is distinct from others and from nearby objects, and characterized by somatic sensations of various qualities experienced from a first-person perspective. But direct evidence of this is still required. The relationship between SPS and the OBT task backs the idea that changing perspective is detrimental to the perception of SPS and that, consequently, SPS contribute to experiencing sensations from the first-person perspective.

According to theories of self-awareness, there is an ever-present background of bodily sensations that may be the basis for constructing the continuity of the experiencing self (Kinsbourne, 1998). This background would maintain the integrity of the body and would be partly responsible for how the self is perceived (Sakson-Obada et al., 2018). Orienting and focusing attention toward the self would enable the representation of one's own body or body parts to arise (Michael and Naveteur, 2011; Michael et al., 2012) and be maintained in consciousness (Wolpert et al., 1998), and this may be the representation over which attention is shifted (Kinsbourne, 1998). The postulated theory behind these accounts is that the sense of self arises due to interaction between the systems and brain structures that contain information about the body (e.g., somatosensory and interoceptive) and those that control attention. Interestingly, both attention and body-related processes are altered in schizotypy and schizophrenia spectrum disorders (Lenzenweger, 2000; Chang and Lenzenweger, 2005; Moe and Docherty, 2014; Ettinger et al., 2015; Ferri et al., 2016; Michael et al., 2020), one consequence of which may be aberrant bodily perceptions. It is not absurd to imagine that disordered attention processes operating over body representations are the origin of aberrant perceptual phenomena, such as body-related illusions, tactile and bodily hallucinations, and bodily perceptual distortions (Behrendt, 2006). We believe that when attention operates normally over the somatosensory and interoceptive cortices, SPS may be perceived (Michael et al., 2012, 2015), particularly given that activity in the primary and secondary somatosensory cortices does relate to these phenomena (Bauer et al., 2014a,b). However, in cases of altered attention, this may lead to distorted perception of such sensations (Borg et al., 2015), body perceptual alterations (Echalier et al., 2020), phantom limbs (Kinsbourne, 1998), asomatognosia (Berlucchi and Aglioti, 1997), and tactile hallucinations (Behrendt, 2006). Another theory would be that the spontaneous cortical activity that confers the characteristics of normal SPS may be easily mistaken as coming from outside the body if the internal origin is not correctly appreciated (Larøi and Woodward, 2007). In this last case, not only may bodily hallucinations arise, but the implicit bodily experience one has of one's own body may be altered, giving rise to experiences such as abnormal feelings of transformation (Stanghellini et al., 2014).

Limitations

One limitation of the present study is the unbalanced number of male and female participants, with female participants outnumbering males. This mostly stems from the fact that participants were undergraduate students in Social Sciences and Humanities where, at least in France, female students are as much as four times more numerous than male students. Furthermore, within the 15 years of scientific investigation of SPS, we found that the probability of males being excluded from the study is high because of regular use of substance and drugs. An unbalanced sample may prevent from detecting gender-related effects, and indeed previous investigations found such gender differences in both the OBT task (Mohr et al., 2006) and SPS (Naveteur et al., 2015). Yet, except from the fact that gender differences were not one of the main factors under investigation in the present study, research showed that the SPS patterns observed in female participants (Naveteur et al., 2015) are more representative of overall performance (i.e., mixing up male and female participants) and can be more easily generalized.

An observation that may appear surprising at first glance is the complete absence of correlation between the OBT task and the SPQ. Previous research found that the higher the schizotypal traits, the slower the performance in this task (Mohr et al., 2006). However, the authors did not use a general schizotypal personality tool, as was used here. They instead used a questionnaire focusing on perceptual aberrations that included multiple assessments of body-related phenomena (Chapman et al., 1978). A closer inspection of the SPQ reveals that unusual body-related experiences are assessed in just two questions (one related to the feeling of presence and one to deformations of faces seen in a mirror). The SPQ therefore covers more global aspects of schizotypy, and this may be why no relationship was found with the OBT task. Interestingly, as explained above, both the OBT task and the SPQ correlated with SPS, despite not correlating with each other, suggesting that SPS may capture those specific aspects of each measure that relate to sense of self and the way in which the body and its boundaries are felt. The interaction found between the total SPQ scale and performance in the OBT task in predicting confidence in the location of SPS may reflect this idea.

Another limitation is that only the spatial distribution and some types of SPS were found to relate with OBT task performance and SPQ score. The remaining SPS parameters did not. This is not surprising, however, since previous research has shown that these parameters may be less sensitive, probably due to significant between-subject variability. One possible reason is the moderate size of our sample. Indeed, as power analyses suggest, the present sample is enough to detect the most common characteristic of SPS, which is the proximo-distal gradient, but it may not suffice for revealing more subtle effects that also may greatly vary between participants.

CONCLUSION

The present study provides a coherent picture of the relationship between *feeling* oneself, as assessed through the perception of SPS, and embodiment, as assessed through the OBT task and as seen in the schizotypal personality. Embodiment is needed in order to correctly feel and sense oneself. These findings complement previous research, which found that SPS may be interoceptive in nature (Michael et al., 2015), and show that feeling oneself is not only related to the perception of internal visceral signals, but also to the perception of tactile sensations that arise on the surface of the body without any external triggers. We believe that this study helps us understand normal and disordered bodily awareness and that the methodology associated with the assessment of SPS could be used as a research tool for addressing issues that are difficult to induce experimentally, such as tactile and bodily hallucinations, and phantom limbs. Finally, dissemination of the findings could help therapists to better apprehend disturbances of embodiment and their relationship to the schizophrenia spectrum, and develop behavioral methods and practices for the treatment and prevention of disordered body image and the self. For instance, giving precise information about the nature of sensations that are spontaneously perceived at rest may constitute a prevention practice, while helping patients with disorders of the self to focus on relevant bodily and interoceptive sensations, and providing them with techniques to scan their body and interpret those sensations may contribute to reduce feelings of anxiety.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/supplementary material.

ETHICS STATEMENT

This study involving human participants was reviewed and approved by the Comité de Protection des Personnes Sud-Est II (reference number IRB Groupement Hospitalier Est, 59 boulevard Pinel, 69500 Bron, France. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

GM supervised the research, conducted the statistical analysis, and wrote the majority of the manuscript. DG and ET created the code for the OBT task and collected and analyzed data. SS and MC provided technical assistance. All the authors made a significant contribution to drafting the article and revising it critically for important intellectual content, discussed the results, commented on the manuscript, and gave their final approval of the version for publication, contributed to the article and approved the submitted version.

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Gender Brain Structural Differences and Interoception

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Interoception, the ability to perceive inner body sensations, has been demonstrated to be different among genders, with a stronger female attention toward interoceptive information. No study correlated this capability with brain differences between males and females. This study aims to detect behavioral variances and structural neuroimaging interoception correlates in a sample of healthy volunteers matched for age. Seventy-three participants (37 females, mean age 43.5; 36 males, mean age 37.4) completed the Self-Awareness Questionnaire (SAQ) for interoceptive sensibility and underwent a structural MRI session. A *t* test corrected for Bonferroni multiple comparisons was performed to compare brain morphological parameters (cortical thickness and parcel volume) in both groups. A multivariate analysis of variance was performed to assess the effect of gender on scores obtained on the SAQ. A moderation model through multiple linear regression analysis was performed between gray matter volumes or parcels, cortical thickness, and the interoception score. Group analysis showed significant differences in morphometric brain data between males and females, both for cortical and subcortical volumes, but not for cortical thickness analyses. MANOVA underlined a significant difference in SAQ scores between males and females with higher values for the second ones. Moreover, a significant correlation between the interoception scores and gray matter volumes of the two groups has been detected, with a sharp prevalence for the female gender in the left insula with F1, F2, and SAQ interoception scores ($R^2 = 0.41$, $p < 0.001$). Our results demonstrated that in the female group, a stronger predisposition was found toward interoceptive sensations, and that multiple brain areas were correlated with interoceptive measure. These data sustain a female advantage in the attention toward this process and support the idea that interoception in females is a process more shared across several regions that participate in creating the sense of self.

Keywords: interoception, sex differences, structural MRI, gray matter volume, SAQ score

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INTRODUCTION

Interoception is a multifaceted construct, reflecting the capability in perceiving inner body signals. The self-evaluation of subjective interoceptive sensations returns the interoceptive sensibility (Garfinkel et al., 2015). Substantial sex-related variations in paying attention to one's bodily states have been demonstrated in several independent samples (Longarzo et al., 2020), where women exhibit higher attention to internal states and somatic complaints but reduced objective interoceptive accuracy (Grabauskaitë et al., 2017), understood as the objective accuracy to detect bodily sensations (Garfinkel et al., 2015). Murphy et al. (2019) in their review argued about the known sex differences in interoception, whereby women with respect to men report heightened attention to internal signals, and they hypothesized that interoceptive differences might be due to the amount of physical and hormonal changes experienced by women through life due to experiences of menstruation, pregnancy, and menopause. Interoception is closely related with visceral sensations; in fact, it is also a factor of the Self-Awareness Questionnaire (SAQ), a questionnaire focused on interoceptive stimuli (Longarzo et al., 2015). Gender seems to cover a role in abdominal pathologies such as irritable bowel syndrome: several authors such as Chang and Heitkemper (2002) reported that women experienced more constipation, nausea, bloating, and extraintestinal symptoms than men. As a brain correlate, it has been found that neural networks respond differently to visceral stimuli in men and women with irritable bowel syndrome (IBS).

However, such difference has not been related to possible differences between males and females in brain structures involved in interoception capability.

Convergent results from neuroimaging studies support the existence of significant differences between males and females in brain cytoarchitecture. At a global level, Gur et al. (1999) found differences between males and females in gray and white matter, where females have more gray matter, whereas males have more white matter and cerebrospinal fluid. It has been reported that the brain of males is 10% larger than that of females (Goldstein et al., 2001) even after adjustment (Cosgrove et al., 2007). Frontal and medial paralimbic brain regions are larger in women, whereas the hypothalamus, amygdala, and angular gyrus seem to be larger in men (Rezzani et al., 2019). In females, the volume of the corpus callosum and temporal and parietal regions (surrounding the Sylvian fissure) engaged in language processing is comparatively larger, whereas males have larger parietal cortical area associated with visual–spatial function (Grabowska, 2017).

It is largely recognized that insula and cingulate cortices are related to interoceptive stimuli processing. The anterior insular cortex is a station of encoding and representing interoceptive information and has been defined as an interoceptive cortex (Critchley et al., 2004; Craig, 2009). The insula has reciprocal projections with the anterior cingulate cortex that guides attention on physiological information and provides autonomic responses. However, little is known about sex-related differences in the engagement of brain areas related to interoceptive stimuli.

The present work aims to explore interoception among males and females at different levels and to determine whether there are differences in interoceptive awareness as a function of gender. Studying sex-related differences in the interoceptive process and how it relates to morphological brain aspects allows researchers to target specific populations in order to understand what makes them more susceptible. Firstly, we compared brain morphological parameters in the two groups to identify both global and specific differences. Next, differences between genders in attention toward interoceptive information have been investigated through an interoceptive sensibility measure. Finally, we investigated how behavioral results were related to brain regions in the two samples.

MATERIALS AND METHODS

Participants

The study sample consisting of 73 healthy subjects (37 females, mean age 43.5 ± 14.6; 36 males, mean age 37.4 ± 12.5) participated in a research protocol conducted at the IRCCS SDN that included a clinical evaluation and a magnetic resonance imaging (MRI) protocol. All participants were recruited if they met the following criteria: (i) lack of current or past history of alcohol or drug abuse; (ii) lack of current or past history of major psychiatric illnesses; (iii) lack of history of brain injury, stroke, or any other major clinical condition; and (iv) lack of current or past use of psychoactive medications. The eligibility criteria were assessed through a brief clinical interview performed by an expert psychologist.

Each participant provided written informed consent approved by the local Ethics Committee of IRCCS Pascale and performed according to the ethical standards laid down in the 1964 Helsinki Declaration and its later amendments. All individuals were naive to the scope of the study and gave their written informed consent to participate without any reward.

Neuropsychological Assessment

All participants in the study completed the SAQ, a self-report tool devised to evaluate the perception of a wide range of bodily sensations and, in particular, investigate the frequency with which volunteers perceive signals from their own body (Longarzo et al., 2015).

The SAQ consisted of 28 items to be rated on a five-point Likert scale (0 = never; 1 = sometimes; 2 = often; 3 = very often; 4 = always). The total score ranges 0–112 with higher scores meaning higher interoceptive awareness. The SAQ proved to have a bifactorial structure: the first factor (F1) comprises items related to visceral sensations, whereas the second one (F2) is related to somatosensory sensations.

For the present study, the multivariate analysis of variance (MANOVA) was performed to assess the effect of gender on demographics and scores obtained on SAQ. Statistical analyses were conducted using SPSS (IBM Corp. Released 2016. IBM SPSS Statistics, Version 24.0).

MRI Scanning and Brain Morphometry

Structural MRIs were collected from a 3-Tesla PET-MR Siemens Biograph mMR unit (housed at IRCCS SDN in Naples) using a 12-channel head coil with an axial structural 3D-T1-weighted sequence (TR = 2,400 ms, TE = 2.25 ms, flip angle = 8°, voxel size 0.8 × 0.8 × 0.8 mm, matrix 256 × 256, field of view 214 × 214). Structural images were also reviewed for incidental brain abnormalities by an experienced neuroradiologist (CC). The parcellations of morphological T1-weighted 3D images of subjects were processed with FreeSurfer v5.1 toolkit (Dale et al., 1999; Alfano et al., 2020). Briefly, this processing includes spatial inhomogeneity correction, non-linear noise reduction, skull-stripping, subcortical segmentation, intensity normalization, surface generation, topology correction, surface inflation, registration to a spherical atlas, and thickness calculation (Fischl and Dale, 2000). To map all subjects' brains to a common space, reconstructed surfaces were registered to the Desikan-Killiany atlas using a non-linear procedure that optimally aligned sulcal and gyral features across subjects. Brain morphological parameters, including cortical and subcortical volume and cortical thickness, were calculated using processed and segmented FreeSurfer data. Then, they were normalized by the ratio with the estimated total intracranial volume (eTIV). A moderation model through multiple linear regression analysis was performed between gray matter volumes or parcels, cortical thickness, and the interoception score in both female and male groups using gender as the moderator. Furthermore, a type I and type III sum of squares was performed with the interoception score (F1, F2, SAQ total) in order to indicate whether a variable brings significant information or not, once all the other variables are already included in the model. Then, for the model estimation, the adjusted R^2 was used to consider the number of predictors in the model. Finally, a two-tailed two-sample t test, corrected for Bonferroni multiple comparisons (significant p value < 0.0004), was performed to compare brain morphological parameters in both groups.

RESULTS

MANOVA revealed significant differences between males and females (Wilks' Lambda = 0.89; $F = 4.5$). The analyses on single measures showed significant differences between males and females on SAQ total score ($p = 0.008$) and on both factors, F1 ($p = 0.004$) related to visceral sensations and F2 ($p = 0.049$) related to somatosensory sensations. Statistical analysis of behavioral data underlined significant differences in interoceptive awareness between genders. Mean age did not differ between the two groups (**Table 1**).

Regarding brain morphometry, group analysis showed significant differences in the male subjects compared to the female group: brain parcels that survived at multiple comparisons test are resumed in **Table 2**. Multiple linear regression analysis showed a significant model with correlations between gray matter brain parcels and F1, F2, and total SAQ score (female group: left inferior parietal $R^2 = 0.17$, $p = 0.04$; left posterior cingulate $R^2 = 0.17$, $p = 0.04$; left precentral $R^2 = 0.21$, $p = 0.02$; left insula $R^2 = 0.41$, $p < 0.001$; left parahippocampal $R^2 = 0.31$, $p = 0.002$; right pars opercularis $R^2 = 0.18$, $p = 0.04$; right post central $R^2 = 0.27$, $p = 0.005$; right posterior cingulate $R^2 = 0.18$, $p = 0.03$; right supramarginal $R^2 = 0.17$, $p = 0.04$. Male group: left precuneus $R^2 = 0.20$, $p = 0.03$) (**Figure 1**). In both groups, different values of F1, F2, and total SAQ score allow us to explain an amount of the variability of the brain parcels (**Table 3**); no correlation was found with cortical thickness parcels.

TABLE 1 | Demographics and neuropsychological characteristics.

	Male	Female	*p* value	Group differences
Age	37.4	43.5	>0.05	\
F1	7	11	0.004	F > M
F2	12	14	0.049	F > M
SAQ	18	25	0.008	F > M

Values are expressed as mean. SAQ, Self-Awareness Questionnaire; F1, first factor of SAQ; F2, second factor of SAQ.

DISCUSSION

In the present study, we aimed to investigate interoceptive capability and interoceptive brain correlates in a sample of healthy males and females. The SAQ was used to measure subjective interoceptive sensibility, and similar to previous reports, women obtained scores significantly higher with respect to men on the SAQ total score and on both factors of the SAQ, related to visceral sensations and somatosensory sensations. Firstly, we investigated morphological differences in brain volumes among the two groups. Previous studies have demonstrated that dimorphism exists between males and females for volume and surface area, and reported that men display global larger brain volume. Similarly, we found that male subjects reported larger volume in several areas across the brain, even if the female group reported major volume in some parcels on both brain sides, such as the insula and central areas (Wierenga et al., 2014).

Moreover, and for the first time, behavioral results on interoception have been correlated with brain areas among males and females. Positive correlations have been found between interoception scores and several brain region volumes. In the male group, total score and both F1 and F2 factors of the SAQ correlated with the precuneus, a major association area that may subserve a variety of behavioral functions. Converging evidences from functional imaging studies in healthy subjects indicate that the precuneus covers a role in the internal mentation processes of self-consciousness (Cavanna and Trimble, 2006), but to date, no specific correlations were demonstrated between the precuneus and interoception, and it was not specifically investigated among genders.

The precuneus has reciprocal connections with many cortical areas, afferent to the parietal lobe such as the operculum, and extra parietal zones such as the cingulate cortex, which is primarily involved in interoceptive processing and which, in our sample, is significantly related with interoceptive scores in the female group. Furthermore, the connection of the precuneus with the temporo-parieto-occipital cortex functionally responds to the integration of somatosensory information.

Kircher et al. (2000) demonstrated that self-descriptive traits activate a network comprising the bilateral precuneus, superior parietal lobe, prefrontal cortex, and cingulate cortex. Also, Gusnard et al. (2001) attributed to the precuneus, cingulate, and medial prefrontal areas the role of engaging continuous information and representation of the self when a person is awake and alert (Cavanna and Trimble, 2006). In the present sample, we found that besides the precuneus, in the female group,

TABLE 2 | Morphological differences of normalized brain parcels' volume between the male (M) and female (F) subject groups.

Left brain parcels	*p*	*M* mean	*F* mean	Right brain parcels	*p*	*M* mean	*F* mean
Cuneus	8.0E-05	0.00097	0.00096	Cuneus	2.0E-06	0.00101	0.00100
Fusiform	1.6E-07	0.00188	0.00189	Fusiform	1.2E-07	0.00188	0.00186
Inferior temporal	2.0E-06	0.00209	0.00208	Inferior temporal	9.6E-08	0.00203	0.00197
Lateral occipital	2.7E-07	0.00313	0.00310	Lateral occipital	1.1E-05	0.00313	0.00315
Lingual	6.8E-06	0.00187	0.00184	Lingual	3.1E-07	0.00194	0.00191
Middle temporal	5.4E-06	0.00200	0.00201	Middle temporal	1.1E-05	0.00217	0.00219
Paracentral	2.8E-05	0.00083	0.00085	Paracentral	2.4E-05	0.00094	0.00094
Post central	5.0E-06	0.00256	0.00264	Post central	1.3E-04	0.00247	0.00255
Precentral	2.1E-04	0.00309	0.00324	Precentral	2.8E-05	0.00305	0.00316
Precuneus	1.8E-07	0.00234	0.00233	Precuneus	7.0E-07	0.00242	0.00243
Superior frontal	2.5E-05	0.00457	0.00464	Superior frontal	1.7E-07	0.00447	0.00439
Superior parietal	4.4E-04	0.00332	0.00345	Superior parietal	5.0E-05	0.00325	0.00335
Superior temporal	2.6E-06	0.00251	0.00255	Superior temporal	6.5E-05	0.00225	0.00235
Temporal pole	2.3E-04	0.00028	0.00029	Temporal pole	3.8E-05	0.00027	0.00028
Transverse temporal	1.5E-04	0.00029	0.00029	Transverse temporal	2.7E-04	0.00021	0.00022
Insula	2.9E-07	0.00151	0.00154	Insula	1.3E-06	0.00147	0.00148
Pericalcarine	2.1E-04	0.00089	0.00087	Supramarginal	1.5E-05	0.00226	0.00227
Rostral anterior cingulate	4.5E-08	0.00052	0.00045	Medial orbitofrontal	5.9E-05	0.00115	0.00117
Rostral middle frontal	4.3E-04	0.00356	0.00365				
Posterior cingulate	3.8E-04	0.00074	0.00076				
Caudal anterior cingulate	1.5E-04	0.00040	0.00038				
Isthmus cingulate	4.3E-06	0.00064	0.00063				

also the parietal and temporal areas display a strong connection with our interoceptive measure, sustaining the hypothesis that this network, also if not directly implied in, probably cooperates to interoceptive monitoring and self-processing. The interaction between the precuneus and prefrontal cortex has been postulated in a state of consciousness characterized by a high level of reflective self-consciousness (Kjaer et al., 2002).

The interconnected medial prefrontal regions and the posterior medial parietal represent a network through which personal identity forms, permitting to build the self-awareness. Wang et al. (2019) found activation of subsequent brain regions involved in interoceptive attention: the inferior parietal lobule, post central, and supramarginal. One possibility is that all of these regions concur to create a personal perspective of the proper bodily status and that females have a stronger predisposition to achieve the contents of proper mind about bodily condition.

In the female group, the correlation we found between the insula and interoceptive sensitivity measure is noteworthy since wide neuroimaging evidences identify it as the brain site of interoceptive processes. The existence of several subdivisions of the insular cortex is important when considering the mechanisms of learning and memory that involve the insula (Von Bernhardi et al., 2017). In particular, the anterior one is involved in emotional awareness; the mid insula influences one's physical self-perception, promotes goal-directed cognition, and is active during external and internal stimuli integration; the posterior part is involved in somatosensory functions and contributes to interoceptive processing. The latter one is a site of convergence of interoceptive and limbic systems inputs (Klabunde et al., 2016). Relevant to the central networks involved in learning are the neural connections of the rostral agranular insular cortex with the amygdala and hippocampal formation, which, in the present study, has demonstrated to be correlated with the interoceptive measure. Basing on the close relationship between the insula and hippocampus, we could speculate that its correlation with the SAQ may reflect the "proper corporeal memory" useful for building a quite stable interoceptive identity, with which one can compare the physical state of the moment in order to catch personal variations that allow answering the question "how do you feel?." Another region closely related with the insula is the cingulate cortex, even if previous studies have reported a larger volume of the cingulate cortex in women (Mann et al., 2011). In the present study, this finding was not replicated, but a significant correlation was found between both the anterior and posterior cingulate cortex with the interoceptive measure, in the women subgroup. The cingulate is the area that, together with the insula, most of all contributes to elaborate the interceptive information, particularly in choosing the most appropriate response to the perceived stimuli. Also, from a functional perspective, the cingulum showed gender differences, mainly in studies on emotional processes, closely related to interoception (Mann et al., 2011).

The carelessness of males in paying attention toward proper bodily signs could be explained based on the data by Sun et al. (2015), who demonstrated a higher global efficiency of males, suggesting a predilection for global information integration rather than for detailed information. Considering this data, we could speculate that interoception entails more detailed information, not globally but at a specific level, that needs more attention to be captured.

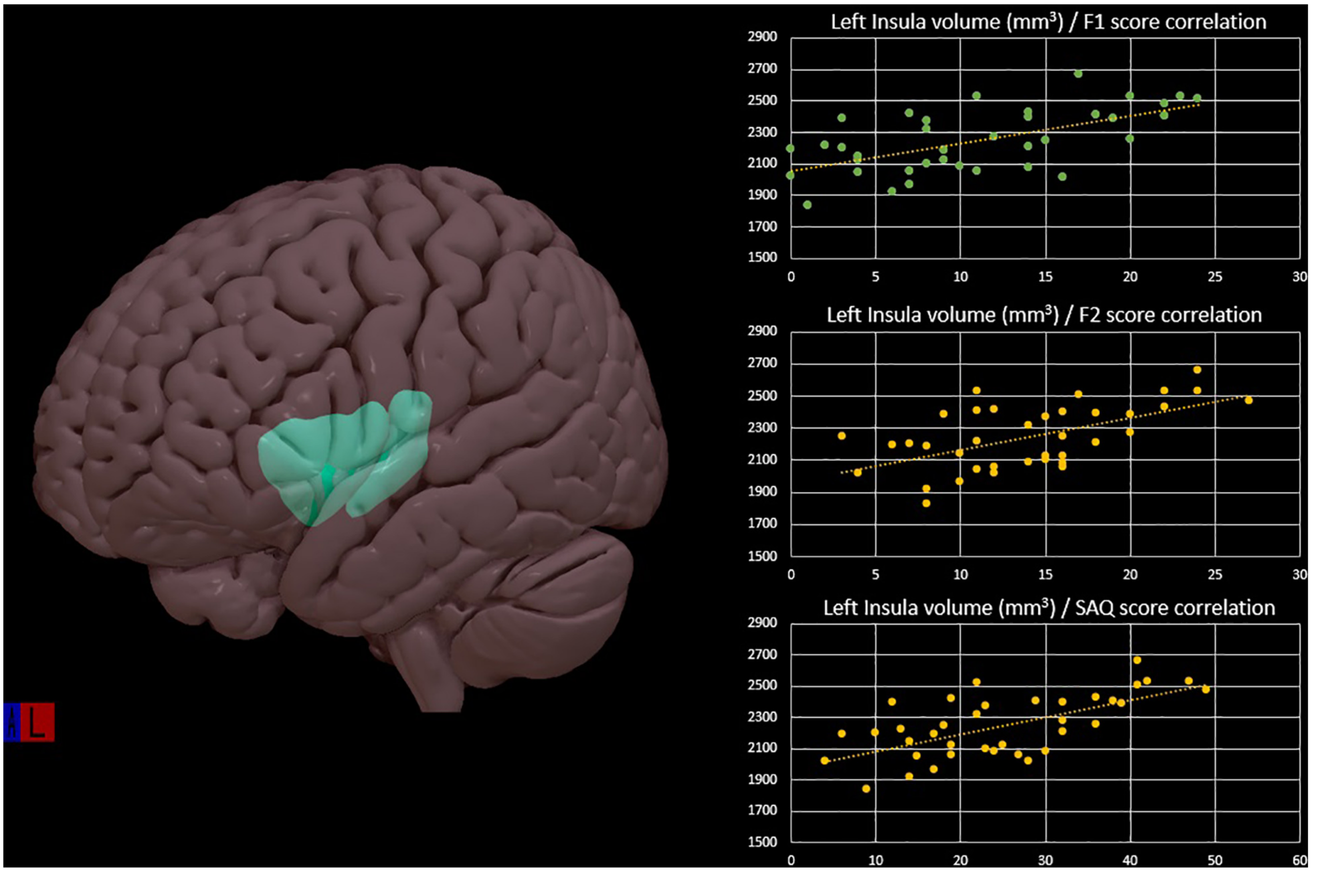

FIGURE 1 | Left insula cortex representation with positive correlation of the left insular volume and the interoceptive scores: F1, F2, and SAQ in the female group, from multiple linear regression analysis.

TABLE 3 | Multiple linear regression model in the female and male groups between gray matter volumes and interoception scores (F1, F2, and SAQ total score).

	Goodness of fit			***F1***		***F2***		***SAQ***	
	R^2	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Female									
Left inferior parietal	0.169	3.459	0.043	0.014	0.908	3.922	0.056	5.314	0.027
Left posterior cingulate	0.173	3.549	0.040	3.537	0.069	0.004	0.948	6.349	0.016
Left precentral	0.212	4.565	0.018	0.215	0.646	6.146	0.018	5.914	0.020
Left insula	0.412	11.918	0.000	5.136	0.030	2.437	0.128	24.475	<0.0001
Left parahippocampal	0.309	7.616	0.002	13.072	0.001	2.059	0.160	7.098	0.012
Right pars opercularis	0.175	3.610	0.038	0.135	0.715	2.790	0.104	6.625	0.014
Right post central	0.269	6.255	0.005	0.341	0.563	4.488	0.042	11.584	0.002
Right posterior cingulate	0.182	3.778	0.033	4.677	0.038	0.071	0.791	5.974	0.020
Right supramarginal	0.171	3.500	0.041	0.210	0.650	4.843	0.035	4.474	0.042
Male									
Left precuneus	0.198	4.083	0.026	5.633	0.024	0.998	0.325	4.715	0.037

The second column displays the goodness of fit of the model and Fisher's F test, while in the F1, F2, and SAQ columns, type III sum of squares is represented to indicate whether a variable brings significant information or not, once all the other variables are already included in the model.

Our results demonstrated that in the female group, a stronger correlation of multiple areas with interoceptive measure was found. These data sustain a female advantage in the attention toward this process and support the idea that interoception in females is a process more shared across several regions that participate in creating the sense of self.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Ethics Committee of IRCCS Pascale, Naples. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

ML conceptualized the study and wrote the manuscript. CC conceptualized the study and critically revised the manuscript. VA and GM collected the data and performed the behavioral and neuroimaging analyses. MS revised and approved final version of manuscript. All authors approved the submitted version.

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Anisotropic Psychophysical Trends in the Discrimination of Tactile Direction in a Precision Grip

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Tactile cues arising from interactions with objects have a sense of directionality which affects grasp. Low latency responses to varied grip perturbations indicate that grasp safety margins are exaggerated in certain directions and conditions. In a grip with the ulnar-radial axis vertical, evidence suggests that distal and downward directions are more sensitive to task parameters and have larger safety margins. This suggests that, for the purpose of applying forces with the fingers, reference frames with respect to the hand and gravity are both in operation. In this experiment, we examined human sensitivities to the direction of tactile movement in the context of precision grip in orientations either orthogonal to or parallel to gravity. Subjects performed a two-alternative-forced-choice task involving a textured cube which moved orthogonal to their grip axis. Subjects' arms were placed in a brace that allowed for finger movement but minimized arm movement. Movement of thumb and index joints were monitored via PhaseSpace motion capture. The subject was presented with a textured cube and instructed to lightly grasp the cube, as if it were slipping. In each trial the object was first translated 1 cm in 0° (proximal), 90° (radial), 180° (distal), or 270° (ulnar) and returned to its origin. This primary stimulus was immediately followed by a 10 mm secondary stimulus at a random 5° interval between −30° and 30° of the primary stimulus. Response from the subject after each pair of stimuli indicated whether the test direction felt the same as or different from the primary stimulus. Traditional bias and sensitivity analyses did not provide conclusive results but suggested that performance is best in the ulnar-radial axis regardless of gravity. Modeling of the response curve generated a detection threshold for each primary stimulus. Lower thresholds, indicating improved detection, persisted in the ulnar-radial axis. Anisotropic thresholds of increased detection appear to coincide with digit displacement and appear to be independent of the grasp orientation.

Keywords: precision grip, psychophysics, sensitivity, bias, anisotropic

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INTRODUCTION

Achieving success in motor tasks requires viable and interpretable somatosensation, especially as the task's nature becomes finer. Removing somatosensation severely hinders motor ability, leaving a person to rely on visual feedback or learned motor patterns, both incurring high levels of error (Marsden et al., 1984). Even with complete somatosensory functionality, there are limits in perceptual abilities associated with fine motor tasks as they provide incomplete data that must be subjectively interpreted. Understanding these subjective limits will help identify the properties of normal somatosensation. A key aspect of successfully performing accurate grip movements is discriminating finite differences between movements across fingertips. The directional element of tactile input is useful in informing grasp intent and response to perturbations. This directional tactile discrimination plays an important role in catching falling objects and adjusting grip on moving objects.

Studies of angular discrimination have concentrated on passive poses, such as a hand or finger placed facing down (Webster et al., 2005). These investigated the absolute threshold of directional discrimination in the coronal plane utilizing a passive touch in which subjects placed their index fingers on a rotating ball device. This device's direction varied in 5° increments and subjects identified the direction as either "angled" or "straight." The average least noticeable angular difference in slip direction was determined to be between 20° and 25°. A similar study incorporating various textures found this least noticeable angular difference to be between 3.6° and 11.7°, depending on the surface texture (Salada et al., 2004). While the information provided by texture from movement across the relaxed hand is useful in the exploration and identification of new objects, directional discrimination is more intrinsically related to active tasks. In addition, it has been shown that proprioception from large arm movements affects the ability to determine slip speed (Salada et al., 2004), so it is important to limit the inclusion of proprioceptive information as much as possible by limiting movement proximal to the wrist when investigating perceptual thresholds at the fingertips. These referenced studies did not utilize practical hand postures such as precision grips so knowledge regarding this tactile direction discrimination threshold in precision grip is limited. This information is necessary to understand directional discrimination in the context of fine motor actions during practical tasks.

Anisotropic sensitivities of directional discrimination have been observed in numerous studies, but not in precision grip. Psychophysical static groove orientation detection favors grooves oriented perpendicularly to the fingerpad (Essock et al., 1997). Detection and discrimination of grooved indentations scanned across the finger produces increased psychophysical and median nerve responses in the distal-proximal axis (Wheat and Goodwin, 2000). In an investigation of static groove detection anisotropies at different sites, it was found that the fingertip was more sensitive to grooves oriented along the distal-proximal axis, and the finger base was more sensitive along the lateral axis, and the fingerpad was anisotropic (Gibson and Craig, 2005). Finally, primary somatosensory cortex neural activity during discrimination of static indented bars demonstrates tuning in the distal-proximal directions during scanning studies (Bensmaia et al., 2008). These textural features pass across the fingers' dermal ridges and generate varied vibrational power, activating mechanoreceptors used in such detection (Maeno et al., 1998). At the tip of the finger, neural encoding of force loading direction is also sensitive to the distal direction, noted to be perpendicular to the papillary ridges (Birznieks et al., 2001). With respect to angular slip direction, slip speed, and slip texture, anisotropic sensitivities in detection thresholds favor the distal-proximal direction as opposed to ulnar-radial. However, the studies discriminating scan direction were examined under passive, non-grip tasks which leaves us with an opportunity to explore these trends and properties in an active task.

In an active precision grip, more variables are at work than in passive states, and this creates heightened direction sensitivities which allow for quicker and stronger responses. We can glean some anisotropic trends in this grip setting. Literature reports that a reactionary pinch force to a precision grip stimulus is increased for distally traveling stimuli (Jones and Hunter, 1992). There is also lower grip force latency and greater grip force safety margin in distal directions and in the direction of downward gravity, confirmed by utilizing inverted grip but not an orthogonal grip (Häger-Ross et al., 1996). While these are quantitative measures of our intrinsic grip reactions, they also imply that subjective directional grip discrimination may be biased in certain critically dangerous directions. If these subjective anisotropies are consistent with environmental factors such as gravity, we can infer that our tactile discrimination is externally referenced. However, reducing gravity does not affect grip performance or cyclic loading, but does affect force scaling necessary for appropriate safety margins, suggesting internal reference frames for subjective responses (Augurelle et al., 2003).

The necessary grip force during normal gravity would, however, apply higher shear forces on the finger pad in the direction of gravity and would likely induce lateral finger movement more easily. Since the glabrous skin of the finger pad is anisotropic, with stiffness relating to the orientation of the papillary ridges, movements across these ridges would induce more deformation (Wang and Hayward, 2007). The orientation of the papillary ridges is not consistent across the finger pad, but the center has ridges primarily orthogonal to the ulnar-radial axis. Mechanoreceptor sensitivity seems to follow similar patterns of this anisotropy, showing ridge-orthogonal tuning for SA systems and ridge-parallel tuning for certain mechanoreceptors (Birznieks et al., 2001). Skin stretch is tied to directional detection (Seizova-Cajic et al., 2014), so it is our hypothesis that the axis with more deformation, the radial-ulnar axis, will likely align with the axis of sensitivity.

Directional tactile sensitivities exist in different directions for multiple contexts but can be generally reduced to variable and contextual biomechanical loading. Precision grip tends to not rely on scanning across the finger, so the deformation due to shear forces is likely the method of activation. Axes sensitive to tactile direction in precision grip are unclear, but likely will align with the ulnar-radial axis as it is less stiff and more deformable. Whether those sensitivities are referenced to internal biomechanics or to external effects such as gravity must be jointly determined. An internal reference would support that environmental factors like gravity are superseded by mechanoreceptor information for contextually informing perception, grip structuring, and future planning.

Here we examine the effect of changing the grip orientation with respect to gravity on the perception of slip direction during active grip. We report that the sensitivity to movement direction is largely aligned along the radial-ulnar axis.

MATERIALS AND METHODS

Using a precision grip, 14 subjects (8 female, 6 male, 20–32 years old) held a 50 mm cube textured with 60 grit sandpaper that was attached to a six degree of freedom DENSO (Long Beach, CA, United States) VS-G series robotic arm. Each subject was instructed to lightly hold onto the cube, maintaining contact, but not attempting to immobilize the object. Stimuli were delivered to the subject via a custom LabVIEW (National Instruments, Austin, TX, United States)/Python program. Experimental protocols were reviewed and approved by the Institutional Review Board at Arizona State University.

Based on a two-alternative, forced-choice task, subjects were presented with two stimuli and asked to determine if they were the “same” or “different.” Each stimulus was a 10 mm movement of the gripped cube at 20 mm/s in varied sagittal directions. A randomized primary stimulus in the proximal, radial, distal, or ulnar direction was followed by a randomized 300–700 ms interstimulus interval. Then a secondary stimulus with a randomized angular difference of ±30° on intervals of 5° was delivered (**Figure 1**). Subjects were asked to determine whether the stimuli were in the “same” or “different” directions. In order to explore the reference frame of potential grip sensitivities, two grip orientations were used (**Figure 1**): horizontal (nine subjects; five female, four male) and vertical (five subjects; three female, two male). The primary stimulus definitions were aligned with the arm, and thus rotated by 90° between these two orientations. Grip and task instructions were identical for each grip orientation.

To avoid unwanted visual and proprioceptive feedback, subjects were blindfolded with their wrist mounted in a cushioned brace attached to a rigid frame. Coordinates from a PhaseSpace motion capture unit (PhaseSpace Inc, San Leandro, CA, United States) were referenced to the robotic arm so that the Y- and Z-axes corresponded with the subject’s sagittal plane. Motion capture markers were placed on the robotic arm, metacarpophalangeal joints (MCP), and the tip of the distal phalanges (DP) of digits 1 and 2 (MCP1, MCP2, DP1, and DP2), and the forearm just proximal to the wrist for each subject (**Figure 1**). Motion capture marker distance was defined as the maximum sagittal distance for each trial. Movement for each joint was evaluated using a two-way interaction ANOVA with grip orientation and primary stimuli and Tukey-Kramer tests are used for *post hoc* analysis on significant effects.

Sensitivity (d′) and bias (β) definitions were obtained for each primary stimulus using Eqs 1 and 2, respectively (Stanislaw and Todorov, 1999). Equation 1 is also divided into the necessary variables for clarification. Z(H) is the z-score conversion of the probability the subject has a hit (H) and identifies a “Different” trial correctly (True Different – TD). Z(F) is the z-score conversion of false alarms (F): when the subject identifies any “Same” trial incorrectly (False Same – FS). Sensitivity and bias were evaluated using a two-way interaction ANOVA with grip orientation and primary stimuli.

To determine thresholds of detection, we obtained a Point of Subjective Detection (PSD) by first defining the detection rate (DR) for each secondary stimulus (Eq. 3), with correctly identified trials as true and incorrectly identified trials as false. As shown in Eq. 3, the PSD is the angle where the proportion of true responses exceeds the false responses, i.e., when the DR becomes greater than 50%. The DR values were fit for all subjects grouped and for each subject individually using a second order polynomial regression and solutions for 50% are calculated. These solutions were considered the detection threshold and used to ascribe response trends to specific primary stimuli. Accuracy for each primary stimulus was calculated as the total correct responses of that primary stimulus over its total trials. Increased response accuracy and lower psychophysical PSD provide support for directional anisotropies. Detection thresholds were evaluated using a two-way interaction ANOVA with grip orientation (two levels) and primary stimuli (four levels). In a second analysis, primary stimuli were grouped into primary axes as proximal-distal and radial-ulnar rather than individual directions.

$$d'(Pri) = \frac{Z(H) - Z(F)}{\sqrt{2}}, \tag{1}$$

$$H(Pri) = \frac{TD\ (Pri)}{TD(Pri) + FD(Pri)} \tag{1a}$$

$$F(Pri) = \frac{FS(Pri)}{TS(Pri) + FS(Pri)} \tag{1b}$$

$$\beta(Pri) = \frac{Z(H) + Z(F)}{2} \tag{2}$$

$$DR(Pri, Sec) = \frac{T(Pri, Sec)}{T(Pri, Sec) + F(Pri, Sec)} \tag{3}$$

RESULTS

Motion capture data were used to calculate the absolute maximum distance traveled in the sagittal plane for each trial. Significant movement between grip orientation and primary stimulus for each joint of interest was determined by constructing respective two-way ANOVAs (**Table 1**). The wrist demonstrated no significant displacement for factors nor interactions. In both the thumb (digit 1) and index finger (digit 2), the MCP and tip of the DP had significantly less movement in the horizontal orientation than the vertical. For primary stimuli and the interaction effect, only the DP1 and DP2 produced significant differences. Tukey-Kramer *post hoc* analyses were conducted for these significant effects (**Figure 2**). Analysis of the primary stimulus factor revealed that the DP1 moved less during distal movements than ulnar movements but did not indicate any significant differences for DP2. As for the interaction effect *post hoc* analyses, DP1 demonstrated significant results in the horizontal orientation, but not the vertical orientation: distal and proximal trials produced less movement than radial and ulnar trials. DP2 was similar, except proximal

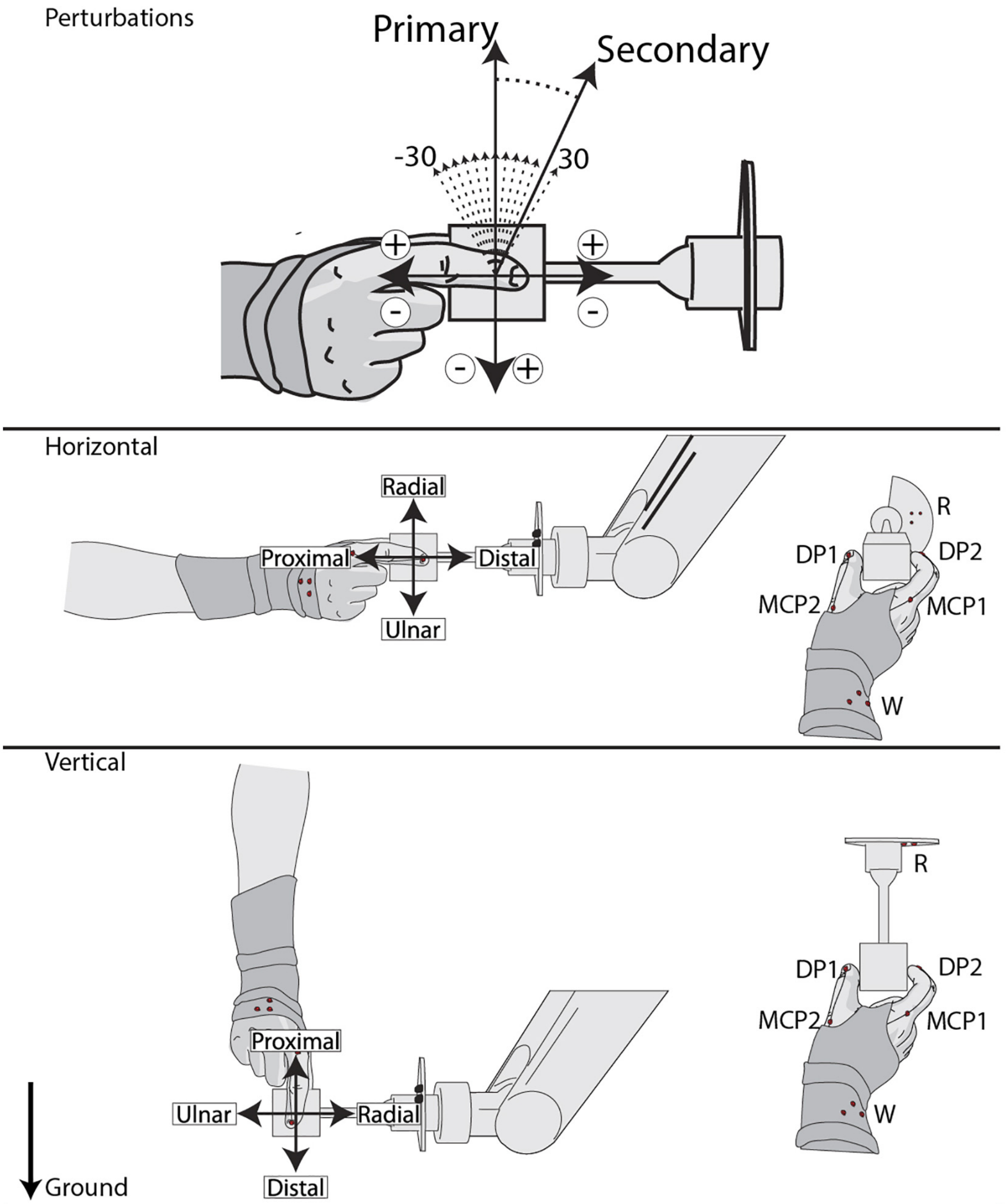

FIGURE 1 | Experimental setup and task. Task: a two-alternative, forced-choice paradigm consisting of both a primary and secondary stimulus, with a randomized 300–700 ms interstimulus interval. The primary stimulus is a 10 mm (20 mm/s) center-out-center movement in the proximal, radial, distal, or ulnar direction. The equidistant and equal velocity secondary stimulus differs within ±30° on 5° increments from the primary stimuli, indicated by respective sign conventions. Each subject responds "Same" or "Different" to the stimuli pair. Grip Orientations: primary stimulus definitions are defined by the rotation of the grip with respect to the ground. PhaseSpace markers on the M, DPs, Wrist, and Robot are also represented as red dots.

trials' movement was not significantly different than ulnar trials. Across all digits and conditions movement was less than 3 mm, less than the 10 mm the gripped cube actually moved. In significant cases, the difference in means ranged from 0.6 to 1.02 mm.

Bias (β) and sensitivity (d′) values were calculated for each set of grip orientation and primary stimuli trials. A two-way interaction ANOVA was performed with grip orientation and primary stimuli. No significant differences for bias nor sensitivity were found. Distal and proximal axes mostly exhibit increased β values, implying a preference of responding "different" in these directions. A higher bias would suggest a decreased ability to detect "same" trials. In addition, the d′ values are slightly higher for the distal-proximal axis in the horizontal grip and the vertical grip. With no significant β or d′ results, we explored threshold of detection.

TABLE 1 | Summary of two-way ANOVA on digit movement.

	Wrist	MCP1	DP1	MCP2	DP2
Motion capture					
Orientation	0.947	***p* < 0.005** H < V	**0.0002** H < V	***p* < 0.005** H < V	**0.0178** H < V
Primary Movement	0.9131	0.5365	**0.0058** Significance (Δmm) D < U (0.453)	0.5203	**0.042** No Tukey-Kramer
Interaction	0.5963	0.2147	**0.0005** Significance (Δmm) Horizontal P < R (0.6), P < U (0.71) D < R (0.91), D < U (1.02)	0.2668	**0.025** Significance (Δmm) Horizontal P < R (0.65) D < R (0.89), D < U (0.75)

Individual two-way ANOVAs were constructed for each finger's MCP and DP markers as well as the wrist. Any significant factor is bolded and accompanied by the significant post hoc comparisons and relevant differences in means, except for the DP2 Primary Stimulus effect, which did not provide significant post hoc results.

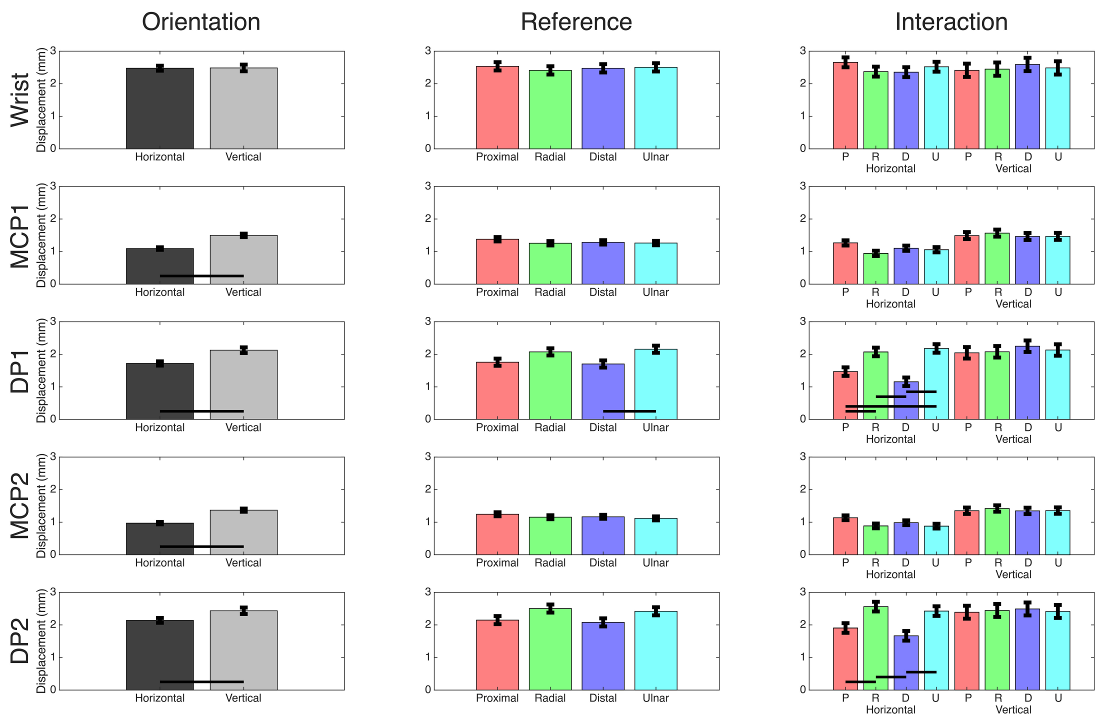

FIGURE 2 | Motion capture comparisons. Mean values for each two-way ANOVA performed on the motion capture marker's two-way ANOVA using orientation and primary stimuli as effects. Black bars indicate a significant *post hoc* Tukey-Kramer result of $p<0.05$. Comparisons between orientations in the interaction plots are removed as they are not of interest, but significant results between references movements within orientation are shown.

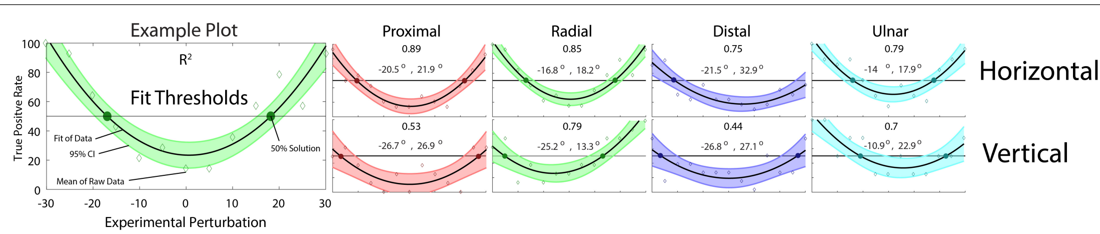

FIGURE 3 | Polynomial regression fits of response sensitivity. For each primary stimulus in each grip condition, detection rate (DR) is calculated as a secondary stimuli's True Positives over the sum of respective True Positives (TP) and False Negatives (FN). The PSD mark represents where TP ≥ FN. Subjects who showed a DR ≤ 50% for ±30° or 0° secondary stimuli were excluded due to lack of attention or focus during the experiment. For all subjects, the mean DR is overlaid with a second order polynomial regression fit and respective 95% confidence intervals. Solutions for 50%, and R^2 are given for each plot.

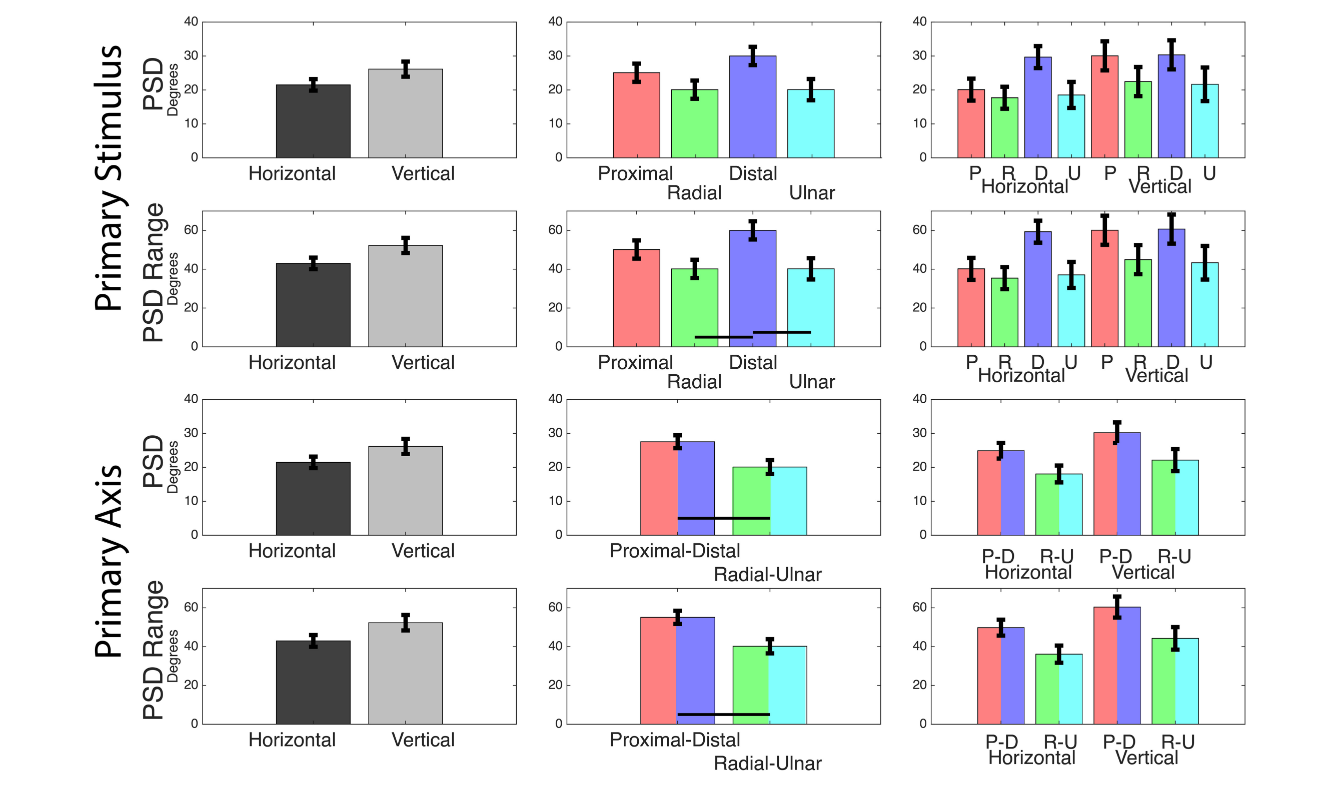

FIGURE 4 | Points of subjective detection. Mean values for each two-way ANOVA performed on the calculated PSD values and PSD windows. Tests were performed with primary stimuli grouped into four levels (movements) and two levels (axes). The latter grouped radial with ulnar and grouped distal with proximal. Black bars indicate a significant *post hoc* Tukey-Kramer result of $p < 0.05$.

The task was designed to exceed existing reports of directional discrimination limits and required the subjects' attention. Subjects whose DR was less than 50% for ±30° or 0° trials were excluded, and the high error was attributed to lack of attention or task vigilance. These rules revealed two horizontal grip exclusions and one vertical grip exclusion. To determine the PSD, data were modeled with second order polynomial regressions, 95% confidence intervals were calculated, and solutions for 50% DR calculated (**Figure 3**). Using the Akaike Information Criterion (AIC), it was determined that utilizing a fourth order polynomial model overfits the data and second order models provide a higher quality fit. The full results are summarized in **Table 2**, including accuracy calculations for each primary stimulus under each grip treatment and AIC values for the second and fourth order models. The R^2 values included are representative of the chosen second order model. Determined PSD values occurred within 10.9° to 32.9°, depending on axis and grip orientation.

Using second order models to fit individual subject's DR values, we calculated PSD values for each primary stimulus. A two-way ANOVA of PSD values using grip orientation and primary stimuli (four levels) reports that primary stimuli is a significant effect. *Post hoc* Tukey-Kramer analysis reports that distal thresholds are greater than radial and ulnar. A second two-way ANOVA of grip orientation and primary axis rather than stimuli (two levels) reports that primary axis is a significant effect. *Post hoc* Tukey-Kramer analysis reports that distal-proximal thresholds less than radial-ulnar thresholds (**Figure 4** and **Table 3**). The PSD values in **Table 2** also imply some asymmetry along certain axes, primarily the radial-ulnar axis, where the positive and negative PSD values deviate in magnitude. Due to this axial asymmetry, it is hard to define specific PSDs for the directional discrimination, but the range within the determined PSDs informs us of windows that would provide subjective uncertainty. A two-way ANOVA of the window ranges using grip orientation and primary stimuli reports that primary stimuli is a significant effect. *Post hoc* Tukey-Kramer analysis reports that the distal uncertainty windows are greater than radial and ulnar. A second two-way ANOVA of the window ranges using grip orientation and primary axis reports that primary axis is a significant effect. *Post hoc* Tukey-Kramer analysis reports that distal-proximal thresholds greater than radial-ulnar thresholds (**Figure 4** and **Table 3**).

DISCUSSION

The β and d′ calculations offered valuable suggestions in directional bias and sensitivity. Specifically, that there is a subjective bias to answer "different" and an increased sensitivity in the distal-proximal axis, largely regardless of grip orientation. These suggestions were statistically insignificant and further

TABLE 2 | Summary of analytical results for each primary stimulus under grip orientations.

		Primary stimulus			
		Proximal	**Radial**	**Distal**	**Ulnar**
Horizontal grip	+	21.9	18.2	32.9	17.9
PSD	–	20.5	16.8	21.5	14
	Δ	42.4	35	54.4	31.9
	AIC (2°)	57	58.5	52.7	57
	AIC (4°)	61.1	62.9	56.7	61.6
	R^2	0.89	0.85	0.75	0.79
	Accuracy	47.8	59.3	37.3	63.1
	Standard error (n = 7)	1.73	1.04	2.45	1.34
Vertical grip	+	26.9	13.3	27.1	22.9
PSD	–	26.7	25.2	26.8	10.9
	Δ	53.6	38.5	53.9	33.8
	AIC (2°)	35.4	38.5	34	37.4
	AIC (4°)	39.5	42.8	38.9	41.6
	R^2	0.53	0.79	0.44	0.7
	Accuracy	37.5	54.8	36.5	59.6
	Standard error (n = 4)	4.1	0.9	3.18	4.26

*Accuracy: correct responses over total trials for each primary stimulus. Detection thresholds: (+) and (–) indicate the solutions at the PSD for the polynomial fit of the mean subject response, respective to the sign convention indicated in **Figure 1**. Δ is the range between PSDs. Akaike Information Criterion (AIC) values are listed for second and fourth order polynomials. In all cases, the second order models had lower AIC values and therefore are considered better fits. R^2: fit coefficient of determination for the second order polynomial.*

analysis contradicted the suggested trend, as Points of Subjective Detection (PSD) indicated a significant anisotropy where discrimination improved in the radial-ulnar axis. Distal-proximal PSD values were near literature values, between 20.5 and 32.9°, but the radial-ulnar axes had significantly lower PSDs, between 10.9 and 25.2°. The ulnar-radial axes were lower in PSD value but also in uncertainty window range. This addresses the concern over the asymmetry of PSDs in **Table 1**, as the narrow range supports better detection even if it is slightly offset. Results indicate that increased detection ability occurs in the radial-ulnar axis, referenced to the orientation of the hand rather than the environment. To arrive at these conclusions, we find it important to address the statistical limitations of our analysis and process. While analyzing primary stimuli directions independently, limited or no significant results were found. However, grouping the primary stimuli into primary axes provides significant anisotropic differences. While this is likely exacerbated by the limited sample size, we believe this provides insight toward subjective understanding of somatosensory and proprioceptive integration.

From the analysis, heightened directional discrimination ability in the radial-ulnar axis supports that this discrimination is referenced to the subjects' hand orientation, and we offer the explanation of increased distal-phalange movement in that axis. Statistically, the DP1 and DP2 demonstrated increased movement during trials in the radial-ulnar axis. Therefore, the increased detection ability could be explained by these movements, even when the significant differences are less than a millimeter. While the gripped cube moved 10 mm and the motion capture only indicates DP movement less than 3 mm, it is clear that proprioceptive information from these significant displacements is the primary explanation for increased detection ability.

As a consideration, the results are likely not solely due to displacement as the majority of object movement, near 70%, is left to be absorbed and interpreted with other means. Multisensory integration of somatosensation and proprioception is occurs even at miniscule additions of tactile information, so it is not unreasonable to think the combination of miniscule but significant joint displacement and complex tactile information are both being utilized (Rincon-Gonzalez et al., 2011). The somatosensation component could be explained by surface friction inducing skin deformation. Passive slip literature indicates that slip texture, speed, and direction sensitivity should exist in the distal-proximal axis, potentially attributed to factors such as the anisotropic properties of the fingertip surface's dermal ridging (Maeno and Kobayashi, 1998; Maeno et al., 1998). However, the finger pad is also anisotropic in its ability to deform, and the combination of dermal ridging and glabrous tissue interactions may provide an answer. Somatosensory cortex possesses multimodal representations of passive lateral finger displacement and cutaneous touch (Kim et al., 2015). Contextual activation of the finger pad informs these multimodal representations during precision grip cued by weight, texture, and increased friction (Salimi et al., 1999a,b,c). The different cues are directionally influenced by the anisotropic properties of the finger pads' glabrous skin. First, papillary ridges at the middle

TABLE 3 | Summary of two-way ANOVA on points of subjective detection.

Detection thresholds	**Primary direction**		**Primary axis**	
	PSD	**PSD range**	**PSD**	**PSD range**
Orientation	0.1029	0.0679	0.0969	0.0678
Primary movement	**0.0385**	**0.0183**	**0.0093**	**0.005**
	No Tukey-Kramer	Significance (Δ°)	Significance (Δ°)	Significance (Δ°)
		D > R (19.84), D > U (19.82)	P-D > R-U (7.45)	P-D > R-U (14.90)
Interaction	0.6654	0.5659	0.8254	0.8057

Two-way ANOVAs were constructed for the calculated PSD values and PSD window ranges. This is performed grouping trials into primary directions (four levels) and primary axes. Any significant factor is bolded and accompanied by the significant post hoc comparisons and relevant differences in means, except for the primary direction ANOVA for the PSD values, which did not provide significant post hoc results.

of the finger are orthogonal to the radial-ulnar axis, predicting increased deformation in the respective axis. With increased skin stretch comes increased perception of tactile information (Wang and Hayward, 2007; Provancher and Sylvester, 2009; Seizova-Cajic et al., 2014). During the previously observed passive slip tasks, the glabrous skin is not likely heavily engaged and the tactile stimuli are superficial. By utilizing precision grip, our task engages more of the inherent biomechanical properties of the fingers and fingertips. Directional grip detection sensitivity, but not superficial slip sensitivity, is a function of the amount of observed digit displacement and, potentially, skin stretch in respective directions. Further investigation focused on the latter variable.

CONCLUSION

Precision grip responses are modulated by task context as seen in forces, latencies, and orientation sensitivity. We studied the perception of the task not the response properties, and observed an internally referenced source of information independent of hand posture. This tactile directional discrimination is claimed to be biomechanically referenced as a result of increased digit movement and hypothesized to be influenced by anisotropic fingerpad properties. These are not inherently competing results but argue that perceptual responses stem from directionally dependent activation of the parallel inputs.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Arizona State University Institutional Review Board. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

JT and NN contributed to the experimental design, data collection, analysis of the data, and preparation of the manuscript. SH provided mentorship and advice, as well as editing and oversight. All authors contributed to the article and approved the submitted version.

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ORIGINAL RESEARCH
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Cardiac and Proprioceptive Accuracy Are Not Related to Body Awareness, Perceived Body Competence, and Affect

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Interoception in the broader sense refers to the perception of internal states, including the perception of the actual state of the internal organs (visceroception) and the motor system (proprioception). Dimensions of interoception include (1) interoceptive accuracy, i.e., the ability to sense internal changes assessed with behavioral tests, (2) confidence rating with respect to perceived performance in an actual behavioral test, and (3) interoceptive sensibility, i.e., the self-reported generalized ability to perceive body changes. The relationship between dimension of cardioceptive and proprioceptive modalities and their association with affect are scarcely studied. In the present study, undergraduate students (N = 105, 53 males, age: 21.0 ± 1.87 years) filled out questionnaires assessing positive and negative affect (Positive and Negative Affect Schedule), interoceptive sensibility (Body Awareness Questionnaire), and body competence (Body Competence Scale of the Body Consciousness Questionnaire). Following this, they completed a behavioral task assessing cardioceptive accuracy (the mental heartbeat tracking task by Schandry) and two tasks assessing proprioceptive accuracy with respect to the tension of arm flexor muscles (weight discrimination task) and the angular position of the elbow joint (joint position reproduction task). Confidence ratings were measured with visual analog scales after the tasks. With the exception of a weak association between cardioceptive accuracy and the respective confidence rating, no associations between and within modalities were found with respect to various dimensions of interoception. Further, the interoceptive dimensions were not associated with state and trait positive and negative affect and perceived body competence. In summary, interoceptive accuracy scores do not substantially contribute to conscious representations of cardioceptive and proprioceptive ability. Within our data, non-pathological affective states (PANAS) are not associated with the major dimensions of interoception for the cardiac and proprioceptive modalities.

Keywords: proprioception, cardioception, interoceptive accuracy, interoceptive sensibility, affect, body awareness

INTRODUCTION

Interoception refers to the processing of information originating from within the body (Cameron, 2002). Originally, it was a synonym for visceroception; later, the inclusion of somatosensory and proprioceptive information was also proposed (Vaitl, 1996; Ceunen et al., 2016; Berntson et al., 2018). The current paper applies this broad approach to interoception. Thus, conscious aspects of interoception include body sensations associated with emotions, awareness of non-emotive body processes and the perception of the actual state of the locomotor system.

The recently accepted conceptualization of conscious aspects of interoception describes at least two major dimensions (Ceunen et al., 2013; Garfinkel and Critchley, 2013; Garfinkel et al., 2015a). Interoceptive accuracy (IAc or sensitivity) refers to the acuity of perception of internal changes and states as assessed by behavioral methods. Its self-report counterpart, i.e., the perceived performance in an a behavioral test of acuity, is called confidence. Finally, the perceived general ability to sense body changes is called interoceptive sensibility (IS) or awareness in the literature. Empirical evidence shows that the association between these three dimensions of cardiac interoception is weak or non-existing (see below).

It is worth noting that there is an inconsistency in the literature with respect to the concept of interoceptive sensibility. Unfortunately, it is not clear which questionnaires should be used to assess the dispositional aspect of interoceptive sensibility. Garfinkel et al. (2015a) recommend the Body Awareness Scale of the Body Perception Questionnaire (Porges, 1993). The Body Awareness Questionnaire (BAQ) (Shields et al., 1989) and the Multidimensional Assessment of Interoceptive Awareness (Mehling et al., 2012) have been also used in the literature (Meessen et al., 2016; Ferentzi et al., 2019). Although the former does not make a distinction between visceroception and proprioception, whereas the latter includes only visceroceptive modalities, a recent study indicated a substantial overlap between the two constructs (Ferentzi et al., 2020).

Concerning the emotional experience, the primary importance of visceroception has been suggested by many authors (James, 1884, James, 1890; Lange, 1885; Damasio, 1994), whereas others emphasize the role of the somatosensory system (Darwin, 1872; Tomkins, 1962, 1981; Izard, 1971). These models assume the causal role of interoceptive information in the development of affective experience thus they are called peripheral theories of emotion. Central theories do not suppose such a causal link (Cannon, 1927, 1931; Panksepp, 1982, 1991; Oatley and Johnson-laird, 1987; Davis, 1989; LeDoux, 1990); still, they accept that emotions are typically characterized by peripheral changes that prepare the organism for the behavioral response. As a proportion of these changes, both visceral and somatosensory, may reach conscious awareness, an association between the emotional experience and the perception of body changes can be explained by central theories too.

Cardiac response plays a central role in the physiological component of emotional reactions, as they are usually characterized by an increased energetic demand (Lacey and Lacey, 1978). It is widely assumed that, in line with the tenets of peripheral theories of emotion, the accuracy of perception of cardiac activity, dubbed cardioceptive accuracy, contributes to the emotional experience (Wiens et al., 2000; Pollatos et al., 2005). On the other hand, a more intense emotional reaction (e.g., if it is accompanied by sympathetic activation) can improve the perception of heartbeats (Schandry et al., 1993; O'Brien et al., 1998; Fairclough and Goodwin, 2007). Empirical studies revealed a positive association between the intensity (arousal) component of emotions and cardioceptive accuracy (Wiens et al., 2000; Barrett et al., 2004; Pollatos et al., 2005, 2007b; Herbert et al., 2007, 2010). Also, improved cardiac accuracy was found to be related to the actual level of anxiety in a number of studies (Schandry, 1981; Ludwick-Rosenthal and Neufeld, 1985), whereas no such associations were reported in others (Pollatos et al., 2007a; Werner et al., 2013). From a theoretical point of view cardioceptive confidence may also contribute to the affective experience. For example, manipulated feedback on heart rate was enough to intensify the emotional reaction (Valins, 1966, 1967). Even more intriguingly, if actual and perceived heart rate did not correspond, the latter influenced the perceived level of arousal (Thornton and Hagan, 1976; Kerber and Coles, 1978; Woll and McFall, 1979; Parkinson, 1985).

Proprioceptive information is also assumed to play a substantial role in the formation of emotional experience. According to different theories (for a review, see Moors, 2009), somatic and/or motor changes, modulated by cognitive processing, are cornerstones of the arising of affective feelings. Changes in the musculoskeletal system can modulate the emotional experience. Shafir et al. (2015) showed that different affective feelings can be evoked by specific, complex movement patterns. Power posing may also change the affective experience; however results with respect to behavioral (more risk-taking) and hormonal responses (i.e., increased testosterone and decreased cortisol level) are controversial (Carney et al., 2010; Ranehill et al., 2015; Simmons and Simonsohn, 2017). In the same vein, EMG activity increases in many muscles and muscle groups in stressful situations (Lundberg et al., 1994; Wahlström et al., 2002; Krantz et al., 2004; Luijcks et al., 2014), and it is possible to reduce stress and anxiety through relaxation techniques (e.g., progressive relaxation, autogenic training), which operate (at least partially) through the systematic relaxation of muscles (Kanji et al., 2006; Rausch et al., 2006). Finally, Cacioppo et al. (1993) showed that the activation of arm flexor muscles activates the approach system, which biases the judgment of neutral stimuli to the positive direction. By contrast, activation of arm extensors stimulates the avoidance system, resulting in the opposite effect. Neumann and Strack (2000) drew a similar conclusion in a categorization task. Overall, these findings support the idea that the actual state of muscles can impact the emotional experience.

Based on the aforementioned role of proprioceptive information in the formation of the affective experience, it is logical to assume that, similar to cardioceptive information, individual differences in the accuracy of processing of proprioceptive information (aka proprioceptive accuracy) are related to differences in emotional processing. In accordance with this assumption, alterations in processing and integration of proprioceptive input can be associated with pathological conditions. For example, a greater reliance on proprioception during the completion of a motor task is associated with impairments in imitation and empathy in autism spectrum, and attention deficit hyperactivity disorder (Gao et al., 2019). In fibromyalgia, however, patients were found to be less reliant on proprioceptive information than healthy controls (Bardal et al., 2016). Also, decreased proprioceptive accuracy was found in chronic pain (Tsay et al., 2015) and schizophrenia (Rosenbaum et al., 1959, 1965; Leventhal et al., 1982; Chang and Lenzenweger, 2005). In contrast, somatoform disorders are accompanied by higher proprioceptive accuracy (Scholz et al., 2001). It is also important to note that an emotionally intense state, e.g., the high level of stress, decreases proprioceptive accuracy (Şenol et al., 2018). However, not all studies confirmed the aforementioned relationships, there are null findings too, for example with respect to schizophrenia (Ritzler and Rosenbaum, 1974; Ritzler, 1977), fibromyalgia (Akyol et al., 2013; Ulus et al., 2013), and chronic pain (Tsay et al., 2015). Moreover, Horváth et al. (2019) found that there is no association between trait affect and proprioceptive accuracy, as assessed with the Joint Position Reproduction test in the elbow joint. Additionally, proprioceptive accuracy was not correlated with body awareness–a construct that overlaps with interoceptive sensibility (Ferentzi et al., 2020)–and perceived body competence (Ferentzi et al., 2017; Horváth et al., 2019).

When investigating the role of interoceptive accuracy, it is a fundamental question whether individual characteristics in information processing established in one modality (e.g., cardioception) can be generalized to other modalities (e.g., proprioception). Ferentzi et al. (2018) reported no association between modalities of interoception. A significant association was found only between measures within the same modality for three visceroceptive modalities (i.e., pain threshold and tolerance, gastric fullness and unpleasantness, and the intensity and unpleasantness of bitter taste), but there was no association between the two included measures of proprioceptive accuracy (ipsilateral and contralateral version of the joint position reproduction test in the elbow joint). These and other results (Garfinkel et al., 2017) show that interoceptive accuracy cannot be generalized across interoceptive modalities.

With respect to joint-related proprioceptive accuracy, a number of measurement paradigms were developed (Han et al., 2016). Studies investigating the association between different tests in one joint (Barrack et al., 1984; Grob et al., 2002; Jong et al., 2005; Elangovan et al., 2014; Li et al., 2016; Niespodziński et al., 2018; Yang et al., 2020) consistently report that accuracy is test-specific. The same conclusion can be drawn with respect to cardioception: accuracy scores obtained by heartbeat discrimination methods that use forced-choice methods and methods that use heartbeat tracking (i.e., counting) typically show no or only weak associations (Pennebaker and Hoover, 1984; Weisz et al., 1988; Phillips et al., 1999; Schaefer et al., 2012; Hart et al., 2013; Schulz et al., 2013; Michal et al., 2014; Garfinkel et al., 2015a,b; Forkmann et al., 2016; Ring and Brener, 2018). Moreover, proprioceptive measurement methods can be conducted with respect to different joints; Han et al. (2013) and Waddington and Adams (1999) revealed that accuracy, assessed with the same paradigm (active movement extent discrimination apparatus) is joint-specific, and only the same joints of the left and right side of the body show an association. The actual exertion (or tension) of muscles represents another proprioceptive modality; a fundamental difference is that activation of the muscles is controlled by a feed-forward mechanism thus the efferent information plays a similarly important role in the processing of the actual state as the afferent input (Miall and Wolpert, 1996; Cullen, 2004). Further, joint-related acuity primarily relies on receptors located in the joints (Ruffini end organs), whereas muscle-related accuracy is impacted by afference from receptors in the muscles (muscle spindles) (Batson, 2009; Jha et al., 2017).

Confidence rating, the self-reported dimension of interoception, appears to be independent of interoceptive accuracy for healthy participants (e.g., Ehlers et al., 1995). In another study, accuracy and confidence were associated among high performers in both applied heartbeat perception tasks, i.e., the mental tracking and the discrimination task (Garfinkel et al., 2015a). The authors interpret their results as a dissociation of the assessed dimensions of interoception which was replicated by others regarding the mental tracking task (Forkmann et al., 2016; Meessen et al., 2016). A weak positive association between cardioceptive accuracy and confidence was found in another study (Köteles et al., 2020a). Besides heartbeat perception, interoceptive confidence with respect to respiration has been also investigated and the dissociation between accuracy and confidence was confirmed (Garfinkel et al., 2016). In the field of proprioception, however, confidence has not been assessed to date.

The major goal of the present study is to shed more light on the associations within and between the dimensions of cardioception and two modalities of proprioception, i.e., the sense of joint position and muscle tension. We also wanted to explore the associations between affect and the behavioral and self-report measures of these modalities.

The following hypotheses were tested. First, accuracy and confidence show a weak positive association within the same modality (H1). Second, accuracy and confidence between modalities are independent of each other (H2). Third, cardioceptive accuracy and confidence are associated with affect, whereas proprioceptive accuracy and confidence are not (H3). Finally, we assumed that proprioceptive accuracy and confidence would not be associated with perceived body competence and body awareness (H4).

MATERIALS AND METHODS

Participants

A priori sample size calculation for $r = 0.3$, $\alpha = 0.05$ (one-tailed), $1\text{-}\beta = 0.9$ indicated a minimum required sample size of $N = 92$ (Faul et al., 2007). Participants were undergraduate students of Eötvös Loránd University ($N = 105$, 53 males, age: 21.0 ± 1.87 years, 95 right handed). Participants consuming alcohol and/or taking psychoactive drugs within 8 h before the experiment, and those with severe injury/disability of the arm were excluded. Participation was rewarded with partial course credit. Joint Position Reproduction test was missing for nine individuals due to technical problems. The study was approved by the Research Ethics Committee of the university. Before participation, everyone signed an informed consent form.

Behavioral Measures

Proprioceptive Accuracy–Joint Position Sense

Joint Positions Sense was assessed with a version of the Joint Position Reproduction Test (JPR) (Goble, 2010), where participants had to reproduce elbow joint positions. We tested the non-dominant arm of the participants. Participants were blindfolded, seated, and asked to keep a standard posture (upper arms parallel with the ground and in line with the body). During the measurement, they placed their upper arm on a rotatable lever, which was connected to a motor, and made possible the accurate (±0.1 degree) measurement and movement of the elbow joint. They had to hold a handle and keep their hand on a button. 180 degree indicated fully extend elbow. From starting position, the machine moved the arm of the participant to the target positions with a speed of 12 degree/s. After spending 4 s there, the device moved back the lever to the starting position. After 1 s, the lever started to move again, with a speed of 8 degree/s. The task of the participants was to press the button, when they felt that their arm reached the target position. Following this, the lever moved the arm back to the starting position again and a new trial begun. The starting position was always 160 degree, while the target position changed from trial to trial. Overall, nine trials were conducted, with nine different target positions (150, 135, 120, 105, 90, 75, 60, 45, and 30 degree). Every target position was presented once; the order of presentation was randomized. To calculate the accuracy of Joint Position Reproduction, an error score (i.e., the difference between the target and the reproduced position (i.e., the difference between the target and the reproduced position) was calculated for each trial. Outliers above and below two standard deviation were removed and missing values were imputed by using the fully conditional specification (MCMC) and linear regression model options of SPSS v20 software. To determine accuracy, we used two error scores: constant and variable error (Schutz and Roy, 1973; Boisgontier et al., 2012; Goble et al., 2012). Constant error is the mean of the error scores and shows the magnitude and direction of the systematic distortion in position judgments. Negative values of constant error score indicate bias toward the inside direction, whereas positive values indicate bias toward the outside direction. Internal consistency of constant error was acceptable (Cronbach's alpha: 0.751). Variable error is the standard deviation of the error scores and shows the inconsistency of judgments (i.e., higher variable error shows higher level of inconsistency.

Proprioceptive Accuracy–Weight Discrimination

To assess weight discrimination ability, participants had to compare the weight of two objects (Chang and Lenzenweger, 2005). These objects were glass bottles filled with water, identical in shape and size. During the measurement, participants eyes' were covered; they had to keep a standing posture, keep their left upper arm next to their body, and their lower arm in a flexion of approximately 90 degree.

Overall, 32 comparisons were made. The weight of one of the presented bottles was always 200 g. In one half of the trials (16), the other bottle was 200 g (identical pairs), while in the other half (16), it was 215 g (different pairs). The presentation order of the pairs and that of the bottles within pairs were randomized. Participants had to hold every bottle for 8 s, verbally judge if they were the same weight or one was heavier. For heavier judgments, it also had to be indicated which weight was heavier. Weight discrimination ability was calculated by dividing the number of correct trials by the number of all trials.

Cardioceptive Accuracy

Cardioceptive accuracy was assessed with a mental heartbeat-counting paradigm (Schandry, 1981). Participants had to count their heartbeats silently, while sitting on a chair, with their hands on their laps. They were explicitly encouraged to count if they had the lightest heartbeat sensation in any part of their body but were also asked not to count if they did not have any sensation. After a practice trial, which lasted for 15 s, three test trials of different lengths (25, 35, and 50 s) were conducted. The test trials were presented in a randomized order. The number of heartbeats were recorded with the NeXus recording system (NeXus Wireless Physiological Monitoring and Feedback: NeXus-10 Mark II, Version 1.02; BioTrace + Software for NeXus-10 Version: V201581; Mind Media BV, Herten, the Netherlands). For every interval, an accuracy score was calculated as: 1–| (HB recorded–HB counted)/HB recorded|. For every individual, the scores of the three intervals were averaged to calculate cardioceptive accuracy. Internal consistency of the Schandry task was high (Cronbach's alpha = 0.906).

Questionnaires and Questions

Confidence Ratings

After every task (Joint Position Sense, Weight Discrimination, Cardioceptive accuracy), participants' subjective judgment about their performance ("*How do you think you performed in this test?*") was recorded. For this purpose, they had to indicate their perceived performance on a 10 cm-long, vertical visual analog scale. The anchor points were "*The best possible*" and "*The worst possible*." We measured the distance of the crossed part of the line from the bottom of the visual analog scale in millimeters. Higher values indicate higher levels of confidence.

Interoceptive Sensibility–Body Awareness

Body Awareness Questionnaire measures the self-reported sensitivity to bodily processes, and the ability to anticipate bodily reactions (Shields et al., 1989; Köteles, 2014). Participants have to answer 18 questions on seven-point Likert-scales (e.g., "I notice distinct body reactions when I am fatigued"), where higher scores mean higher levels of body awareness (except one reversed item). Internal reliability in this sample was good (Cronbach's α = 0.848).

Body Competence

Body Competence was assessed with the Body Competence Scale of Miller's Private and Public Body Consciousness Questionnaire (Miller et al., 1981). The scale consists of four questions (e.g., "*I'm better coordinated than most people*"), rated on a five-point Likert scale. Higher values indicate higher levels of perceived physical competence. Internal consistency of the scale in this study was good (Cronbach's $\alpha = 0.835$).

Affect

We used the Positive and Negative Affect Schedule (PANAS) to asses affect (Watson, 1988; Gyollai et al., 2011). The questionnaire can be used with two different instructions, to measure state and trait aspects of affect. The questionnaire is divided into two subscales, positive affect (PA) (e.g., enthusiasm), and negative affect (NA) (e.g., nervousness); both measured with 10 items. Participants have to rate how intensely they feel the given emotional state on a five-point Likert scale, from 1 ("*Very slightly or not at all*") to 5 ("*Very much*"). Higher scores refer to higher levels of positive and negative affect, respectively. Cronbach's α values indicated acceptable to high levels of internal consistency in this study (Positive Trait: 0.872, Positive State: 0.922, Negative Trait: 0.854, Negative State: 0.794).

TABLE 1 | Descriptive statistics of the assessed variables.

***N* = 105**	**M ± SD**	**Min–max**
Cardioceptive accuracy	0.51 ± 0.270	0.0 to 0.963
Cardioceptive confidence	46.80 ± 26.042	1 to 96
Weight discrimination accuracy	15.66 ± 3.622	9 to 29
Weight discrimination confidence	40.74 ± 22.419	0 to 94
Joint Position Sense–constant error	6.5 ± 4.652	–11.341 to 21.386
Joint Position Sense–variable error	6.76 ± 2.277	2.287 to 12.352
Joint Position Sense confidence	61.094 ± 22.239	0 to 98
State NA	12.54 ± 3.190 (15.8 ± –5.9)*	10 to 24
Trait NA	17.22 ± 5.181 (19.5 ± 6.0)*	10 to 36
State PA	31.60 ± 8.247 (29.0 ± 8.0)*	12 to 49
Trait PA	36.429 ± 6.090 (35.7 ± 6.2)*	17 to 50
Interoceptive sensibility–BAQ	80.95 ± 15.449	40 to 122
Body competence	14.45 ± 3.581	4 to 20

*Weight discrimination and proprioception of the angle of the elbow joint were conducted with the subdominant hand. NA, negative affect; PA, positive affect; BAQ, Body Awareness Questionnaire. *Normative data reported by Watson and Clark (1994).*

TABLE 2 | Correlations between accuracy and confidence for the three interoceptive modalities.

Interoceptive modality	**Spearman correlation (p)**	**Bayesian Kendall's Tau (BF_{10})**
Cardioception	0.25* (0.011)	0.182 (5.063)
Weight discrimination	0.05 (0.643)	0.032 (0.144)
Joint Position Sense–constant error	–0.09 (0.433)	–0.058 (0.191)
Joint Position Sense–variable error	–0.05 (0.640)	–0.050 (0.176)

**p < 0.05.*

Procedure and Statistical Analysis

Data was collected in two phases. Participants had to fill out the questionnaires (with the exception of state PANAS) at home in an online form. The order of the questionnaires was: demographic data, trait PANAS, BAQ, Body Competence. Behavioral measures were conducted individually in the laboratory in a randomized order. Before the behavioral tasks, participants had to fill out the state PANAS questionnaire. Statistical analysis was conducted using the Jasp v0.11 software (JASP Team, 2019) using both the frequentist and Bayesian approach. Due to violations of the requirement of normality, associations were estimated using non-parametric correlations, i.e., Spearman's rho in the frequentist analysis and Kendall's Tau in the Bayesian analysis. For the Bayesian analysis, values below 0.33 indicated the superiority of the null-hypothesis, and values over 3 indicated the superiority of the alternative hypothesis (Wetzels and Wagenmakers, 2012).

RESULTS

Descriptive statistics of the assessed variables are presented in **Table 1**.

No significant associations but one between accuracy and confidence ratings (H1) within the included interoceptive modalities were revealed (**Table 2**). For cardioception, accuracy was weakly ($r_s = 0.25$, $p < 0.05$) related to confidence (**Figure 1**); this was supported by the Bayesian analysis ($BF_{10} = 5.063$). The null model (i.e., the lack of association) was more probable for all other modalities.

Concerning associations between indicators of accuracy (H2), no significant correlation was found. Only the two joint position sense related indices (i.e., constant and variable error) showed a moderate association ($r_s = 0.41$, $p < 0.001$; $r_\tau = 0.28$,

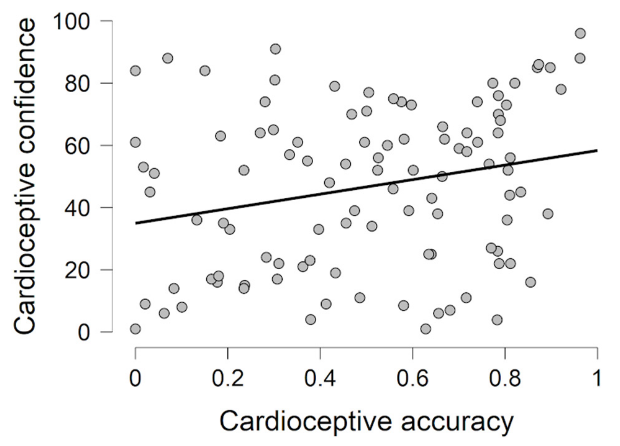

FIGURE 1 | Association between cardioceptive accuracy and cardioceptive confidence ratings.

TABLE 3 | Correlations between accuracies for the three interoceptive modalities.

***N* = 105**	**Cardioception**	**Weight discrimination**	**Joint Position Sense–constant error**	**Joint Position Sense–variable error**
Cardioception	–	0.00 (0.987)	−0.08 (0.455)	−0.09 (0.399)
Weight discrimination	−0.003 (0.127)+	–	0.09 (0.395)	−0.01 (0.938)
Joint Position Sense–constant error	−0.058 (0.188)+	0.059 (0.188)+	–	0.41 (<0.001)***
Joint Position Sense–variable error	−0.051 (0.174)+	−0.004 (0.133)+	0.281 (500.816)***	–

*Upper triangle: frequentist analysis with Spearman's rho coefficients (p-values); Lower triangle: Bayesian analysis with Kendall's Tau coefficients (BF^{10} values). ***$p < 0.001$/$BF10 > 100$. +: $BF10 < 0.33$.*

TABLE 4 | Correlations between confidence ratings for the three interoceptive modalities.

***N* = 105**	**Cardioception**	**Weight discrimination**	**Joint Position Sense**
Cardioception		0.09 (0.374)	0.135 (0.198)
Weight discrimination	0.07 (0.212)+		−0.07 (0.518)
Joint Position Sense	0.09 (0.314)+	−0.04 (0.155)+	

*Upper triangle: frequentist analysis with Spearman's rho coefficients (p-values); Lower triangle: Bayesian analysis with Kendall's Tau coefficients (BF^{10} values). ***: $p < 0.001$/$BF10 > 100$. +: $BF10 < 0.33$.*

$BF_{10} = 500.816$); Bayesian analysis indicated the superiority of the null hypothesis for all other cases (**Table 3**).

With respect to confidence ratings, no significant association was found between cardioceptive and weight discrimination related confidence ($r_s = 0.09$, $p = 0.374$; $r_\tau = 0.067$, $BF_{10} = 0.212$), between cardioceptive and joint position sense related confidence ($r_s = 0.14$, $p = 0.198$; $r_\tau = 0.092$, $BF_{10} = 0.314$), and joint position sense and weight discrimination related confidence ($r_s = -0.07$, $p = 0.518$; $r_\tau = -0.037$, $BF_{10} = 0.155$). Again, Bayesian analysis indicated the superiority of the null hypothesis for all cases (**Table 4**).

Between measures of interoception and questionnaire scores (H3, H4), correlation analysis indicated no significant correlations (**Table 5**). Bayesian analysis indicated the superiority of the null hypothesis for most of the cases and was inconclusive (i.e., in the 0.33–3 domain) for the remaining associations (**Table 6**).

DISCUSSION

The goal of the present study was to investigate the associations between different modalities (cardioception and two proprioceptive modalities) of interoception and their dimensions (accuracy, confidence ratings and sensibility). Associations with positive and negative affect and perceived body competence were also investigated. Overall, accuracy and confidence were associated with respect to the cardiac modality only; further, no between-modality associations and associations with interoceptive sensibility, affect, and body competence were found.

Interoceptive Accuracy and Confidence

Contrary to our first hypothesis, accuracy and confidence were found to be independent of each other with respect to the two proprioceptive modalities. In other words, people are not able to sense their actual performance in these tasks. In the cardioceptive modality, however, similar to previous studies (Garfinkel et al., 2015a), we found a weak positive association between accuracy and confidence. This latter finding is in line with the insight that top-down information substantially impacts performance in the mental tracking task (Ring et al., 2015; Ring and Brener, 2018; Zamariola et al., 2018; Desmedt et al., 2020). Although a strict instruction was applied (i.e., participants were explicitly encouraged not to count if they did not have any sensation to report), which presumably decreases the impact of top-down factors (Ehlers et al., 1995; Desmedt et al., 2018), the involvement of conscious processes in the tracking task is substantial. If one combines knowledge on the usual frequency of his or her heartbeats with the number and timing of actually sensed and counted heartbeats, performance in the task can be estimated (Desmedt et al., 2020). In the case of the proprioceptive modalities, however, no such information is available, thus actual and perceived accuracy show complete dissociation.

In line with our second hypothesis, interoceptive accuracy and the respective confidence ratings proved to be modality-specific. We replicated the findings of Ferentzi et al. (2018), namely that cardioceptive accuracy, as assessed with the mental heartbeat tracking task, does not correlate with measures of proprioceptive accuracy (joint position reproduction and weight discrimination tests in this study). Moreover, in accordance with the findings of other studies (Barrack et al., 1984; Grob et al., 2002; Jong et al., 2005; Elangovan et al., 2014; Li et al., 2016; Niespodziński et al., 2018; Yang et al., 2020), no association between accuracies with respect to two proprioceptive modalities was found. This lack of association might reflect the actual independence of the two abilities; however, conceptual differences (i.e., the weight discrimination test does not involve a reproduction element and it was measured with a forced choice paradigm) can also explain this finding.

The confidence-related findings were similar to those for accuracy: there were no associations between cardioceptive and proprioceptive tasks, and between the two proprioceptive tasks. Empirical results concerning interoceptive confidence across modalities are scarce. Garfinkel et al. (2015a) found a strong positive association between confidence ratings of two heartbeat perception tasks (i.e., mental heartbeat tracking task and the discrimination task). In our data, this indicates that the perception of performance is not only more or less independent of actual performance, but also differs between modalities; cardioception-related confidence rating show closer connection than those of proprioceptive confidence. This also suggests that top-down factors that usually impact perception, such as previous experiences and expectations, may show considerable modality-specific differences.

Interoception and Affect

Contrary to our expectation (H3), we did not find any association between state and trait positive and negative affect and cardioception-related accuracy and confidence In fact, Bayesian analysis supported the lack of association for the majority of the analyses. The same was true for the two proprioceptive modalities. There are several possible explanations for these null-findings. Cardioceptive accuracy showed associations with arousal but not with valence in studies where emotions were experimentally evoked and the two dimensions were assessed independently (Wiens et al., 2000; Barrett et al., 2004; Pollatos et al., 2005, 2007b; Herbert et al., 2007, 2010; Köteles et al., 2020b). The approach used in the present study, however, primarily measures affective states that are accompanied with high arousal (Lox et al., 2010) thus cannot separate these components. Further, the actual affective state of participants was measured, which is necessary less intense than experimentally evoked affective states. Under such conditions, the already weak association between cardioception and emotional experience may disappear. Concerning chronic (trait-like) emotional states, previous studies assessed anxiety, an affective state accompanied with marked vegetative changes (i.e., sympathetic activation), particularly for patients with related disorders (e.g., Domschke et al., 2010). For positive and negative affect in healthy participants, however, the intensity of the emotions, including both the experience and the vegetative changes, are much lower. Also, we did not asses other interoceptive channels that might be associated with the emotional experience. This holds particularly true for proprioceptive accuracy, where the investigation of a single joint and task represent only one aspect of the proprioceptive accuracy of the whole body (Han et al., 2013). Secondly, emotions assessed with self-report might not be at the same level of consciousness as accuracy and confidence related decisions (Smith and Lane, 2015).

Proprioception and Body-Related Questionnaires

Finally (H4), we replicated the findings on the independence of proprioceptive accuracy and interoceptive sensibility and body competence (Horváth et al., 2019) and extended them to another proprioceptive modality (weight discrimination) and confidence rating. The lack of association between interoceptive sensibility, a construct that integrates interoceptive experience across multiple channels, and interoceptive confidence ratings is particularly intriguing.

Also, our results indicate that the self-reported acute dimension of interoception is also modality-specific, i.e., cannot be generalized. As both constructs represent perceived abilities and the former is embedded in the latter (at least theoretically), their independence is clearly worthy of further investigation.

TABLE 5 | Associations between indicators of interoceptive accuracy and confidence ratings and questionnaire scores.

N = 105	State NA	Trait NA	State PA	Trait PA	BAQ	Body competence
Cardioceptive accuracy	0.128 (0.192)	0.065 (0.512)	−0.041 (0.674)	−0.007 (0.947)	0.020 (0.840)	−0.10 (0.331)
Cardioceptive confidence	−0.026 (0.797)	−0.065 (0.519)	0.024 (0.809)	0.132 (0.187)	0.112 (0.262)	0.0 (1)
Weight discrimination–accuracy	0.044 (0.658)	−0.099 (0.316)	−0.021 (0.834)	−0.114 (0.248)	0.043 (0.664)	−0.019 (0.850)
Weight discrimination–confidence	−0.163 (−0.163)	−0.131 (0.189)	0.131 (0.189)	0.041 (0.681)	0.171 (0.084)	0.012 (0.900)
Joint Position Sense–constant error	−0.064 (0.534)	−0.026 (0.802)	−0.152 (0.140)	−0.123 (0.231)	0.117 (0.255)	0.005 (0.963)
Joint Position Sense–variable error	−0.078 (0.448)	0.005 (0.640)	−0.103 (0.317)	−0.075 (0.465)	−0.161 (0.177)	−0.138 (0.179)
Joint Position Sense–confidence	0.048 (0.646)	0.019 (0.854)	0.085 (0.414)	0.027 (0.794)	0.185 (0.073)	0.070 (0.503)

Frequentist analysis, Spearman's rho coefficients (p values). None of the associations reached the $p < 0.05$ level of significance. NA, negative affect; PA, positive affect; BAQ, Body Awareness Questionnaire.

TABLE 6 | Associations between indicators of interoceptive accuracy and confidence ratings and questionnaire scores.

N = 105	State NA	Trait NA	State PA	Trait PA	BAQ	Body competence
Cardioceptive accuracy	0.102 (0.412)	0.044 (0.159)$^{+}$	−0.026 (0.318)$^{+}$	−0.006 (0.128)$^{+}$	0.011 (0.129)$^{+}$	−0.07 (0.223)$^{+}$
Cardioceptive confidence	−0.021 (0.136)$^{+}$	−0.045 (0.161)$^{+}$	0.020 (0.135)$^{+}$	0.095 (0.346)	0.079 (0.258)$^{+}$	0.001 (0.129)$^{+}$
Weight discrimination accuracy	0.030 (0.141)$^{+}$	−0.067 (0.211)$^{+}$	−0.014 (0.130)$^{+}$	−0.081 (0.269)$^{+}$	0.033 (0.144)$^{+}$	−0.019 (0.133)$^{+}$
Weight discrimination–confidence	−0.123 (0.680)	−0.088 (0.305)$^{+}$	0.093 (0.337)	0.024 (0.137)$^{+}$	0.107 (0.462)	0.012 (0.131)$^{+}$
Joint Position Sense–variable error	−0.06 (0.195)1^{+}	4.507e-4 (0.133)$^{+}$	−0.063 (0.201)$^{+}$	−0.052 (0.176)$^{+}$	−0.106 (0.422)	−0.095 (0.341)
Joint Position Sense–constant error	−0.051 (0.174)$^{+}$	−0.018 (0.137)$^{+}$	−0.107 (0.462)	−0.081 (0.264)$^{+}$	0.085 (0.278)$^{+}$	0.003 (0.133)$^{+}$
Joint Position Sense–confidence	0.034 (0.150)$^{+}$	0.014 (0.137)$^{+}$	0.060 (0.193)$^{+}$	0.014 (0.137)$^{+}$	0.126 (0.677)	0.048 (0.169)$^{+}$

Bayesian analysis, Kendall's Tau coefficients (BF^{10} values). +: $BF10 < 0.33$. NA, negative affect; PA, positive affect; BAQ, Body Awareness Questionnaire.

LIMITATIONS

We investigated a sample of young people without known pathology; in this population, strong emotions were rarely presented. This leads to the decrease of variance in affective ratings which in turn makes the detection of associations difficult. The Schandry task has received considerable criticism recently (Ring et al., 2015; Desmedt et al., 2018, 2020; Ring and Brener, 2018; Zamariola et al., 2018); thus, although we applied a strict instruction which decreases the role of top-down factors, cardioception-related findings of the study might be flawed. Also, the joint reproduction task involves memory processes. Thus, cognitive abilities unrelated to interoception might also influence participants' performance.

CONCLUSION

Our findings indicate that interoceptive accuracy and confidence ratings are independent from each other in two proprioceptive modalities (joint reproduction with respect to the elbow joint and weight discrimination using the arm flexor muscles) and they are only weakly associated in the cardioceptive modality. There are no associations between accuracy and confidence ratings within the three interoceptive modalities. Finally, proprioceptive and cardioceptive accuracy and confidence ratings are not related to the acute and chronic affective state, interoceptive sensibility/body awareness and perceived body competence.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Research Ethics Committee of the Faculty of Education and Psychology at ELTE Eötvös Loraìnd University. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

All authors contributed to the conception and design of the study, read and commented on the last version of the manuscript. ÁH and LV contributed to the assessment of data. FK processed the data and performed the statistical analyses. ÁH wrote the first draft of the manuscript. EF and FK wrote sections of the manuscript. All authors contributed to the article and approved the submitted version.

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Interoception and Empathy Impact Perspective Taking

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Adopting the perspective of another person is an important aspect of social cognition and has been shown to depend on multisensory signals from one's own body. Recent work suggests that interoceptive signals not only contribute to own-body perception and self-consciousness, but also to empathy. Here we investigated if social cognition – in particular adopting the perspective of another person – can be altered by a systematic manipulation of interoceptive cues and further, if this effect depends on empathic ability. The own-body transformation task (OBT) – wherein participants are instructed to imagine taking the perspective and position of a virtual body presented on a computer screen – offers an effective way to measure reaction time differences linked to the mental effort of taking an other's perspective. Here, we adapted the OBT with the flashing of a silhouette surrounding the virtual body, either synchronously or asynchronously with the timing of participants' heartbeats. We evaluated the impact of this cardio-visual synchrony on reaction times and accuracy rates in the OBT. Empathy was assessed with the empathy quotient (EQ) questionnaire. Based on previous work using the cardio-visual paradigm, we predicted that synchronous (vs. asynchronous) cardio-visual stimulation would increase self-identification with the virtual body and facilitate participants' ability to adopt the virtual body's perspective, thereby enhancing performance on the task, particularly in participants with higher empathy scores. We report that participants with high empathy showed significantly better performance during the OBT task during synchronous versus asynchronous cardio-visual stimulation. Moreover, we found a significant positive correlation between empathic ability and the synchrony effect (the difference in reaction times between the asynchronous and synchronous conditions). We conclude that synchronous cardio-visual stimulation between the participant's body and a virtual body during an OBT task makes it easier to adopt the virtual body's perspective, presumably based on multisensory integration processes. However, this effect depended on empathic ability, suggesting that empathy, interoception and social perspective taking are inherently linked.

Keywords: empathy, interoception, perspective taking, bodily self-consciousness, illusion

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INTRODUCTION

Empathy is characterized as the ability to be sensitive to, to understand, and to experience the emotions of others (Ochsner et al., 2008; Singer et al., 2009; Reniers et al., 2011), requiring both affective/emotional and cognitive processes. Given that some authors have argued that emotion is an inherently embodied experience (Damasio, 2000), it has been suggested that individual differences in empathy might be linked to differences in the sensitivity to internal bodily signals (interoception). In line with this argument, there is evidence that individuals who are more sensitive to internal bodily signals tend to experience emotions more intensely and have a better understanding of their emotions (Critchley et al., 2004; Herbert et al., 2011). Empathy for pain has been linked to interoceptive accuracy (Grynberg and Pollatos, 2015) and a cortical index of interoception – the heartbeat evoked potential – correlates with self-reported empathic concern (Fukushima et al., 2011). Interoceptive awareness – measured via a questionnaire – was shown to correlate with both cognitive and affective aspects of empathy in a mixed group of individuals with and without autism (Mul et al., 2018). Interestingly, neuroimaging studies show that the insula, a primary interoceptive brain region, is also activated during the subjective awareness of feelings, including empathy (Ochsner et al., 2008; Craig, 2009; Singer et al., 2009; Zaki et al., 2012; Ernst et al., 2013), suggesting that learned associations between interoceptive signals and emotions observed in others may contribute to empathy (Bird and Viding, 2014; Quattrocki and Friston, 2014).

On the other hand, some authors have argued that empathy is strongly related to perspective taking ability because the ability to adopt the perspective of another person is an important aspect of social cognition (Adolphs, 2001), and perspective taking ability correlates with trait empathy (Mohr et al., 2010; Gronholm et al., 2012). One way to assess perspective-taking is the so-called own-body transformation task (OBT). In this task participants are asked to imagine adopting the perspective and position of a front- or back-facing virtual body presented on a screen, and to decide whether its marked hand would correspond to their own left or right hand (Parsons, 1987; Blanke et al., 2005). Longer reaction times are observed for front- as compared to back-facing figures, arguably due to the process of mental own body transformation required to imagine having perspective and position of the front- vs. back facing virtual body (Parsons, 1987; Blanke et al., 2005). This is further supported by the fact that the reaction times of mental transformation tasks also depend on the angle of rotation between the participant's body and the imagined body or body part (Arzy et al., 2006a; Tadi et al., 2009; Heydrich et al., 2017).

There is evidence that spatial perspective taking involves a mental transformation of the observer's own body, relying on motor, proprioceptive, and vestibular information, and it has been linked to multisensory brain regions (Blanke et al., 2005). During the OBT task, the brain regions that are selectively activated overlap with multisensory brain regions implicated in out-of-body experiences, e.g., the temporo–parietal junction (Blanke et al., 2005; Arzy et al., 2006b). Moreover, a patient who had out-of-body experiences was shown to behave differently in an OBT task (Overney et al., 2009).

We have previously shown that it is possible to modulate self-related processing and self-consciousness using a virtual body and visuo-tactile (Lenggenhager et al., 2007; Ionta et al., 2011) or visuo-interoceptive cues [cardio-visual stimulation (Aspell et al., 2013; Heydrich et al., 2018)]. In the latter case, presenting an illuminated outline around a virtual body flashing in synchrony with the participant's heartbeat was found to increase illusory self-identification with the virtual body (the avatar's body feels like one's own body), shift self-location and alter somatosensory processing, as compared to an asynchronous control condition.

In the present study, we adapted the cardio-visual paradigm to an OBT task and aimed to investigate whether performance on a mental OBT task would be facilitated by online cardio-visual stimulation. To do this we visually projected heartbeat timing information onto the OBT virtual body (creating an illuminated outline around the virtual body), whose perspective participants were asked to take. We also tested whether this facilitatory effect would depend upon participants' empathic ability measured via a validated empathy questionnaire (Baron-Cohen and Wheelwright, 2004).

METHODS

Participants

A power calculation (*F* tests, ANOVA, repeated measures, within-between factors, assuming a power of 0.8; effect size of 0.3; significance level $\alpha = 0.05$, four repetitions, correlation among repeated measures 0.5) using the software G*Power (Faul et al., 2007) revealed that a sample size of at least 18 participants would be necessary. The estimation of a correlation of 0.5 was based on previous work using the OBT task where a correlation around 0.8 among repeated measures was found (Arzy et al., 2006b). A total of 20 healthy right-handed participants took part (nine females, mean age 26.7 ± 5.6 years). No participant had previous experience with the task or related experimental paradigms. All participants had normal or corrected to normal vision and had no history of neurological or psychiatric conditions. Participants gave written informed consent and were compensated for their participation. The study protocol was approved by the local Ethics Research Committee – La Commission d'éthique de la Recherche Clinique de la Faculté de Biologie et de Médecine – at the University of Lausanne, Switzerland and was performed in accordance with the ethical standards laid down in the Declaration of Helsinki.

Materials and Procedure

Setup, Electrocardiogram (ECG), Signal Analysis

The present protocol adapted an experimental setup that has been used previously to study bodily self-consciousness and cardio-visual stimulation (Aspell et al., 2013; Heydrich et al., 2018). Raw data (ECG) were acquired with the BioSemi Active II^{TM} system (Biosemi, Netherlands) at a sampling rate of 2048 Hz. A custom signal processing software computed, at 60 Hz, the instantaneous derivative of the ECG signal (buffered data) to detect the high-amplitude signal change between the Q and R peaks of the ECG. Continuous adjustment of the algorithm to cumulatively averaged extrema allowed for an automatic adaptation to inter-participant differences and signal amplitude variations. Triggers were sent when the instantaneous signal change in the ascending Q to R phase of the ECG approached the averaged minimum to maximum amplitude difference (i.e., threshold of 90%). To guarantee maximum detection accuracy, ECG signals, and triggers were monitored (for largest amplitude and lowest noise) during the placement of the electrodes in order to find their optimal position on the chest, and the threshold was adjusted by the experimenter. A custom-made display software, created using Open Graphics Library, was programmed to superimpose a flashing outline onto the virtual body, that was characterized by a mean intensity of opacity (alpha) over the 800 × 600 pixels of 6%. In the synchronous condition, the silhouette surrounding the virtual body flashed for a duration of 100 ms and with a sinusoidal opacity of 0% starting at 0 ms to 100% at 50 ms and vice versa, aiming at a synchrony with the theoretical blood flow at the aortic root, and thus with the systolic heart contraction of the participant. The imprecision of the R-peak detection in the software is maximally 1 frame before or after the peak (33 ms). As the flash animation has a fixed duration of 100 ms, the "peak" of the flash therefore occurs on average at 73 ± 16 ms after the R peak [for details see Aspell et al. (2013)]. In the asynchronous conditions everything remained the same except that the virtual body/object was illuminated with a fixed delay of 400 ms with respect to the participant's heartbeat (see Aspell et al., 2013; Heydrich et al., 2018).

OBT Task

Stimuli in the OBT task consisted of a schematic virtual body either facing toward (front facing condition) or away from the participant (back facing condition; **Figure 1**). Front and back figures had the same outline and were therefore scaled to the same proportions (dimensions: 2.8 × 6.1°). One of the virtual body's hands was marked as if it were wearing a dark glove around the wrist, either on the right or left hand. Thus, there were a total of four figures: 2 (Front or Back) × 2 (right or left hand marked).

In the OBT task, the participants were asked to imagine themselves in the position and orientation of the virtual body displayed on the screen and to indicate which hand was marked. Stimuli were presented for 200 ms in the center of a computer screen. Participants sat at a distance of approximately 50 cm from the screen. Successive stimuli were only displayed after a response was given. The participants had to respond with their right hand as quickly and as accurately as possible – by pressing one of two buttons arranged vertically – to indicate whether the marked hand was the left or the right one.

Procedure

There were two different conditions, presented in a counterbalanced fashion between: (1) virtual body with flashing outline synchronous with the heartbeat (Heart Sync) and (2) virtual body with flashing outline asynchronous with the heartbeat (Heart Async).

For each condition we presented two blocks of 100 randomized (front/back) OBT trials. Within each block, five repetitions of 20 OBT trials were interleaved with 35 s periods of viewing the virtual body with an outline flashing synchronously (Heart Sync) or asynchronously with respect to the heartbeat (Heart Async, see **Figure 1**). This resulted in a total of 400 OBT trials across all conditions (i.e., 200 trials for Heart Sync and 200 trials for Heart Async). The duration of the experimental procedure was approximately 18–20 min per subject (without filling out the questionnaire).

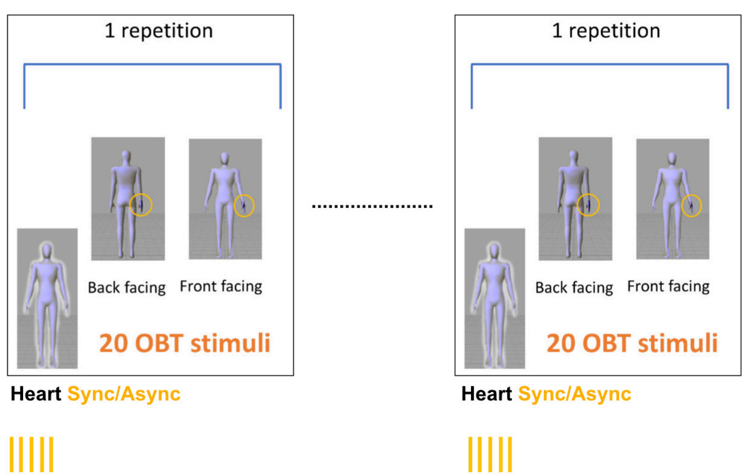

FIGURE 1 | Stimulus presentation. Stimuli in the OBT task consisted of a schematic virtual body either facing toward (front facing) or away from the participant (back facing). The participants were asked to imagine themselves in the position and orientation of the virtual body displayed on the screen and to indicate which hand (right/left) was marked. Each experimental block consisted of five consecutive repetitions 20 OBT trials that were interleaved with periods of 35 s of seeing the virtual body with a flashing outline either synchronous (Heart Sync condition) or asynchronous (Heart Async condition) with respect to the heartbeat. This resulted in 100 OBT trials per experimental block. Because each experimental block was repeated twice per condition, a total of 400 OBT trials across conditions was recorded.

Empathy

Empathy was assessed with the empathy quotient (EQ) questionnaire before the experimental procedure (Baron-Cohen and Wheelwright, 2004). The EQ comprises 60 questions: 40 items assessing empathy and 20 filler items. Each of the items were scored from 0 to 2 points (no, mild, strong empathic behavior), resulting in a maximum score of 80 and minimal score of 0 points.

Statistical Analysis

In order to assess the effect of synchronous cardio-visual stimulation and empathic ability on OBT performance, we conducted a two-tailed 3-way repeated-measures ANOVA with between-subject factor empathy (low/high) and within-factors orientation (front/back) and synchrony (synchronous/asynchronous). Participants were assigned to a low empathy group (median split, EQ Score < 42) or a high-empathy group. In order to follow up on the results of the ANOVA, a t-test (two-sided, paired) was used for *post hoc* testing and the significance (alpha) level used was $p = 0.05$ (corrected for multiple comparisons). The same statistic was applied to the accuracy data.

We also calculated a "synchrony effect size" by subtracting the reaction times for the synchronous condition from the asynchronous condition, e.g., yielding a positive value if the reaction time during the synchronous condition was shorter as compared to the asynchronous condition. We then used spearman's correlation in order to assess the link between EQ and the synchrony effect size during front and back facing conditions separately.

RESULTS

Own Body Transformation Task

We assessed the OBT effect and whether seeing a virtual body flashing synchronously or asynchronously with respect to the heartbeat as well as empathic ability had an influence on reaction times during the OBT task. Participants were split into low EQ (below median EQ score of 42, $n = 10$) and high EQ (above median EQ, $n = 10$) empathy scorers. The mean EQ Score was 41 points (SD $\pm$ 7.4). The median EQ Score was 42 points.

As predicted, statistical analysis revealed a significant effect of orientation [$N = 20$, $F(1,18) = 56.271$, $p = 0.000$, $\eta p2 = 0.758$]. Thus, reaction times were significantly shorter if the virtual body was presented back-facing (mean reaction time = 406.2 ms, SD $\pm$ 105.2) as compared to front-facing (mean reaction time = 500.2 ms, SD $\pm$ 124.6, $p < 0.001$, see **Figure 2**). No

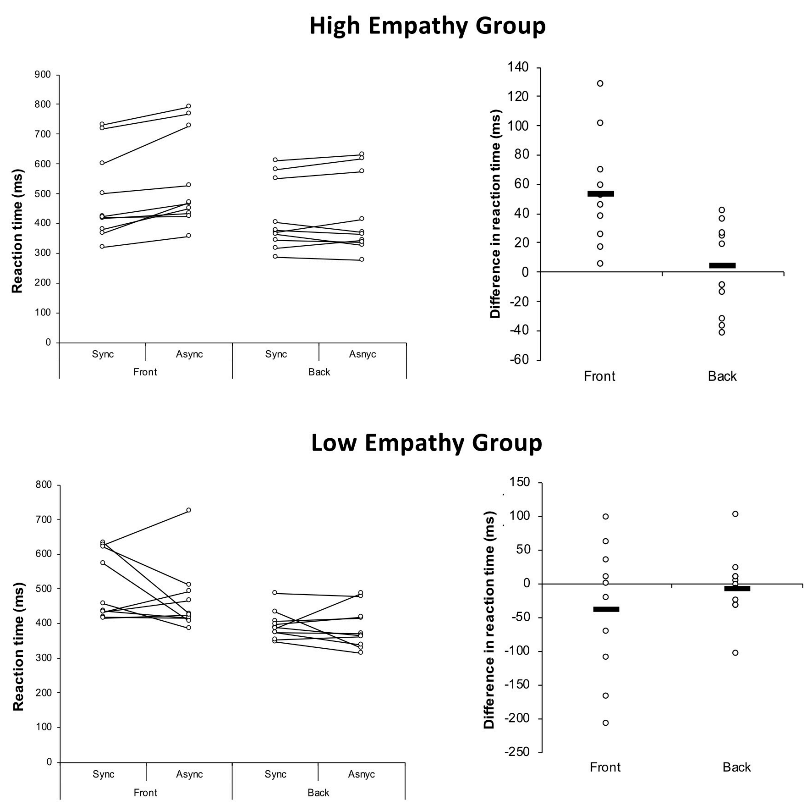

FIGURE 2 | Results. Participants were split into low and high empathy scorers. Reaction times were significantly shorter if the virtual body was presented back-facing as compared to front facing. A significant interaction of synchrony and empathy group and a significant three-way interaction of synchrony, orientation, and empathy group was due to shorter reaction times in the condition in which the virtual body was flashing synchronously as compared to when the virtual body was flashing asynchronously in the high EQ group only.

main effect of synchrony [$N = 20$, $F(1,18) = 0.084$, $p = 0.77$, $\eta p2 = 0.004$], empathy [$N = 20$, $F(1,18) = 1.318$, $p = 0.25$, $\eta p2 = 0.018$] and no significant interaction between orientation and synchrony was found [$N = 20$, $F(1,18) = 0.31$, $p = 0.58$, $\eta p2 = 0.016$].

However, we found a significant interaction of synchrony and empathy [$N = 20$, $F(1,18) = 4.735$, $p = 0.043$, $\eta p2 = 0.208$] and a significant three-way interaction of synchrony, orientation and empathy [$N = 20$, $F(1,18) = 9.308$, $p = 0.007$, $\eta p2 = 0.341$]. The latter was due to shorter reaction times in the condition in which a front facing virtual body was flashing synchronously (mean 487.78 ms, SD $\pm$ 146.41 ms) as compared to when the virtual body was flashing asynchronously (mean 541.83 ms, SD $\pm$ 159.04 ms, $t = 4.50$, df = 9, $p = 0.007$), in the high EQ group only. No significant difference was found for the back-facing condition in the high EQ group (synchronous condition: mean 420.20 ms, SD $\pm$ 100.18 ms; asynchronous condition: mean 424.66 ms, SD $\pm$ 103.64 ms, $t = 0.49$, df = 9, $p = 0.6$) nor for the low EQ group (front facing synchronous condition: mean 512.58 ms, SD $\pm$ 103.29 ms; asynchronous condition: mean 463.87 ms, SD $\pm$ 104.30 ms, $t = -1.2$, df = 9, $p = 0.26$; back facing synchronous condition: mean 395.17 ms, SD $\pm$ 43.98 ms; asynchronous condition: 376.54 ms, SD $\pm$ 52.00 ms, $t = -0.4$, df = 9, $p = 0.69$).

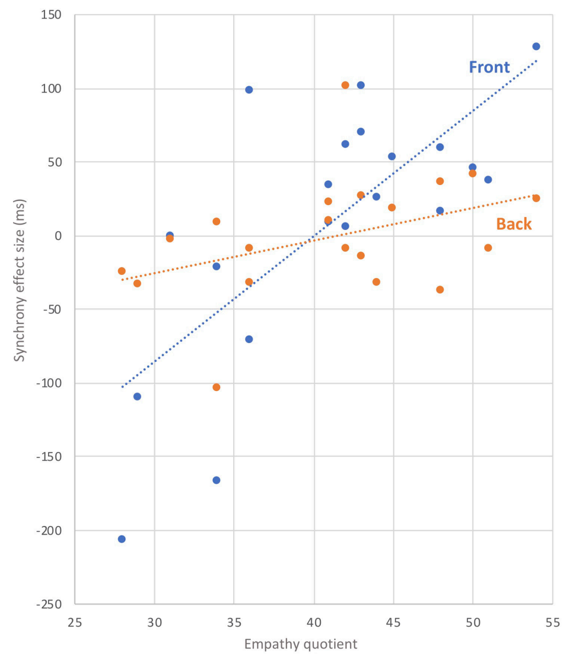

FIGURE 3 | Correlation.

Correlation

There was a significant correlation between EQ and "synchrony effect size" during the front-facing condition (rho = 0.69, dF = 18; $p = 0.001$, see **Figure 3**). No significant correlation was found between EQ and synchrony effect size during the back-facing condition (rho = 0.3, dF = 18, $p > 0.05$).

DISCUSSION

In the present study, we investigated whether performance on a mental OBT task would be modulated by online cardio-visual stimulation that has previously been shown to induce illusory changes in self-identification with a virtual body. We did this by visually projecting the participant's heartbeat onto the virtual body that indicated the cue for the mental transformation. We further tested whether this potential modulatory effect would depend upon participants' empathic ability. We found that for participants with high empathy ratings, reaction times during the OBT task were shorter for avatars in blocks where a flashing outline was synchronous with the participant's heartbeat, as compared to blocks where a flashing outline was asynchronous with the heartbeat. This effect was only observed for the front facing virtual body (e.g., with higher OBT requirements) and was absent for the back facing virtual body. This was further corroborated by a significant correlation between EQ scores and the synchrony effect size for the front facing virtual body. Finally, OBT performance in low EQ participants was not modulated by the cardio-visual synchrony of the flashing outline.

Our findings support previous suggestions of a link between interoceptive processing and empathy (Fukushima et al., 2011; Herbert et al., 2011; Mul et al., 2018). Importantly, we were able to demonstrate that in participants with high empathic ability a marker of empathic ability –visuo-spatial perspective taking during the OBT task – can be systematically modulated by an online visualization of interoceptive activity –synchronous cardio-visual stimulation.

Why does synchronous cardio-visual stimulation result in an improved performance during the OBT task in participants with high empathic ability? Böffel and Müsseler (2018) have reported that perspective taking depends on perceived ownership over an avatar, while Ferri et al. (2011) have demonstrated that seeing one's own hand as compared to someone's else's hand improves laterality judgments that involve a sensory-motor mental simulation.

We have previously shown that synchronous cardio-visual stimulation – i.e., presenting an illuminated outline flashing around a virtual body in synchrony with the participant's heartbeat – results in increased self-identification with a virtual body, and alters somatosensory processing [cardio-visual full body illusion (Aspell et al., 2013; Heydrich et al., 2018)]. Although changes in bodily self-consciousness were not measured directly in the present study, based on previous findings (Aspell et al., 2013; Heydrich et al., 2018) we speculate that synchronous cardio-visual stimulation likely also enhanced self-identification with the virtual body and may have induced a drift in self-location toward the body during the OBT task, thereby improving visuo-spatial perspective taking ability required to imagine oneself in the position and orientation of the front facing body. Because this effect was absent for the back facing virtual body, where no visuo-spatial perspective shift is required, and since it was also absent for participants with lower empathic ability, synchrony-driven shifts in attention could be ruled out as an explanation.

We also note there was no main effect of synchrony found by the analysis.

The effect of synchronous cardio-visual stimulation on visuo-spatial perspective taking was only present in participants with high empathic ability, while the correlation between EQ and the synchrony effect size for front facing avatars was observed across all participants. This suggests that the susceptibility to the effect of interoceptive cues on visuo-spatial perspective taking performance depends on empathic ability. This is in line with recent findings showing a link between empathy and the amplitude of the heartbeat-evoked potential (Fukushima et al., 2011) and the suggestion that intra-individual differences in empathy might be linked to differences in the sensitivity to internal bodily signals (Damasio, 2000). Our findings are also in keeping with evidence that people with higher empathic ability are more susceptible to a related multisensory (visuo-tactile) body illusion (Mul et al., 2019).

While visuo-spatial perspective taking and interoception have traditionally been considered to be based on distinct neural networks – i.e., perspective taking has been linked to the temporo–parietal junction (Blanke et al., 2005) and the representation of internal states to the insula (Craig, 2009) – here we show that the visual presentation of self-specific internal (cardiac) states alters performance of the OBT task in participants with high empathic ability. Based on this finding we speculate that in participants with high empathic ability the two systems are more tightly connected than in participants with low empathic ability. This would be in line with recent studies demonstrating that connectivity patterns depend on empathic ability (Esménio et al., 2019) and parieto-insular connectivity (Uddin et al., 2017). Stronger connectivity between parietal and insular regions would thus contribute to empathic ability by integrating both visuo-spatial perspective taking and processing of one's internal states, including online interoceptive signals.

There are several limitations to the current study. Although a sample size calculation was performed in order to provide enough power for a repeated measures ANOVA, an even bigger sample size would have allowed us to perform a linear regression analysis, using EQ as a continuous predictor. Thus, a future study with a bigger sample is needed in order to confirm the robustness of these results. Also, the link between self-identification with the virtual avatar, synchronous cardio-visual stimulation and performance during the OBT task would need to be assessed directly using a questionnaire.

CONCLUSION

Our finding that performance on a perspective taking task can be enhanced by synchronous cardio-visual stimulation and that this effect depends on empathic ability suggests that interoceptive processing, perspective taking and empathy are inherently inter-linked.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the La Commission d'éthique de la Recherche Clinique de la Faculté de Biologie et de Médecine – at the University of Lausanne, Switzerland. The participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

LH and JA were responsible for the study design, data analysis, and writing of the manuscript. FW was responsible for data collection. LB helped with data analysis. BH helped with the study design and technical aspects of the setup. OB helped with the writing of the manuscript and supervision of the study. All authors contributed to the article and approved the submitted version.

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On the Relationship of Interoceptive Accuracy and Attention: A Controlled Study With Depressed Inpatients and a Healthy Cohort

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Objective: Previous research has shown reduced interoceptive accuracy (IAcc) in depression. Attention deficit represents a key symptom of depression. Moreover, IAcc is positively correlated with attention. There is no study that investigates the effect of depression on IAcc and attention. The aim of this study is to examine the mediating effect of IAcc on depression and attention.

Methods: Thirty-six depressed patients from the Psychosomatic Clinic in Windach were matched with 36 healthy controls according to age and sex and were assessed at Ulm University. All participants completed the Beck Depression Inventory-II, the heartbeat perception task to examine IAcc, and the d2 test assessing selective attention.

Results: Depressed patients showed attention deficits—both for general visual attention and IAcc—compared to healthy controls. The mediation analyses revealed that the relationship between depression and attention is not mediated via IAcc. Furthermore, depression predicts IAcc and attention, but these effects are direct and largely unaffected by the respective other variable.

Discussion: The results of the present study highlight both interoceptive as well as attention deficits in depressed patients. No clear mediation between these variables could be shown in this study. More elaborative research is needed to clarify whether different approaches to improve IAcc are effective for these deficits in depressed patients and could therefore be of importance as an additional aspect of therapy in depression.

Keywords: depression, interoception, heartbeat perception, attention, psychosomatic

INTRODUCTION

Affecting over 300 million people (4.7%) worldwide, major depression is one of the most common mental diseases (World Health Organization [WHO], 2017). Moreover, due to the high number of affected people, it represents a severe public health burden (Greenberg and Birnbaum, 2005; Wittchen et al., 2011; Ferrari et al., 2013; World Health Organization [WHO], 2017). Depressed people experience impairments of different domains, including affective and cognitive symptoms (e.g., loss of interest, feelings of guilt, or concentration problems) as well as somatic distress. Moreover, depressive episodes are characterized by a loss of appetite, psychomotor retardation, or agitation (World Health Organization [WHO], 2009).

Typical problems in depressed patients such as decreased perception and regulations of emotion and stress as well as the perceptions of hunger and satiety are related to the concept of interoception, which is described as the ability to perceive and sense internal bodily signals (Vaitl, 1996; Cameron, 2001; Craig, 2002). Garfinkel et al. (2015) proposed a three-dimensional model of interoception, which includes interoceptive accuracy (IAcc), interoceptive sensibility (IS), and interoceptive awareness (IAw). IAcc is described as the perception of internal bodily signals and is objectively measured by the heartbeat perception task (Schandry, 1981). The second dimension, IS, denotes a subjective parameter and is thereby usually measured by self-rating questionnaires [e.g., Body Perception Questionnaire (BPQ); Porges, 1993, 2015, Multidimensional Assessment of Interoceptive Awareness (MAIA); Mehling et al., 2012), and confidence ratings directly after an IAcc task (Garfinkel et al., 2015). IAw as the third dimension represents the congruence of IAcc and IS, which is defined as the meta-cognitive level of interoceptive processes. In this article the focus is on IAcc, which represents the main dimension of interoception and is associated with IS as well as IAw.

One important association in the context of interoception is its relationship with emotion. This association is based on different emotion theories. James (1884) and Lange (1887) described in their James–Lange theory that emotions result from visceral and vascular changes; Schachter and Singer (1962) added that the interpretation of an arousal is important to form an emotion. In addition, Damasio's (1994) somatic marker hypothesis exemplified the body-relatedness of emotional signals. All theories emphasize the visceral and somatic feedback to the brain, which in turn influences emotional behavior and facilitates decision-making processes (Damasio, 2000). Overall, several studies support the idea of these theories, showing a close relationship of interoception and emotions (Dunn et al., 2007; Herbert et al., 2011; Füstös et al., 2013). Findings mostly indicate that decreased IAcc is associated with higher alexithymia scores (Herbert et al., 2011; Shah et al., 2016; Murphy et al., 2018; Pollatos and Herbert, 2018; Zamariola et al., 2018), reduced arousal ratings (Dunn et al., 2010), and downregulation of affect (Füstös et al., 2013). Besides emotion regulation, different studies found an impaired IAcc in several clinical and subclinical samples (e.g., anorexia nervosa, fibromyalgia, somatoform disorder; Pollatos et al., 2008; Weiss et al., 2014; Fischer et al., 2016; Duschek et al., 2017).

Depression symptoms are also associated with problems in IAcc in non-clinical and clinical samples (Dunn et al., 2007; Pollatos et al., 2007, 2009; Furman et al., 2013). For instance, Pollatos et al. (2007, 2009) showed that higher depression scores are linked with an impaired IAcc in a non-clinical sample. Similarly, these findings could also be demonstrated for clinical samples: Dunn et al. (2007) and Furman et al. (2013) found that depressed patients had a significantly lower IAcc in comparison to healthy controls. It should be mentioned that Furman et al. (2013) investigated only women and that the findings in the study of Dunn et al. (2007) could not be supported among patients with severe depression. Moreover, reduced positive affectivity, impaired emotion regulation strategies, and changes in visceral feedback from the body were also found in previous studies (Silk et al., 2003; Joormann and Gotlib, 2010; Wiebking et al., 2010; Furman et al., 2013), which could explain the decreased IAcc.

Cognitive processes are another influencing factor on IAcc. The assumption that heightened attention to interoceptive signals is required to perceive them, is shown in two studies (Gregory et al., 2003; Matthias et al., 2009). Exemplarily, Matthias et al. (2009) found that participants with higher IAcc performed better in the d2 Test of Attention, which represents a better (visually selective) attention. Nonetheless, these results are only revealed by a correlational design of a healthy cohort. Beyond that, different neuroimaging studies showed an overlap between attention and different neural networks (e.g., insular cortex, prefrontal cortex, anterior cingulate), which also underlines the relationship between attentional performance and interoceptive sensation (Corbetta et al., 1991; Phan et al., 2002; Nebel et al., 2005). Based on the defined symptoms of the International Classification of Disease, tenth revision (ICD-10), attention and concentration problems are common symptoms in depressed patients (Paelecke-Habermann et al., 2005; McDermott and Ebmeier, 2009; World Health Organization [WHO], 2009). Even though specific findings on the relationship between IAcc in depressed patients and attention remain scarce, cognitive processes seem to have an impact on both IAcc and depression and would be of interest for further research.

So far, research shows that a higher IAcc, so called attention for bodily signals, has a higher visually selective attention (Matthias et al., 2009). Until now, there is no study that investigates the influence of depression in this field. Therefore, interoception and attention were investigated in a sample with depressed patients in comparison to matched healthy controls. Based on this, we hypothesize reduced IAcc in depressed patients in comparison to healthy controls. Similarly, we assume that depressed patients exhibit decreased attention (d2 test) compared to healthy controls. Moreover, we assume a negative relationship between depression and IAcc as well as the attention level. To expand the research question, it is important to bring all these variables together and to investigate whether the negative association between attention and depression is mediated by a reduced IAcc. To examine the interrelations between the concepts of depression, interoception, and attention, it is hypothesized that a possible relationship of depression to decreased attention is mediated by reduced interoceptive abilities.

MATERIALS AND METHODS

Participants

All descriptive data are summarized in **Table 1**. The depressive sample comprised 36 patients (17 male) with a mean age of 41.19 years (*SD* = 11.13). All patients fulfilled the ICD-10 criteria for a major depression and were recruited from the Psychosomatic Clinic in Windach am Ammersee, Germany. Semi-structured diagnostic interviews according to ICD-10 criteria were used to determine the diagnosis of major depression. Testing procedures were conducted in the first or second week of inpatient therapy. Regarding former therapy experiences, 18 patients specified that they were in an ambulant setting, one took part in another inpatient setting, 15 had previously received therapy as inpatients and outpatients. Only two patients did not have any previous experience of a therapy setting. Furthermore, 22 patients were treated with antidepressants. Most of the patients (n = 23) had at least one comorbid psychiatric disorder, including personality disorder (n = 11), somatoform disorder (n = 6), and agoraphobia (n = 6).

Depressed patients were matched according to age and gender to 36 healthy controls with a mean age of 40.92 years (SD = 11.51). Healthy controls were excluded if they reported any medication intake (except of contraceptives) or a current psychiatric/somatic disorder.

Table 1 shows that depressed patients scored significantly higher on the Beck's Depression Inventory (BDI-II) than healthy controls. It should be noted that none of the healthy controls scored higher than 19 on the BDI-II, meaning no healthy control exhibited a critical score at the time of the study (Kendall et al., 1987). No significant differences were found regarding age, sex, and educational level (see **Table 1**).

At the end of the testing procedure, participants received 10 € for taking part in the study. The study was conducted in accordance with the Declaration of Helsinki. Ethical approval was obtained from the Institutional Review Board of Ulm University.

Instruments

Participants had to answer questions regarding demographic information such as age, sex, and education. Moreover, they received a test battery with standard psychology questionnaires. For the results presented in this study, the BDI-II (Beck et al., 1996) is relevant to quantify depressive symptoms over the previous two weeks. This well-validated self-reported questionnaire consists of 21 items, rated on a scale from 0 (=*not at all*) to 3 (=*always*), resulting in score ranges between 0 and 63. Higher scores represent more severe levels of depression (Beck et al., 1996; Steer and Clark, 1997; Arnau et al., 2001). Reliability scores for Cronbach's α differ between $0.84 \leq \alpha \leq 0.94$ for clinical and non-clinical samples (Steer and Clark, 1997; Steer et al., 1998; Arnau et al., 2001; Kühner et al., 2007).

Interoceptive accuracy was measured via the heartbeat perception task by Schandry (1981) to investigate the relationship between IAcc and depression. Consequently, we used this well-validated task characterized by a good test-retest reliability (Schandry, 1981; Knoll and Hodapp, 1992; Mussgay et al., 1999). For reliable measurements, it is important to provide standardized instructions for the heartbeat perception task, including the following different aspects: First, participants were instructed to count their heartbeat silently without taking their pulse or holding their breath. They were told to only focus on their heartbeat, and not on their breathing. If they wanted, participants could close their eyes. Second, they had to choose a relaxed sitting position. It was necessary for participants to stay calm and to not talk during the task. Third, the instructor provided information that the task would include four intervals (25, 35, 45, and 60 s, randomly presented) and that participants would have a break between the intervals to report their counted heartbeats verbally. A 10 s training interval was integrated to familiarize participants with the task. Importantly, participants were neither informed about the length of the different intervals, nor they did receive any feedback regarding their performance. The instructor gave a verbal start- and stop signal for each interval, demonstrating the beginning and the end of heartbeat counting.

For the heartbeat perception task, the IAcc score is of high importance. This score indicates the accordance between counted and recorded heartbeats. The BIOPAC MP35 heart rate monitor (sampling rate of 1,000 Hz) was used for recording the heartbeats. Analyses of cardiovascular signals were performed with the corresponding software AcqKnowledge (version 4.4). The final IAcc score was calculated using the following equation:

$$\text{IAcc score} = \frac{1}{4}\sum 1 - \frac{(|\text{recorded heartbeats} - \text{counted heartbeats}|)}{\text{recorded heartbeats}}$$

This score can vary between 0 and 1. Higher scores indicate better IAcc and consequently a small difference between recorded and counted heartbeats.

For the assessment of attention, the d2 Test of Attention (Brickenkamp, 1998) was used. This test is a standardized method to measure processing speed and performance quality to quantify visual attention and concentration. The test material consists of a sheet of paper with the letters d and p which are arranged in 14 rows, with 47 letters in each row. Above and/or below each letter,

TABLE 1 | Descriptive variables of depressive patients and healthy controls.

	Depressive patients	Healthy controls	Test statistics	*p*
	***n* = 36**	***n* = 36**		
Age in years *M* (SD)	41.19 (11.13)	40.92 (11.51)	$t(70) = 0.104$	0.92
Gender (% male)	47%		$\chi^2(1) = 0.000$	1.00
Education			$\chi^2(1) = 6.32$	0.18
(1)	7	3		
(2)	14	8		
(3)	3	5		
(4)	12	19		
(5)	0	1		
BDI-II mean (SD)	22.81 (9.08)	4.94 (5.02)	$t(70) = 10.32$	≤0.001

M, mean; SD, standard deviation; N, number; % m, percentage of males; BDI-II, Beck Depression Inventory-II; Education: (1) secondary general school certificate, (2) intermediate school certificate, (3) entrance qualification for technical college, (4) entrance qualification for university, (5) other qualification.

there are one to four dashes. To perform the test, participants were asked to cross out only *d*s with two dashes, regardless of whether the dashes were above and/or below the letter. Before the test, participants got the chance to practice the task in one line. The instructor gave verbal start and stop signals and instructed the participant to move on to the next line after 20 s on each line. To evaluate a participant's performance, the total number of processed items and incorrect letters were counted. Incorrect answers were subtracted from the total number of processed items to find the score of correct answers.

Procedure

All participants were informed about the study and provided written informed consent. The testing of the depressed patients took place in the Psychosomatic Clinic in Windach am Ammersee. Healthy participants performed the testing procedure in the laboratories of the Clinical and Health Psychology Department at Ulm University. Both settings were comparable (quiet room, testing situation). All participants first filled out the demographics and BDI-II questionnaires along with other questionnaires not reported here. Next, the heartbeat perception task took place. Afterward, participants had to perform the d2 Test of Attention. In total, each session lasted about 45 min.

Data Analysis

All statistical analyses were conducted using the program Statistical Packages for Social Science (SPSS, version 24). A *p*-value less than 0.05 was considered as significant. In cases where the Levene-test indicated differences in variances, corrected values were used. To analyze differences between depressed patients and healthy controls with regard to IAcc and attention (d2 test), *t*-tests for independent samples were calculated. One-sided correlation analyses were then utilized to investigate the possible influence of depression on attention mediated by IAcc. Mediation analyses were carried out using the SPSS macro-script (Process; Model 4) provided by Hayes (Preacher and Hayes, 2004, Preacher and Hayes, 2008), which uses a bootstrapping resampling strategy in order to examine the significance of the model and the effect of the mediator. As described by Hayes, for indirect effects, 95% bias-corrected bootstrapped confidence intervals were performed using 5,000 repetitions. The hypothesized mediation model tested depression as the independent variable, attention as the dependent variables, and IAcc as mediator. Additionally, a second mediation model with attention as the mediator and IAcc as the dependent variable was computed to test the reverse mediation path. The total effect (sum of the direct and of the indirect effect), the direct effect (effect of the independent variable without the effect of the mediator), the indirect effect (i.e., the mediation), standardized coefficients, and significance levels were reported.

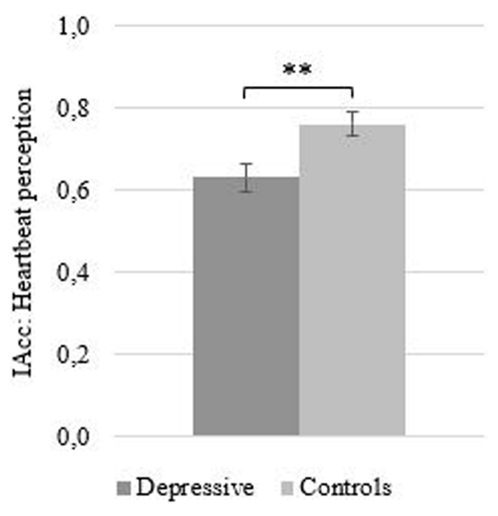

FIGURE 1 | Mean (SE) interceptive accuracy as measured by the heartbeat perception task as a function of group. $^{**}p \leq 0.01$.

RESULTS

Differences in Interoceptive Accuracy and Attention in Depressed Patients

Compared to healthy controls, IAcc scores were lower in depressed patients [$M_{Depr} = 0.62$ ($SD = 0.21$); $M_{Contr} = 0.77$ ($SD = 0.17$)]. Results of the *t*-test for independent samples showed that IAcc scores differed significantly between depressed patients and healthy controls [$t(70) = -3.23$, $p \leq 0.01$; see **Figure 1**]. Moreover, results showed that higher levels of depression are related with lower IAcc ($r = -0.40$, $p \leq 0.01$).

Regarding attention, depressed patients gave significantly fewer correct answers than healthy controls [$t(70) = -2.14$, $p \leq 0.05$; see **Figure 2A**] and also processed fewer items in total [$t(70) = -2.14$, $p \leq 0.05$; see **Figure 2B**] on the d2 test. Thus, they exhibited deficits in two common indicators of attention within the d2 test. Due to the fact that the number of incorrect answers in depressed patients ($M = 1.03$, $SD = 2.18$) and controls ($M = 0.72$, $SD = 1.56$) were close to zero, no significant differences for the incorrect answers in both groups could be found [$t(70) = 0.70$, $p = 0.49$], which likely indicates a floor effect in the data. Therefore, in the following we focus our analysis on the more diagnostic metric of correct and total items completed. As analyses in this study with these two variables were almost identical, calculations for the following analyses were only presented with the total number of processed items. Across the entire sample, depression was significantly negatively correlated to the total number of processed items in the d2 test ($r = -0.26$, $p \leq 0.05$) and correct answers ($r = -0.26$, $p \leq 0.05$), suggesting that higher levels of depression predict lower attention scores. Lastly, no significant relationship between IAcc and attention (total number of processed items, $r = 0.09$, $p = 0.22$) emerged.

Depression, Interoceptive Accuracy, and Attention

To investigate the assumption that impaired IAcc mediates the relationship between depression and attention, a mediation analysis was performed. A representation of the findings is depicted in **Figure 3**.

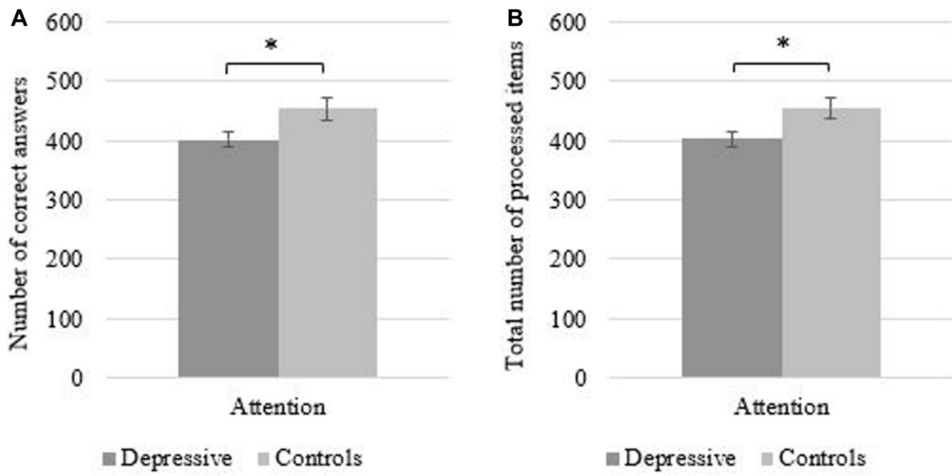

FIGURE 2 | Mean (SE) total number of processed items **(A)** and mean correct answers **(B)** in the d2 test of attention as a function of group. $^*p \leq 0.05$.

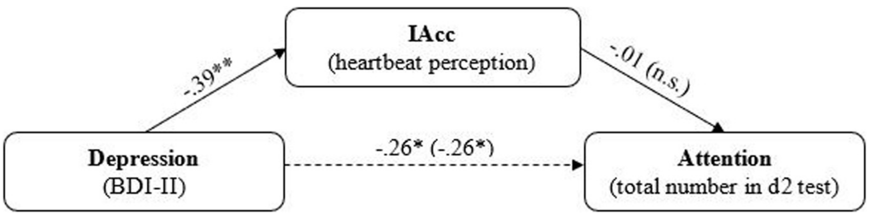

FIGURE 3 | Mediation model for the effect of depressive on attention mediated by IAcc. Standardized regression coefficients are reported arrows. Regression coefficient from the regression analysis without mediator are depicted in parentheses. n.s., not significant. $^*p \leq 0.05$; $^{**}p \leq 0.01$.

The analyses conducted on the first model showed that depression significantly predicted IAcc (β = −0.39, $p \leq 0.001$; see **Figure 3**). Similarly, depression also significantly predicted attention, both when controlling for the mediator (β = −0.26, $p \leq 0.05$) and when performing a linear regression analysis independent of IAcc (β = −0.26, $p \leq 0.05$). Thus, findings indicated a statistically significant total effect [β = −0.26, 95% CI (−0.486, −0.027)] and direct effect [β = −0.27, 95% *CI* (−0.513, −0.008)] of depression on attention, but no significant indirect effect of depression on attention, mediated via IAcc [β < 0.01, 95% CI (−0.111, 0.095)].

The reverse mediation test revealed that although depression significantly predicted attention (see above)—here in the role of the mediator—attention did not significantly predict IAcc [β = −0.01, 95% CI (−0.233, 0.214)], and therefore there was also no indirect effect of depression on IAcc, mediated via attention [β < 0.01, 95% CI (−0.058, −0.061)]. Thus, the results indicate that depression significantly and negatively predicts both IAcc and attention, but these effects are direct and largely unaffected by the respective other variable.

DISCUSSION

The purpose of the study was to investigate the relationship between depression, attention and IAcc. Therefore, depressed participants and healthy matched controls were examined through self-report questionnaires (BDI-II) and behavioral tasks (heartbeat perception task and d2 Test of Attention). Results indicated decreased IAcc and attention for depressed participants compared to healthy controls. Moreover, a negative relationship between depression and IAcc was found and could also be confirmed for depression and attention, but not for IAcc and attention. Mediation analyses revealed that IAcc did not mediate the negative relationship between depression on attention.

Interoceptive Abilities in a Sample With Depressed Patients

It was hypothesized that depressive patients show decreased IAcc. In line with this assumption, depressive patients scored significantly lower than healthy controls on IAcc. Previous data from Furman et al. (2013) support our findings by the fact that participants with higher depression scores exhibited a lower performance in the heartbeat perception task. Additionally, results in our study indicated that higher depression scores are related with lower IAcc. Our findings add to the results of current research investigating the, thus far, inconsistent picture of the relationship of depression and interoceptive abilities (Dunn et al., 2007; Pollatos et al., 2009).

Attention in a Sample With Depressed Patients

Our second main finding supports our hypothesis that depressed patients exhibit impaired attention capacity. Moreover, we found a negative correlation between depression and attention, which is reflected in the result that depression significantly predicted reduced attention. These findings are also supported by previous literature (Paelecke-Habermann et al., 2005; McDermott and Ebmeier, 2009) as well as in the ICD-10, where decreased concentration is listed as a key symptom (World Health Organization [WHO], 2009).

The Relationship of Depression, Interoceptive Abilities, and Attention

Focusing on the last hypothesis, we combined all variables in a meditation analysis, assuming that the negative relationship between depression and attention is mediated by IAcc. Mediation analyses confirmed a negative relationship of depression to IAcc and a direct, negative effect of depression to attention. However, the indirect effect demonstrating the overall mediation did not reach significance. It could therefore not be shown that interoceptive abilities mediate the effect of depression to attention. A more detailed analysis revealed that the correlation coefficient of IAcc and attention was close to zero. This indicates almost no association between IAcc and attention in this study. This missing association of IAcc and attention is somewhat surprising and not in accordance with the research of Matthias et al. (2009). In contrast to the former study our sample consisted of patients with a significant decrease in attention as compared to the healthy controls and therefore other relevant variables such as level of depression or mood could be qualitative discrete additional factors that come into play. Nevertheless, descriptive data showed lower scores in IAcc and reduced attention scores in depressive patients as compared to healthy controls. Due to the novelty of our study approach, further research is needed to shed more light on the interrelations of depression, interoception, and attention.

Strengths, Limitations, and Future Research

In summary, our study highlights the impact of bodily signal processing for basic aspects of depression, focusing on the intensity of depressive symptoms as well as basic aspects of attention. Until now, studies have exclusively investigated attention, and the relationship between IAcc and depression, separately. We have examined these variables and how they interact with each other, therefore showing a more concise picture as compared to former studies.

There are several limitations of the current study relating to sample characteristics and measurements, which should be considered in future research. For example, with a larger sample size, it could be useful to differentiate between the severity of depression, comparable to the study of Dunn et al. (2007). An important avenue for future research could also be investigating the influence antidepressant and comorbidities have on interoceptive abilities. Moreover, additional examinations of the heartbeat evoked potential (HEP) could be of interest. Montoya et al. (1993) examined HEP's in two different conditions of attention (directed attention versus distraction) and found significant differences in central HEP amplitudes. Finally, it could be interesting for future research to measure depressive symptoms and interoception across time to find out more about the evolution of depressive symptoms and its association with IAcc. Following the model of Murphy et al. (2019), a daily assessment of interoceptive abilities in a depressed sample could be also interesting.

CONCLUSION

In summary, results showed that depressed participants have deficits in both interoceptive abilities as well as in basic attention processes. It is an interesting aspect that this stands in contrast to our hypotheses that these deficits seem to be barely connected. This leads to the open question on whether there is a favorable order in therapeutic programs aiming at an improvement of interoceptive abilities or at the improvement of attention deficits. This is a relevant aspect for clinical practice as research so far has shown that through different methods, interoceptive abilities can be increased, including mindfulness meditation (Farb et al., 2013), body scans (Fischer et al., 2017), contemplative mental training (Bornemann et al., 2014; Bornemann and Singer, 2017), and self-focused training (Ainley et al., 2012). Whether this is also true for depressed patients or whether this effect might be more pronounced when attention processes are targeted first, has thus far not been investigated and requires more future research for clarification. Future research should re-examine this model and a possible mediation effect with a larger sample size, including possible influencing factors such as severity of depression, medication, and comorbidities.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The study was conducted in accordance with the Declaration of Helsinki. Ethical approval was obtained from the Institutional Review Board of Ulm University. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

DS, GB, MZ, and OP designed and conceived the study. DS and CS collected the data and wrote the first draft of the manuscript. DS, CS, TE, and OP conducted the statistical analyses. All authors reviewed, edited, and approved the final manuscript.

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The Body Across Adulthood: On the Relation Between Interoception and Body Representations

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Interoceptive information plays a pivotal role in building body representations (BR), but the association between interoception and the different types of BR in healthy individuals has never been systematically investigated. Thus, this study aimed to explore the association between BR and interoceptive sensibility (IS) throughout adulthood. One hundred thirty-seven healthy participants (50 aged from 18 to 40 years old; 50 aged from 41 to 60 years old; and 37 over 60 years old) were given a self-report tool for assessing IS (the Self-Awareness Questionnaire; SAQ), and a specific battery including tasks evaluating three different BR (i.e., the body schema, using the Hand Laterality Task; the body structural representation, using the Frontal Body Evocation task, FBE; and body semantics, using the Object-Body Part Association Task) as well as control tasks (i.e., tasks with non-body stimuli). The older age group (aged over 60 years old) showed lower performances on the tasks probing the body schema and body structural representation than younger groups (aged 18 to 40 and 41 to 60 years old). More interestingly, worse performances on a task assessing the body schema were significantly associated with higher IS with older age, suggesting that higher awareness of one's inner body sensations would decrease the plasticity of this BR. These findings are interpreted according to the neuropsychological model of BR development and the effects of aging on the brain.

Keywords: adulthood, body schema, body structural representation, body semantics, interoception

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INTRODUCTION

Interoception refers to the ability to perceive one's own physical sensations related to internal organ functioning, such as heartbeat, itch, respiration, and satiety (Vaitl, 1996; Cameron, 2001; Craig, 2002; Barrett et al., 2004). It is a multidimensional process that usually occurs outside of conscious awareness, but that may be consciously experienced during instances of homeostatic perturbation (i.e., interoceptive processes, Garfinkel et al., 2015; or interoceptive awareness, Khalsa et al., 2018). Studies that have sought to identify the neural substrates of interoceptive processing point to the pivotal role of the insula, particularly of the anterior insular cortex (Craig, 2002).

A more coherent nomenclature of different components of interoceptive processing (see Khalsa et al., 2018) has been developed, reflecting the need for operationalization in neuroscience and clinical practice. It mainly distinguishes between the *interoceptive attention* (i.e., the process of observing internal bodily sensation), the *interoceptive accuracy* or *interoceptive sensitivity* (i.e., the process of correctly and precisely monitoring the sensation as assessed by comparisons between subjective and objective indices), and the *interoceptive sensibility* (IS; i.e., the self-perceived tendency to focus on interoceptive signals, representing a trait-like feature).

Many studies have shown the role of interoception in cognitive functioning (e.g., in decision-making, memory, and emotion processing) and that its dysfunction is an essential component of different mental health conditions (Khalsa et al., 2009, 2018).

Body Representations and Interoception

The processing of interoceptive information contributes to our sense of body ownership (Berlucchi and Aglioti, 2010) that refers to the feeling that my body belongs to me and "presumably depends on afferent sensations arising within the body itself, but also on the coherence of current sensory input with pre-existing cognitive representations of the body" (Costantini and Haggard, 2007, p. 230). Body ownership is relevant for body representations (BR), since it would act as an essential source of information for the internal BR state that provides forward models generating sensory predictions during voluntary action (Kilteni and Ehrsson, 2017; Grechuta et al., 2019); likewise, BR are relevant for body ownership, since the self-identification of body parts would be achieved through a dynamic multisensory integration process of peripheral inputs interpreted in the context of high-order BR (Makin et al., 2008).

A seminal study by Tsakiris et al. (2011) has nicely shown how interoceptive processing specifically modulates body ownership. They observed a negative correlation between the ability to detect one's own heartbeat (i.e., interoceptive accuracy) and the Rubber Hand Illusion (RHI), such that participants with lower interoceptive accuracy showed a stronger RHI measured both behaviourally and physiologically (i.e., drop in skin temperature). On the other hand, a study by Filippetti and Tsakiris (2017) investigated how changes in body ownership specifically modulates interoceptive processing. They demonstrated that after being exposed to RHI, individuals with initially lower levels of interoceptive accuracy improved the performance at a standard heartbeat-counting task, suggesting that the process of a bodily illusion, biasing the experience of ownership toward an artificial and external limb such as the rubber hand, would improve the ability to accurately detect internal bodily signals in individuals with low interoceptive accuracy. Following this finding, Suzuki et al. (2013) found that participants exposed to a virtual RHI experienced an increased illusion during synchronous cardio-visual feedback with one's own heartbeat compared to asynchronous feedback, confirming the role of interoceptive processing in body ownership. On a similar fashion, several studies focused on the effect of pleasant affective touch, known to engage interoceptive processing (Crucianelli et al., 2013; Lloyd et al., 2013; van Stralen et al., 2014), showing that the pleasant touch (i.e., slow velocity on hairy skin) enhanced the RHI.

At odds with studies on interoception and body ownership mentioned above, less attention has been paid to the role of interoception in building different high order cognitive BR.

According to the dyadic taxonomy, high order cognitive BR can be broadly classified in *body schema,* consisting of a sensorimotor representation of the body that guides actions and enables the body to unconsciously adjust the posture and movement (i.e., an action-oriented BR); and *body image*, grouping all the other perceptual, conceptual or emotional representations about the body that are not used for action (i.e., a non-action oriented BR) (Paillard, 1999; Di Vita et al., 2016).

Subsequently, Schwoebel and Coslett (2005) proposed a triadic taxonomy, further subdividing the concept of body image into *body structural representation*, a visuo-spatial body map of the body that includes information about boundaries of the body parts and their spatial relations; and *body semantics*, a representation that includes names and functions of the body parts and their associations with objects.

While the dyadic and triadic taxonomies do not explicitly refer to the role of interoception in building BR, a study by Longo et al. (2010) is particularly relevant in this context.

Following Longo et al. (2010), Longo (2016), BR can also be distinguished into those mediating somatoperception, which refers to the higher-level percepts about the body, and those mediating somatorepresentation, which refers to the abstract knowledge and beliefs about one's own body and bodies generally. While the body schema is somatoperceptual, the body structural representation and the body semantics are somatorepresentational. According to Longo et al. (2010), critical elements of somatoperception are also the "interoceptive percepts about the nature and state of the body itself" (p. 655). Thus, the processing of interoceptive information can be particularly relevant for building up the body schema. In any case, a recent review of behavioral and neuroimaging studies on non-clinical and clinical populations has also underlined that interoceptive processing might contribute to building up the body image (Badoud and Tsakiris, 2017).

Data from lesion studies on brain-damaged patients with BR and bodily self-consciousness disorders also support the pivotal role of the interoceptive processing in BR. For example, Heydrich and Blanke (2013) found the involvement of the insula, that is a crucial area for processing the body's physiological condition (Craig, 2002), in patients with heautoscopy (i.e., an autoscopic phenomenon in which the person experiences seeing a second own body in the extrapersonal space), suggesting that this bodily self-consciousness disorder arises from the disintegration of the visuo-somatosensory signals with the interoceptive ones. Similarly, damage to the insula has been found in patients with BR disorders defined *disturbed sensation of limb ownership* (e.g., asomatognosia, somatoparaphrenia) (Baier and Karnath, 2008).

Thus, current evidence points toward a key role of interoceptive processing in the complex formation of all BR.

The Effect of Age on Interoception and Body Processing

As underlined by Murphy et al. (2018), the relevance of interoception for cognitive functioning and health has stimulated the study of how it can vary across the lifespan. For example, Khalsa et al. (2009), using a heartbeat detection paradigm with participants ranging in age from 22 to 63 years, found that older adults had poorer detection of their heartbeats than younger and middle-aged adults (i.e., poorer interoceptive accuracy). More recently, Murphy et al. (2018), examining IS from young to very late adulthood (until 90 years of age) by means of a self-report measure (i.e., the short version of the Body Perception Questionnaire; Porges, 1993), found that IS declines with age and suggested that the interoceptive decline due to aging could account for some age-related cognitive impairments (Murphy et al., 2018).

Aging also seems to have an impact on BR. Indeed, the subjective component of body-ownership, investigated experimentally in the lifespan using the RHI, would seem to follow a U-shape curve since young and older adults showed a stronger subjective experience of illusion than the middle-aged (Marotta et al., 2018). This finding suggests that the flexibility of BR would change across the human lifespan.

Cholewiak and Collins (2003) found that the ability to localize touch on body parts decreased with advancing age, which is consistent with an effect of aging on the body structural representation. Similarly, studies investigating the ability to mentally rotate a specific body part (Personnier et al., 2008; Skoura et al., 2008; Saimpont et al., 2009), that is a task probing the body schema (Parsons, 1994), found lower accuracy and slower reaction times in older adults.

Plan of the Study

So far, little attention has been paid to the association between BR and interoceptive processing across the adult lifespan.

Here, to provide a better understanding of the relation between the interoceptive processing, in terms of IS, and BR during adulthood, a sample of healthy adults in different age groups was given (i) a self-report questionnaire to evaluate IS; (ii) specific tasks tapping three different BR (i.e., body schema, body structural representation, and body semantics), and (iii) control tasks (i.e., tasks withouth bodily stimuli but superimposable to the BR tasks in terms of stimuli presentation and response modality) to disentangle the contribution of other cognitive processes (i.e., visual processing, mental imagery, visuo-spatial attention or decision making) necessary to perform the BR tasks.

Based on the previous studies reviewed above, we hypothesized that the relation between age and all BR (i.e., body schema, body structural representation, and body semantics) was affected by IS, as a moderating variable between age and BR (see **Figure 1A**). Indeed, interoceptive information processing declines with age, and can be relevant in building different BR.

MATERIALS AND METHODS

Participants

One hundred thirty-seven healthy individuals participated in this study. They were grouped according to adulthood stages (Collins English and dictionary, 1994; Besedeš et al., 2012; Noh et al., 2015) in three age bands: young adulthood, aged from 18 to 40 years old (including 25 females and 25 males); middle adulthood, aged from 41 to 60 years old (including 30 females and 20 males); and older adulthood, aged over 60 years old (including 26 females and 11 males). Since the sample size was predetermined by study constraints, we performed a sensitivity power analysis that showed that a small effect size of at least Cohen's $d = 0.27$ was required to observe a significant difference between the three age groups at an alpha level of $p < 0.05$ with 0.80 power. Thus, the study would not be able to reliably detect effects smaller than Cohen's $d = 0.27$. Participants were recruited through personal contacts and by word of mouth from "Magna Graecia" University, Catanzaro (Italy), and from the Psychology Department of University of Campania "Vanvitelli," Caserta (Italy). All participants were native Italians, had no current mental health disorder, such as depression and anxiety, according to the Diagnostic and Statistical Manual of Mental Health Disorders, 5th Edition (DSM-5; American Psychiatric Association, 2013), and obtained normal age- and education-adjusted scores on the Mini Mental State Examination (MMSE; Folstein et al., 1975) according to the Italian normative data (Magni et al., 1996) and on the Raven's Colored Progressive Matrices (Raven, 1938) according to the Italian normative data (Spinnler and Tognoni, 1987), that excluded the presence of general cognitive impairment and deficit in abstract reasoning. All participants signed informed consent to participate in the study and did not receive any payments for their participation. The study was designed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and was approved by the local ethics committees (Calabria Region Ethical Committee, Catanzaro, Italy, and Ethical Committee of the University of Campania "Vanvitelli," Caserta, Italy). Descriptive statistics of the three age groups are reported in **Table 1**.

Behavioural Testing

Assessment of IS

To evaluate IS (how frequently individuals feel signals arising from their own body), participants completed a pen-and-paper version of the Self-Awareness Questionnaire (SAQ; Longarzo et al., 2015). The questionnaire included 35 items to be rated on a five-point Likert scale (from 0 = never to 4 = always). The total score was the sum of the responses of all 35 items providing a score range of 0 to 140, with higher scores indicating higher levels of IS. The SAQ shows good internal consistency (Cronbach's alpha ranged between 0.83 and 0.90), as found in wide samples (aged from 18 to 72 years) of Italian and English healthy adults

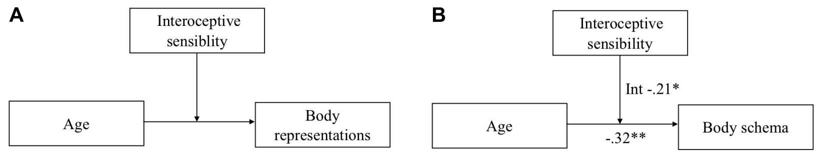

FIGURE 1 | The moderation effect of the interoceptive sensibility on age's direct effect on body representations. Hypothesized **(A)** and significant outcome **(B)** model.

TABLE 1 | Descriptive statistics by age groups.

	Participants aged 18 to 40 years		Participants aged 41 to 60 years		Participants aged over 60 years	
	Mean ± SD	**Range**	**Mean ± SD**	**Range**	**Mean ± SD**	**Range**
Age	33.98 ± 4.26	18–40	48.14 ± 4.16	41–60	69.27 ± 8.53	61–84
Sex (F/M)*	24/25		30/20		25/12	
MMSE	NA	NA	NA	NA	25.66 ± 4.60	13–30
Raven's Coloured Progressive Matrices (age- and education-adjusted scores)*	26.24 ± 4.29	19.2–32.4	26.44 ± 4.10	19.3–31.3	26.92 ± 5.05	19.5–36.3

SD, standard deviation; NA, not assessed; MMSE, mini mental state examination.
**Sex and age- and education- adjusted scores of Raven's Colored progressive Matrices are not statistically different among groups (sex: χ^2 = 2.78, p = 0.248; Raven's Coloured progressive Matrices: H = 0.41 p = 0.812).*

(Longarzo et al., 2015; Hughes et al., 2019) and has been used with non-clinical as well as with clinical populations (e.g., Raimo et al., 2019a; Teghil et al., 2020).

Assessment of BR

According to the triadic taxonomy of Schwoebel and Coslett (2005) the assessment of BR was performed using a specific battery that included the evaluation of three distinct types of BR: the body schema, the body structural representation, and the body semantics. This battery also includes control tasks and was used in a previous study on the development of BR in healthy children and young adults (see Raimo et al., 2019b) and in a previous study on adults with brain damage (Boccia et al., 2020). Here we used for the first time the same apparatus and procedures in a sample of older adults.

Assessment of the body schema

The body schema was assessed using a hand mental rotation task (the Hand Laterality Task, adapted and simplified from Parsons, 1987; see Raimo et al., 2019b). In this task, participants were asked to make, as rapidly and accurately as possible, laterality judgment ("a left or a right hand?") of a single hand (20 stimuli, 10 left, and 10 right stimuli) that could be presented in five different angles of rotation (0, 45, 90, 270, and 315 degrees). In the correspondent control task (the Object Laterality Task, see Raimo et al., 2019b), participants were asked to make, as rapidly and accurately as possible, laterality judgment ("a left or a right hand?") of a flower with a leaf positioned at the right or at the left base of the stem (20 stimuli, 10 left, and 10 right stimuli) that could be presented in five different angles of rotation (0, 45, 90, 270, and 315 degrees). In both tasks, the stimuli presentation order was the same for all participants and the accuracy corresponded to the sum of correct responses digitally recorded; thus, individual scores ranged from 0 to 20, with higher scores indicating better performance.

Assessment of the body structural representation

The body structural representation was assessed using a computerized version of the "Frontal Body Evocation task" (FBE) (Daurat-Hmeljiak et al., 1978; see Raimo et al., 2019b). Although this test has been developed for use with children, it has been extensively used in literature to assess BR in samples of adults (e.g., adults with brain damage: Guariglia et al., 2002; Di Vita et al., 2017, 2019; amputee patients: Palermo et al., 2014, 2018). After watching the picture of a child for 10 s, participants had to re-locate one at time nine specific body parts (left or right leg, left or right hand, left or right arm, left or right part of the chest, and the neck), dragging it with a finger on a touchscreen where only the head of a child was depicted as a reference. Body parts were displayed one at a time on the screen. The computer recorded the position of the body part located by the participant, and then a new body part was shown (number of trials = 9). The control task involved the visuo-spatial processing of non-body related stimuli (the Christmas Tree Task, see Raimo et al., 2019b). After watching the picture of a Christmas tree for 10 s, participants had to re-locate one at time nine specific parts of the tree (left or right lower branches, left or right middle branches, left or right lower branches with trunks, left or right parts of the jar, and the top), dragging it with a finger on a touchscreen where only the star tree topper was shown as a reference. Participants were presented with one specific Christmas tree part at a time. The computer recorded the position of the Christmas tree part located by the participant, and then a new part was shown (number of trials = 9). In both tasks, accuracy was computed in terms of millimeters of deviation from the exact location of the body/tree parts from the correct locations. Thus, a smaller deviation in mm indicated better performance, whereas a higher deviation in mm indicated worse performance.

Assessment of body semantics

Body semantics was assessed using an Object-Body Part Association Task (adapted from Fontes et al., 2014; see Raimo et al., 2019b). In this task, participants were asked to correctly associate an object (e.g., hat) with the related part of the body, choosing between two options (e.g., head and foot). The task included 20 stimuli. The control task, that is the Object-Room Association Task, involved the semantic processing of non-body related stimuli. Participants were asked to correctly associate an object (e.g., armchair) with a room, choosing between two options (e.g., living room and bathroom). The control task included 20 stimuli. In both tasks, the accuracy that corresponded to the sum of correct responses was digitally recorded; thus, individual scores ranged from 0 to 20, with higher scores indicating better performance.

Procedure

All participants completed the cognitive assessment and the entire battery of body and control tasks in a quiet experimental room at the Laboratory of Neuropsychology of University of Campania "Luigi Vanvitelli" and at the Laboratory of Cognitive Processes of 'Magna Graecia' University. First, participants were given, in this order, the MMSE (Folstein et al., 1975), the Raven's Colored Progressive Matrices (Raven, 1938) and the SAQ (Longarzo et al., 2015). Subsequently participants performed the computerized battery of body and control tasks on a laptop (13.3" display) equipped with a touch screen monitor. For these tasks, participants were invited to sit on the chair in front of a desk with the laptop placed upon it. During testing, the participants were instructed to maintain the same position. No time limit was imposed, but they were solicited to respond immediately after the presentation of the stimulus. The order of tasks was counter-balanced across participants, but the presentation order of stimuli was consistent within all tasks.

STATISTICAL ANALYSIS

The normality of data distribution was tested using the Kolmogorov-Smirnov test. Due to non-normal distribution of continuous variables (BR and control tasks and SAQ total scores), non-parametric analyses were performed.

The presence of differences on BR and IS due to the age group was evaluated using Kruskal-Wallis tests. When appropriate, pairwise comparisons were then performed by means of Mann–Whitney *U*-tests.

The next step in our data analyses involved correlation analyses to explore the association between IS and BR across the adult lifespan. First, correlations between age and SAQ total scores, and between age and the BR and control tasks were performed on the whole sample using Spearman's rank correlations. Secondly, correlations between the SAQ total scores and the BR tasks were performed separately for the three age groups and partial correlations between the SAQ total scores and the scores on the three BR tasks controlling for age (i.e., as covariate) on the whole sample were performed. Moreover, to evaluate a possible association between IS and the BR, taking into account other cognitive functions required to perform the body tasks, partial correlations were performed between SAQ scores and the unstandardized residuals of the ranks of the body tasks on the ranks of the control tasks (i.e., the unstandardized residuals of the Hand Laterality Task scores on the Object Laterality Task scores, the unstandardized residuals of the FBE scores on the Christmas Tree Task scores; the unstandardized residuals of the Object-Body Part Association Task scores on the Object-Room Association Task scores), controlling for age (i.e., as covariate).

Finally, moderation analyses were conducted using the bootstrapping technique to assess the moderating role of IS in the relation between aging and BR. The bootstrapping moderation analysis was performed using the PROCESS macro for SPSS (Hayes, 2013), a software used for moderation, mediation, and conditional process analyses that utilizes a regression-based path analytic framework or ordinary least squares to estimate moderation models (Hayes, 2013). Thus, to examine the strength of the relation between age and BR under different values of IS, the age was inputted as the independent variable, BR task scores (Hand Laterality Task, FBE, and Object-Body Part Association Task scores) were inputted as the outcome variables, and SAQ scores were inputted as the moderator variable. Significant moderation effects were followed by models controlling for cognitive abilities (Raven's Colored Progressive Matrix) to assess the extent to which IS's influence was independent of this covariate.

The significance level was set at alpha level <0.05, and Bonferroni correction for multiple comparisons was applied ($p \leq 0.006$). All analyses were performed using SPSS v. 23.0 (SPSS, Inc. Chicago, IL, United States).

RESULTS

Comparison of Behavioural Measures Among Age Groups

The Kruskal–Wallis *H*-test show: (i) a significant main effect of the age group on the task assessing the body schema (the Hand Laterality Task; H = 6.79, $p = 0.033$) and on the respective control task (the Object Laterality Task; $H = 6.47$, $p = 0.039$), this effect was not significant after applying the Bonferroni correction ($p \leq 0.006$); (ii) a significant main effect of the age group on the task assessing the body structural representation (FBE; $H = 59.92$, $p < 0.0001$), but not on the respective control task (the Christmas Tree Task; $H = 1.07$, $p = 0.586$); this effect was significant also after applying the Bonferroni correction ($p \leq 0.006$); (iii) a non-significant main effect of the age group on the task assessing body semantics (Object-Body Part Association Task; $H = 1.30$, $p = 0.520$), and on the respective control task (Object-Room Association Task; $H = 2.03$, $p = 0.362$).

The pairwise comparisons performed by means of the Mann–Whitney *U*-tests showed that scores obtained on the body schema and its control task, and on the body structural representation were significantly lower in the group of participants aged over

60 years than in the two groups of younger participants aged 18–40 years (Hand Laterality Task: $U = 679$, $p = 0.022$; Object Laterality Task: $U = 702$, $p = 0.034$; FBE: $U = 64$, $p < 0.0001$) and 41–60 years (Hand Laterality Task: $U = 679$, $p = 0.023$; Object Laterality Task: $U = 692$, $p = 0.026$; FBE: $U = 119$, $p < 0.0001$).

The pairwise comparisons for the FBE were significant also after applying the Bonferroni correction ($p \leq 0.006$).

The accuracy on the BR and control tasks for each age group are shown in **Figure 2**.

Given these results, to better investigate if aging had only an overall effect on the ability to mentally rotate stimuli (Object Laterality Task) or a specific effect on the ability to mentally rotate body parts (Hand Laterality Task), we performed a Wilcoxon test to compare performances on the Hand Laterality Task and Object Laterality Task of the older age group (over 60 years). Older adults showed significantly lower performances on the Hand Laterality Task ($Z = -2.128$, $p = 0.031$).

The analysis on the total SAQ scores showed no significant differences among the three age groups ($\chi 2 = 2.39$, $p = 0.302$).

Comparison of median total score of SAQ score among three age groups are shown in **Figure 3**.

Correlation Between IS and BR Through the Adult Lifespan

The correlation analysis performed to assess the association between age and SAQ total scores showed no significant correlation. Similarly, no significant correlations were found between age and all control tasks (Object-Room Association Task, Christmas Tree Task, and Object Laterality Task), and between age and the body semantics task (Object-Body Part Association Task). Instead, significant correlations were found between age and the body schema (Hand Laterality Task) and between age and the body structural representation (FBE) task scores (for more details, see **Table 2**). In brief, we found that the older the age, the worse the participants performed on the tasks assessing the body structural representation and body schema ($p \leq 0.013$).

The correlations performed separately on the three age groups show that only in the older adult group there was a significant correlation between the SAQ and the body schema (Hand Laterality Task), and between the SAQ and body structural representation (FBE) (for more details, see **Table 3**).

Furthermore the partial correlations conducted to examine the relation between IS and BR controlling for age (47.5 ± 14.85 years) on the whole sample showed no significant partial correlation ($r = -0.144$, $p = 0.103$) between the SAQ (30.55 ± 12.96) and the task assessing the body schema (Hand Laterality Task; 18.34 ± 3.21). However, the zero-order correlation showed a statistically significant negative correlation between the SAQ and the body schema task (Hand Laterality Task; $r = -0.181$, $p = 0.040$). This indicates that age had a significant influence in controlling for the relation between IS and body schema. As regards the body structural representation, there was still a statistically significant positive partial correlation ($r = 0.274$, $p = 0.002$) between the SAQ (30.55 ± 12.96) and the task assessing the body structural representation (FBE; 96.41 ± 66.01) when controlling for age (47.5 ± 14.85 years).

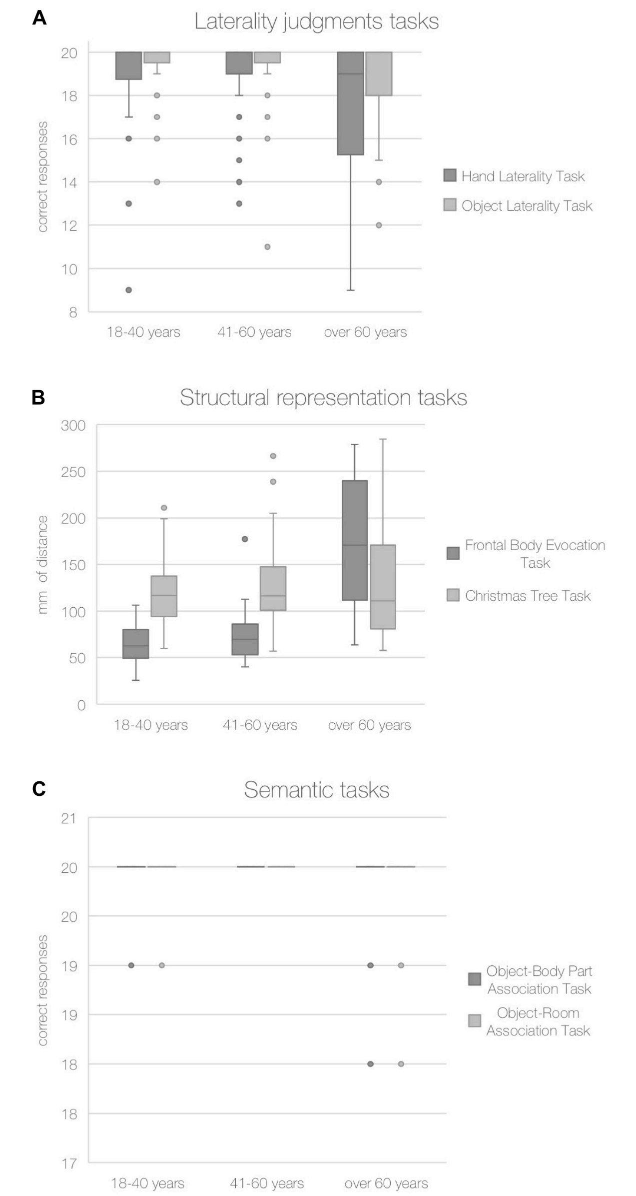

FIGURE 2 | Accuracy in body and non-body tasks. Note: Median number of correct responses for laterality judgments **(A)** and semantic tasks **(C)** and mm of distance from the correct location for structural representation tasks **(B)** are reported for each age group.

The zero-order correlation showed a statistically significant and positive correlation between the SAQ and the body structural representation task (FBE; $r = 0.310$, $p < 0.0001$). This indicates that age had no significant influence in controlling for the relation between IS and body structural representation. As regards the body semantics, there was no significant partial correlation ($r = -0.074$, $p = 0.404$) between the SAQ (30.55 ± 12.96) and the task assessing the body semantics (Object-Body Part Association Task; 19.94 ± 0.27) while controlling for age (47.5 ± 14.85 years). The zero-order correlation showed no

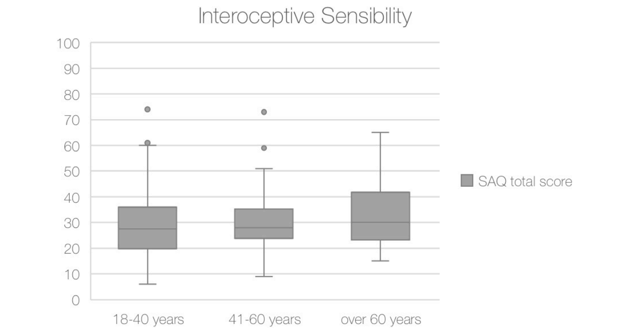

FIGURE 3 | Median total score of Self-Awareness Questionnaire (SAQ) obtained for each age group.

statistically significant correlation between the SAQ and the body semantics task (Object-Body Part Association Task; $r = -0.073$, $p = 0.407$).

Moreover, the partial correlation analyses performed to verify if the association between IS and the BR remained significant regardless of cognitive abilities required to perform tasks per se showed no significant partial correlation ($r = -0.164$, $p = 0.064$) between the SAQ and the unstandardized residuals of the Hand Laterality Task scores on the Object Laterality Task scores while controlling for age. In contrast, the zero-order correlation showed a statistically significant and negative correlation between the SAQ and the unstandardized residuals of the Hand Laterality Task scores on the Object Laterality Task scores ($r = -0.193$, $p = 0.028$). Overall, these results confirmed that IS was significantly correlated with the body schema when controlling for other cognitive skills and that age had a significant influence in this relation.

Regarding the body structural representation, there was a positive partial correlation ($r = 0.250$, $p = 0.004$) between the SAQ and the unstandardized residuals of the FBE scores on the Christmas Tree Task scores while controlling for age, showing that the association remained significant regardless of age. The zero-order correlation also showed a statistically significant and positive correlation between the SAQ and the unstandardized residuals of the FBE scores on the Christmas Tree Task scores ($r = 0.291$, $p = 0.001$). Overall, these results confirmed that IS was significantly correlated with the body structural representation when controlling for other cognitive skills and that age had no influence in controlling for this relation.

Regarding the body semantics, there was no significant partial correlation ($r = -0.080$, $p = 0.369$) between the SAQ and the unstandardized residuals of the Object-Body Part Association Task scores on the Object-Room Association Task scores while controlling for age. The zero-order correlation showed no statistically significant correlation between the SAQ and the unstandardized residuals of the Object-Body Part Association Task scores on the Object-Room Association Task scores ($r = -0.079$, $p = 0.373$).

Moderation Role of IS in the Relation Between Aging and BR

To verify if the effect of age on the BR was conditioned by IS levels, a model 1 (i.e., a simple moderation model to test the

TABLE 2 | Correlation between age and SAQ total scores, BR and control tasks scores in the whole sample.

		Age	SAQ	Hand laterality task	Object laterality task	FBE	Christmas tree task	Object-Body part association task	Object-Room association task
Age	r_{rho}		0.11	−0.23	−0.09	0.54	0.17	−0.01	0.01
	p		0.183	0.013*	0.267	0.001**	0.057	0.939	0.954
SAQ	r_{rho}			−0.19	0.08	0.21	0.15	0.01	0.08
	p			0.024*	0.325	0.014*	0.070	0.844	0.307
Hand laterality task	r_{rho}				0.39	−0.37	−0.29	0.18	−0.02
	p				< 0.0001**	< 0.0001**	0.001	0.030*	0.777
Object laterality task	r_{rho}					−0.23	−0.13	0.11	0.08
	p					0.011*	0.141	0.205	0.315
FBE	r_{rho}						0.32	−0.10	−0.05
	p						< 0.0001**	0.252	0.501
Christmas tree task	r_{rho}							−0.08	0.15
	p							0.327	0.075
Object-Body part association task	r_{rho}								0.18
	p								0.024
Object-Room association task	r_{rho}								
	p								

SAQ, self-awareness questionnaire; FBE, frontal body evocation task.
**p < 0.05.*
***p ≤ 0.001.*

TABLE 3 | Correlations between SAQ total score and scores on the three BR tasks for each age group.

		Hand laterality task	FBE	Object-body part association task
18–40 years				
SAQ	r_{rho}	0.11	0.02	0.17
	p	0.456	0.897	0.235
Hand laterality task	r_{rho}		−0.25	0.19
	p		0.080	0.178
FBE	r_{rho}			−0.09
	p			0.534
Object-body part association task	r_{rho}			
	p			
41–60 years				
SAQ	r_{rho}	−0.01	0.10	0.08
	p	0.924	0.487	0.601
Hand laterality task	r_{rho}		−0.13	0.03
	p		0.362	0.834
FBE	r_{rho}			−0.10
	p			0.477
Object-body part association task	r_{rho}			
	p			
Healthy participants group aged over 60				
SAQ	r_{rho}	−0.68**	0.67**	−0.27
	p	< 0.0001	< 0.0001	0.108
Hand laterality task	r_{rho}		−0.72**	0.39*
	p		< 0.0001	0.017
FBE	r_{rho}			−0.28
	p			0.118
Object-body part association task	r_{rho}			
	p			

SAQ, self-awareness questionnaire; FBE, frontal body evocation task.
$^*p < 0.05$.
$^{**}p \leq 0.001$.

effect of one independent variable on another dependent variable, conditioned on a third moderator variable, see **Figure 1A**) in the PROCESS macro for SPSS was run.

For the body schema (Hand Laterality Task), the overall model was significant (R^2 = 0.13, F(3,133) = 2.971, p < 034) with a significant interaction between age and SAQ scores (b = −003, t = −2.35, p = 0.021). After controlling for cognitive functioning (Raven's Colored Progressive Matrices scores), the overall model remained significant (R^2 = 0.31, F(3,133) = 14.81, p < 0.001), as well as the interaction between the age and SAQ scores (b = −0.002, t = −2.10, p = 0.044). Then, these results showed a total direct effect of SAQ score on age and body schema (see **Figure 1B**).

For the body structural representation (FBE), the analysis indicated the overall model was significant (R^2 = 3.70, F(3,133) = 22.91, p < 0.001); however, the interaction between age and SAQ scores was not significant (b = 0.037, t = 1.38, p = 0.169).

For the body semantics (the Object-Body Part Association Task), the analysis indicated the overall model was not significant (R^2 = 0.02, F(3,133) = 0.674, p < 0.569).

Accordingly, IS appeared to moderate the relation between age and body schema significantly. The moderating effect of IS on the association between age and BR tasks is showed in **Figure 4**.

DISCUSSION

The present study aimed to investigate the relation between IS and BR during the adult lifespan. As a corollary, we also investigated the aging effect on IS and BR per se. The main finding of the present study is that higher levels of IS would worsen the performance on body schema with advancing age. Indeed, results revealed an age-dependent significant negative association between IS and body schema. In contrast, a significant association was found between IS and the body structural representation regardless of age, and no significant association was found between IS and body semantics.

At a closer look, IS also significantly moderated the relation between age and the on-line sensorimotor representation of the body (i.e., the body schema, see **Figure 1B**). Thus, greater difficulties to mentally rotate body parts would be affected by higher IS levels with increasing age, whereas the ability to localize and position correctly body parts (i.e., body structural representation) would be correlated to IS throughout all the adult lifespan and not moderated by it. So, this result would suggest the existence of a specific connection between IS and body schema with advancing age, rather than between IS and all the BR. In particular, the significant relation between IS and the body structural representation found in our correlation analysis could be mediated by the body schema, as these BR result related to each other (see **Table 2**). This possibility fits well with the theoretical co-construction model of BR (Pitron et al., 2018) that suggests that although the body schema and the body image are functionally distinct, their construction is partly based on their interactions and that the body schema, based on multisensory signals and motor expertise, influences the construction of body image (i.e., the body structural representation and the body semantics).

The specific connection between body schema and IS could be interpreted in light of previous research by Tsakiris et al. (2011) that in a sample of young adults (mean age 21.5 years) using the well-known RHI found a negative correlation between interoceptive accuracy (another component of interoceptive processing assessed by means of a heartbeat monitoring task) and body ownership over a fake hand, with low interoceptive accuracy resulting in a stronger sense of body ownership. As outlined in the introduction, body ownership also depends on the "coherence of current sensory input with pre-existing

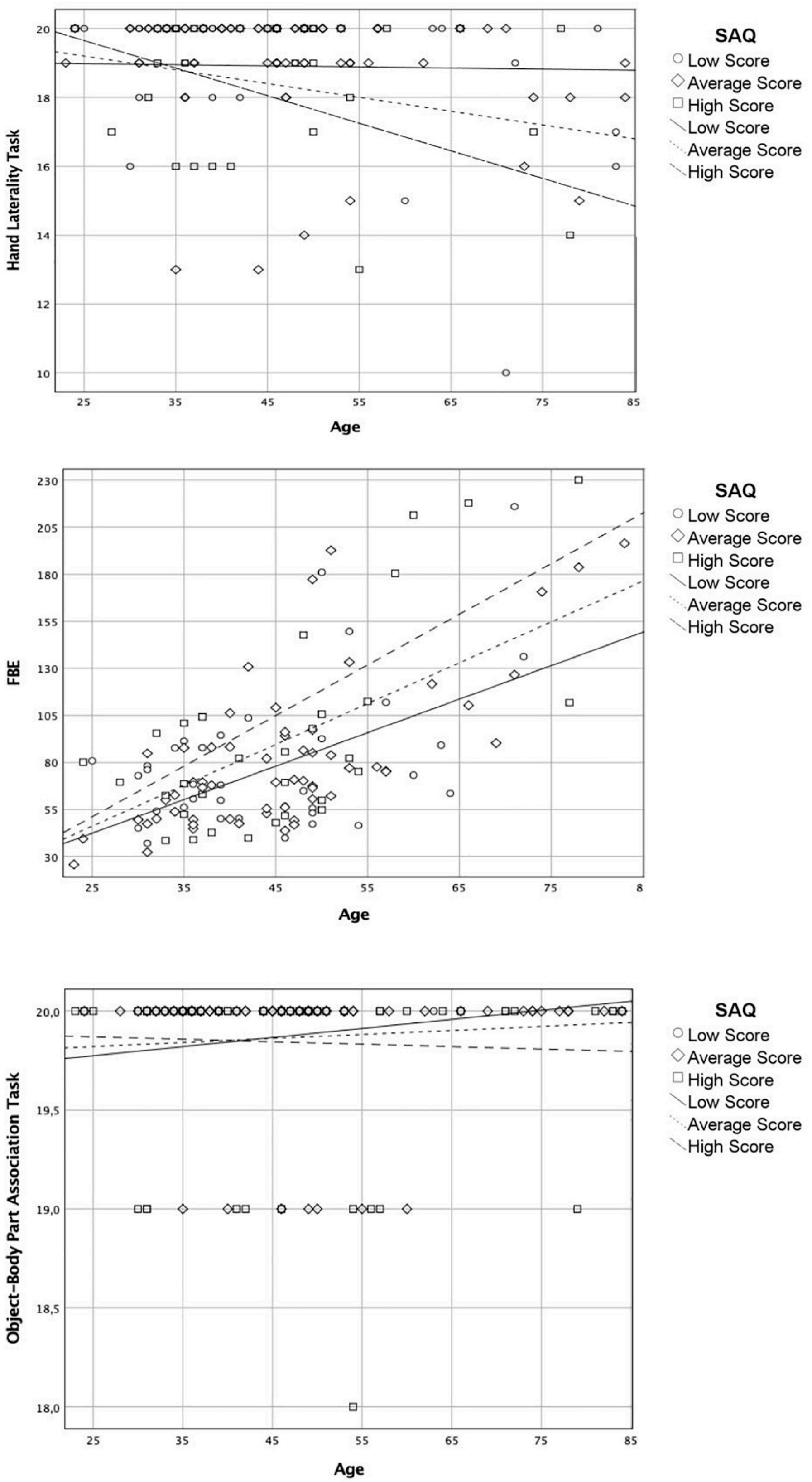

FIGURE 4 | Moderating effect of the interoceptive sensibility on the association between age and body representation tasks.

cognitive representations of the body" (Costantini and Haggard, 2007, p. 230); following Tsakiris et al. (2011) interoceptive accuracy may predict the malleability of the pre-existing BR. A higher awareness of one's inner body sensations would decrease the plasticity of the BR and make it more difficult to feel ownership for artificial body parts that do not pertain to the physical configuration of the actual body. Further evidence of the body schema plasticity can be found in studies with tool use paradigms (Maravita and Iriki, 2004; Cardinali et al., 2009, 2012). Indeed, when actions are performed with tools, the morphology and functionality of specific body parts is modified through a quick and efficient updating of the body schema that allows the maintenance of action accuracy (Cardinali et al., 2009, 2016).

The association between IS and BR in aging could also be due to a reorganization of functional brain networks (Steffener et al., 2012; Bagarinao et al., 2019), and in particular to a decreased within-network and an increased between-network connectivity (Tomasi and Volkow, 2012; Betzel et al., 2014) in the visuospatial, the sensorimotor and the salience network (Bagarinao et al., 2019) associated with BR and interoceptive processing (Takeuchi et al., 2016; Chong et al., 2017). Indeed, studies using graph theory to identify the age-related changes in the brain's network topology, found age- and aging-related decreases in the global measures of integration, segregation, and distinctiveness of the salience and sensorimotor networks (Chan et al., 2014; Shah et al., 2018).

Moreover, unlike previous studies (Khalsa et al., 2009; Murphy et al., 2018) that investigated interoception in older adults, we did not find a significant effect of age on IS likely due to a different method to assess interoception (i.e., a self-report questionnaire rather than a heartbeat detection task, see Khalsa et al., 2009) and to a difference in the age of the assessed samples (participants aged up to 84 years old compared with younger groups in the present study, rather than participants aged up to 90 years old as in Murphy et al., 2018).

Conversely, we found a significant age effect on BR tasks probing the body structural representation and body schema. These results expand on previous findings that point to an age effect on the body schema (e.g., Personnier et al., 2008; Skoura et al., 2008; Saimpont et al., 2009), on the experience of ownership toward an artificial and external limb, such as a rubber hand (Marotta et al., 2018), and on the ability to predict sensory consequences of one's actions (Wolpe et al., 2016), highlighting how the multisensory integration and flexibility of BR may change across the lifespan (Marotta et al., 2018). Also, current findings are aligned with previous neuroimaging studies (McGinnis et al., 2011; Muller et al., 2016; Zhou et al., 2020) that found in older adults cortical thickness, decreased fractional anisotropy, and reduced functional connectivity in brain areas (i.e., insula cortex, primary sensorimotor area, inferior frontal gyrus, superior temporal gyrus, supramarginal gyrus) that are also damaged in patients with clinical conditions that affect BR (Baier and Karnath, 2008; Heydrich and Blanke, 2013; Boccia et al., 2020).

In conclusion, our results provide evidence regarding the relation between IS and BR during the adult lifespan. Nevertheless, some limitations should be acknowledged, such as the smaller sample size of the older group (37 participants over age 60 of which only six participants over age 80), and the sole use of the SAQ to assess IS, focusing mainly on negative visceral and somatic sensations (e.g., "I feel a burning sensation in my stomach;" "I feel that I can't get enough air into my lungs"). Moreover, since almost all participants obtained the maximum possible score on the body semantics task (i.e., ceiling effect), results should be interpreted carefully, considering that the task used to tap body semantics may not be sensitive enough to age-related changes.

Thus, starting from our findings, further studies should enroll a larger sample size of older adults and consider and better investigate the possible moderator and mediator role of other psychological and physical variables (i.e., health anxiety and pain) and their clinical implications for the health maintenance in geriatric populations. Also, future lifespan studies should verify, in the same sample of participants, the effects of different components of interoceptive processing (i.e., interoceptive attention, interoceptive accuracy and IS) on different BR as well as on body ownership, to better understand how far each of them affects the malleability of different aspects of the cognitive body processing.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The study involved human participants and was approved by Local ethics committees (Calabria Region Ethical Committee, Catanzaro, Italy, and Ethical Committee of the University of Campania 'Vanvitelli', Caserta, Italy). The participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

All authors had substantially contributed to the conception and design of the work, to the interpretation of data and to draft and revise the work for important intellectual content. SR, MB, AD, and MC participated in data acquisition and statistical analysis.

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How Proprioception Gives Rise to Self-Others-Knowledge

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INTRODUCTION

The already rich professional literature broadly informs about the role of the body in establishing the self-others distinction (Jeannerod, 2006; Iacoboni, 2009; Kyselo, 2015; Maister et al., 2015; Noel et al., 2017; Palmer and Tsakiris, 2018). The internal sense of ownership and sense of agency are the fundamentals of self-identification (Jeannerod, 2004; Blanke et al., 2015; Tsakiris, 2016; Braun et al., 2018). The lack of these two fundamentals (natural or artificially induced) also conveys important information, specifically that the action was executed by someone else (Iacoboni, 2009; Tsakiris, 2010). In my opinion, owing to its neural fundamentals, bodily self-consciousness (BSC) not only allows us to differentiate between self and others but also leads to the propositional knowledge of the subject and influences the social functioning of the subject (the self-others-knowledge—SOK). Assigning the important role of the body and multisensory integration in the self-others distinction is not new (Keromnes et al., 2019). However, what I add to this opinion is the recognition of the role of proprioception in shaping propositional SOK, i.e., shaping a specific type of metacognition.

THE ROLE OF PROPRIOCEPTION FOR BODILY SELF-CONSCIOUSNESS

The viewpoint presented in this article is in line with the enactivism, which is in turn deeply rooted in the phenomenological tradition (Maturana and Varela, 1998; Gallagher, 2006). According to this line what forms the mind is the body and its interaction with the environment (Wilson, 2002; Di Paolo and De Jaegher, 2012). The role of the body has been described particularly in relation to neural mechanisms underlying BSC—especially multisensory integration constituting proprioception (Blanke and Metzinger, 2009; Blanke et al., 2015; Limanowski, 2017). BSC manifested in the sense of ownership and sense of agency is therefore a psychological outcome of the synchronisation of sensorimotor information (Cf. Jeannerod, 2006; Blanke et al., 2015). However, given that BSC, built from different information including proprioceptive cues, closes the subject in the internal loop at the neuronal level of information processing, the problem arises of a link between self-awareness and awareness of others, i.e., how an individual subject becomes a social subject.

Proprioception can be defined in different ways. On the one hand, it is an unconscious registration in the central nervous system of one's own joint positions (Gallagher, 2006). The information coming from proprioceptors placed in the inner ear and muscles is analysed and integrated by the brain, which on this basis creates a body scheme (Cole, 1995; Gallagher and Cole, 1995). On the other hand, proprioception can be understood as non-conceptual bodily self-awareness (Bermúdez, 2005). In this case it is a kind of direct knowledge about the subject's basic experiences, which are the sense of the body's position and of being embedded in the world (Seth, 2015). Although such sensations are usually consciously inaccessible, they become apparent by paying attention to the subject's own movement, especially by performing certain kinds of action controlling whether the proprioception works properly. The basic multisensory information processing, when integrated, produces an experience being a self—an autonomous minimal selfhood (Blanke and Metzinger, 2009; Blanke et al., 2015).

In ecological psychology represented by Gibson (2002), proprioception is understood as the awareness of the perceiver regarding their existence in the environment, which accompanies the perception of the environment, hence the perception and proprioception come together. Having in mind Gibson's theory of ecological self, I think that the particular constitution of BSC is possible thanks to the sense of vision playing an important role in proprioception by increasing one's self-experience as an individual distinctive from the rest of the world. It is the vision which provides information via exteroception regarding which objects do and do not belong to the body (Gibson, 2002, p. 78). An example is the distinction between object motion and locomotion. In the first case it is perception which reveals the movement of an object in the static environment; in the second case, it is proprioception which informs that the observed movement is the activity of the organism's own body (Cf. Gibson, 2002, p. 78). To illustrate this, one can use the example of an illusion which occurs while sitting on the train; while waiting for its departure, we observe another stationary train through the window and, suddenly, we see windows passing and believe that our train has started to move. However, after a second, we realise that our train is still static and that another train is moving. The example of the illusion of the movement shows how strong the visual information about our position towards other bodies is. The role of vision in the formation of BSC is also featured in the conception of associative system learning, where the motor representation of one's own movements and the sensory representation of this movement connect with each other increasingly whilst self-observation (Heyes, 2016).

SELF-OTHER KNOWLEDGE

I claim that not only BSC but also the particular constitution of a SOK is possible thanks to the sense of vision playing an important role in proprioception by increasing self-experience as being an individual distinctive from the rest of the world (Cf. Jeannerod, 2004; Limanowski and Friston, 2019). Vision serves as the exteroception, i.e., the perception of external objects; proprioception, on the other hand, gives information about the body itself (Gibson, 2002, p. 78). A synchronisation of sensorimotor information coming from vision and proprioception results in representation of the acting body (Cf. Limanowski and Friston, 2019). The recognition whether it is one's own body which is acting is an ultimate factor influencing self-other distinction (Jeannerod, 2004) and establishing self-representation as distinctive from the representation of the others (Palmer and Tsakiris, 2018).

My thesis is that the bodily mechanisms of self-recognition not only lead to distinction me-others (bodily self-others knowledge—BSOK) but also contribute to the formation of propositional SOK (PSOK), i.e., that non-conceptual bodily representations are transformed into conceptual ones, by a recognition of a movement as an action. The meaning is namely an intention: a goal of the movement performed. In other words the ascription of a meaning to the observed movement rests on a connexion of a movement with a goal. I suppose that the recognition of a movement as intentional is the link connecting BSC with metacognition: SK and SOK. The ability to make a distinction between one's own action and the action of others underlies recognition of intentions and, i.e., understanding the actions of others by ascribing them the intention on the basis of the subject's own intentions and goals. As representations can be divided into sensorimotor (bodily) and cognitive (conceptual), the knowledge of others can be divided into sensorimotor and conceptual (Mul et al., 2019). Given that sensorimotor representations underlie the conceptual, BSOK underlies PSOK. In other words, the transition from BSOK to PSOK is the transformation of the sensorimotor representation into conceptual ones.

The claim that vision and proprioception build BSC and consequently SK and SOK is not beyond dispute. For example O'Regan and Noë (2001) trait vision as a way of acting, i.e., active exploration of the environment, which may be an argument against the importance of vision in constructing self-other boundaries. However, this discussion does not apply to the position presented here. I claim, namely, that the internal sense of ownership and sense of agency are the fundamentals of self-identification in BSC. In other words, in BSC resting on vision and proprioception an agent gains the information that it is their body rather than someone else's which is acting and, by using this acting body, they can achieve the intended goal. Thus, the BSC constituted in action provides important information for BSOK: self-others distinction by ascribing the action to oneself or to the other. BSOK underlies the higher-level cognition involving conceptual knowledge. The bodily experience provides a basis for the development of an intentional level of understanding, i.e., PSOK. But why do we need propositional knowledge about others at all if the differentiation has already been made at the bodily level of information processing? The answer is simple: to understand their intentions, to ascribe them mental states, and to interpret them as rational agents. For all this we need a conceptualisation.

A BRIEF DISCUSSION OF ALTERNATIVE APPROACHES

An interesting conception how the neuronal basis gives rise to SOK without the involvement of proprioception refers to the role of mirror neurons system (MNS) in cognition, which facilitates a distinction between an agent's own action and the action of the others. There are two interpretations of the role of mirror neurons in cognition. The first is broader and states that mirror neurons are involved in reading the intentions of others;

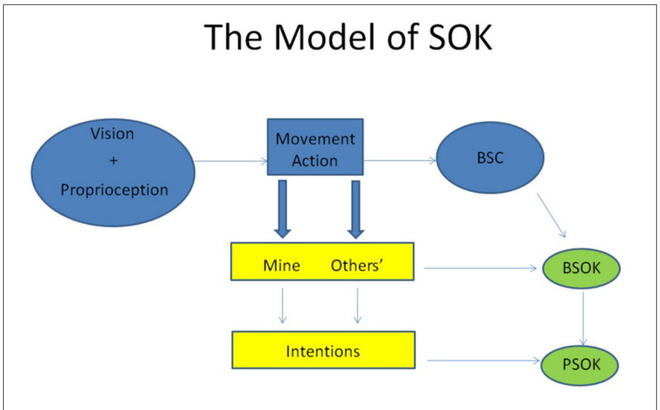

FIGURE 1 | The model of SOK.

moreover, the activation of mirror neurons in humans occurs more often than in primitives, which could be associated with a wider range of interpretation of actions although the effect would be the same: equally fast selection of the appropriate response (Rizzolatti et al., 1996; Iacoboni, 2009). Mirror neurons can distinguish the same movement, but are associated with different intentions (Fogassi et al., 2005).

If the conception of MNS is so useful in the explanation of SOK, why should we look for an alternative? First of all, it is not clear what MNS contributes to. The discussion around the interpretation of mirror neurons revolves around the question of whether MNS is involved only in understanding motor activities or in identifying the intentional states of others, i.e., SOK. The second interpretation of the role of MNS is, by definition, more sceptical and states that the activation of mirror neurons is used to read the sequence of activities that the body has to learn; in other words, mirror neurons are for learning rather than for understanding the intentions of others (Jeannerod, 1994). To compromise rather than fully excluding MNS from the conception proposed in this article it is legitimate to say the reference to the multisensory integration as the neural basis for SOK incorporates MNS. The conception of MNS also contains elements such as movement, action recognition and ascription, the sense of ownership, and the sense of agency.

Another conception regarding how PSOK is created, refers to the ability of perspective taking, i.e., the ability of putting oneself in place of somebody else (Jeannerod, 2006). This conception is based on the Theory of Mind (ToM), which refers to the classical representation-based approach to social cognition where the ability to interact with others rests on the mental constituents of cognition rather than their physical counterparts (Tomasello and Rakoczy, 2003; Tomasello, 2019). Nonetheless, I believe that ToM is good for an explanation of the metacognition, i.e., it explains the mind-social problem but not the body-social problem (Kyselo, 2015). Research on disorders such as Autism and Schizophrenia, where agents have difficulties in interpersonal relations, show that problems with interaction abilities begin at the level of BSC formation, i.e., at the level of multisensory integration. In other words, the problem in SOK starts with the problem with bodily representation of self; specifically, in Autism a subject possesses a sharper self-others boundary which extends beyond the norm whereas in Schizophrenia this boundary is weaker (Noel et al., 2017). The abnormal size of this boundary is determined by disturbances in the processing of information about peripersonal space (Noel et al., 2017). The problems with mindreading or intentions understanding are a consequence of the impaired somatosensory representation of the self.

CONCLUSION

In my opinion the conceptualised knowledge about the others (PSOK), i.e., the recognition of other bodies as intentionally acting individuals necessarily involves the primacy of the non-conceptual bodily self-other knowledge (BSOK). Hence if one wants to build a model of how SOK is created, must refer to the neural constitution of BSC involving the sense of vision and proprioception, triggered and tuned in a goal-directed movement, i.e., an action (**Figure 1**). Vision and proprioception are namely significant indicators of the source of the action—the sense of agency. In such an account not only the individual mind, but also the social mind is shaped by body and its interaction with the world.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

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Effect of Tactile Sensory Substitution on the Proprioceptive Error Map of the Arm

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Proprioceptive error of estimated fingertip position in two-dimensional space is reduced with the addition of tactile stimulation to the fingertip. This tactile input does not disrupt the subjects' estimation strategy, as the individual error vector maps maintain their overall geometric structure. This relationship suggests an integration of proprioception and tactile sensory information to enhance proprioceptive estimation. To better understand this multisensory integration, we explored the effect of electrotactile and vibrotactile stimulation to the fingertips in place of actual contact, thus limiting interaction forces. This allowed us to discern any proprioceptive estimation improvement that arose from purely tactile stimulation. Ten right-handed and ten left-handed subjects performed a simple right-handed proprioceptive estimation task under four tactile feedback conditions: hover, touch, electrotactile, and vibrotactile. Target sets were generated for each subject, persisted across all feedback modalities, and targets were presented in randomized orders. Error maps across the workspace were generated using polynomial models of the subjects' responses. Error maps did not change shape between conditions for any right-handed subjects and changed for a single condition for two left-handed subjects. Non-parametric statistical analysis of the error magnitude shows that both modes of sensory substitution significantly reduce error for right-handed subjects, but not to the level of actual touch. Left-handed subjects demonstrated increased error for all feedback conditions compared to hover. Compared to right-handed subjects, left-handed subjects demonstrated more error in each condition except the hover condition. This is consistent with the hypothesis that the non-dominant hand is specialized for position control, while the dominant is specialized for velocity. Notably, our results suggest that non-dominant hand estimation strategies are hindered by stimuli to the fingertip. We conclude that electrotactile and vibrotactile sensory substitution only succeed in multisensory integration when applied to the dominant hand. These feedback modalities do not disrupt established dominate hand proprioceptive error maps, and existing strategies adapt to the novel input and minimize error. Since actual touch provides the best error reduction, sensory substitution lacks some unidentified beneficial information, such as familiarity or natural sensation. This missing component could also be what confounds subjects using their non-dominant hand for positional tasks.

Keywords: proprioception, multisensory integration, vibrotactile, electotactile, sensory substitution

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INTRODUCTION

Cutaneous and deep sensations have some surprising interactions. The addition of tactile information during proprioceptive tasks provides a reduction in proprioceptive error: tactile cues reduces end-point error in matching tasks, continuous movement tasks, and point-to-point movement tasks (Lackner and Dizio, 1994; Tillery et al., 1994; Rao and Gordon, 2001). Even postural sway can be reduced by light tactile information that offers no mechanical support (Rabin et al., 2008). This multisensory integration is reinforced across the two-dimensional horizontal reaching space, as providing a tactile cue during a positional estimation task reduces error magnitude while maintaining the same spatial properties of the error (Rincon-Gonzalez et al., 2011). These studies suggest that proprioceptive estimation is a result of an internal reference of the body that incorporates internal tactile information. However, many of these prior results rely on a fingertip touching a tabletop, which could induce complex shear forces or small joint forces in addition to normal taction. The focus of this manuscript is to further investigate the effect of tactile input on multisensory integration: specifically we examined how proprioception would interact with artificial sensory substitution.

Sensory substitution has long been used as a method of improving or replacing lost sensory abilities. The implementation of vibrotactile or electrotactile stimulation has been used to replace vision, auditory, or other tactile deficiencies (Kaczmarek et al., 1991). Sensory substitution can also be used to associate actions to feedback, promoting action-sensation coupling and reinforcing body-ownership (Gapenne, 2014), which would promote effective feedback as long as artificial sensations do not disrupt any established proprioceptive estimation strategies. The effect of artificial tactile sensation on this multisensory integration is relatively unexplored. We have previously shown that hand posture can interfere with the perception of artificial sensation: a perceptual illusion elicited by sequential electrotactile stimulation of the fingertips can be abolished by assuming specific hand postures (Warren et al., 2010). Most of the literature investigates the efficiency of singular focused sensory substitution without considering the effects on multisensory integration.

By assessing the limitations and capabilities of vibrotactile and electrotactile sensory substitution, we can gain insight into this multisensory process. Thus, we aimed to investigate the effect artificial sensory substitution has on multisensory integration of tactile and proprioceptive information. We hypothesized that sensory substitution of vibrotactile and electrotactile information would not disrupt proprioceptive strategies and would integrate similarly to natural touch. We report that artificial tactile stimuli and proprioceptive estimation integrate appropriately, maintaining the non-uniform and idiosyncratic spatial distribution of endpoint errors, and reducing overall error although to a lesser degree than natural touch. We also report that sensory feedback increases estimation error in the non-dominant hand, but without changing the spatial properties of the endpoint error map.

MATERIALS AND METHODS

Subjects

For this experiment, 22 subjects were recruited to perform a right-handed proprioceptive estimation task. Two subjects were excluded in the analysis due to handedness discrepancies, addressed below. The task, parameters, and experimental protocols were reviewed and approved by the Institutional Review Board at Arizona State University.

Handedness

Handedness was self-reported from each subject, and the Edinburgh Handedness Inventory questionnaire was used to follow-up and evaluate the handedness of each subject after the experiment (Oldfield, 1971; **Figure 1**). From subject self-reports, there were 11 right-handed subjects and 11 left-handed subjects. One self-reported right-handed subject failed to fill out the Edinburgh Handedness Inventory and that subject was excluded from the right-handed subjects. Only one subject that filled out the questionnaire had a result that differed from their self-report: a self-reported left-handed individual with a handedness score of 0.21. Due to this ambiguity, this subject was excluded from the left-handed subjects. This resulted in 20 subjects included in the analysis: 10 left-handed and 10 right-handed.

Task

Subjects sat in front of a table with a 50 cm wide and 35 cm deep grid, consisting of 280 targets with alphanumeric and color assignments on a 14 × 20 grid illustrated in **Figure 2**. A set of 75 random targets, with at least one from each alphanumeric square on the grid, were chosen for each subject and kept for all iterations of that subject's experiment. For each trial of the task, the subject held their right hand a few centimeters

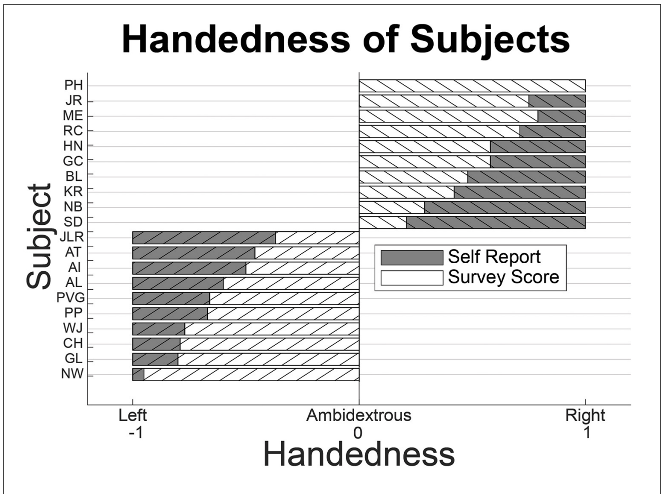

FIGURE 1 | Subject handedness. Self-reporting and results from the Edinburgh Handedness Inventory questionnaire for included subjects. Only a single subject had questionnaire results that deviated from self-reporting. Another subject did not fulfill the questionnaire. Both were excluded from analysis.

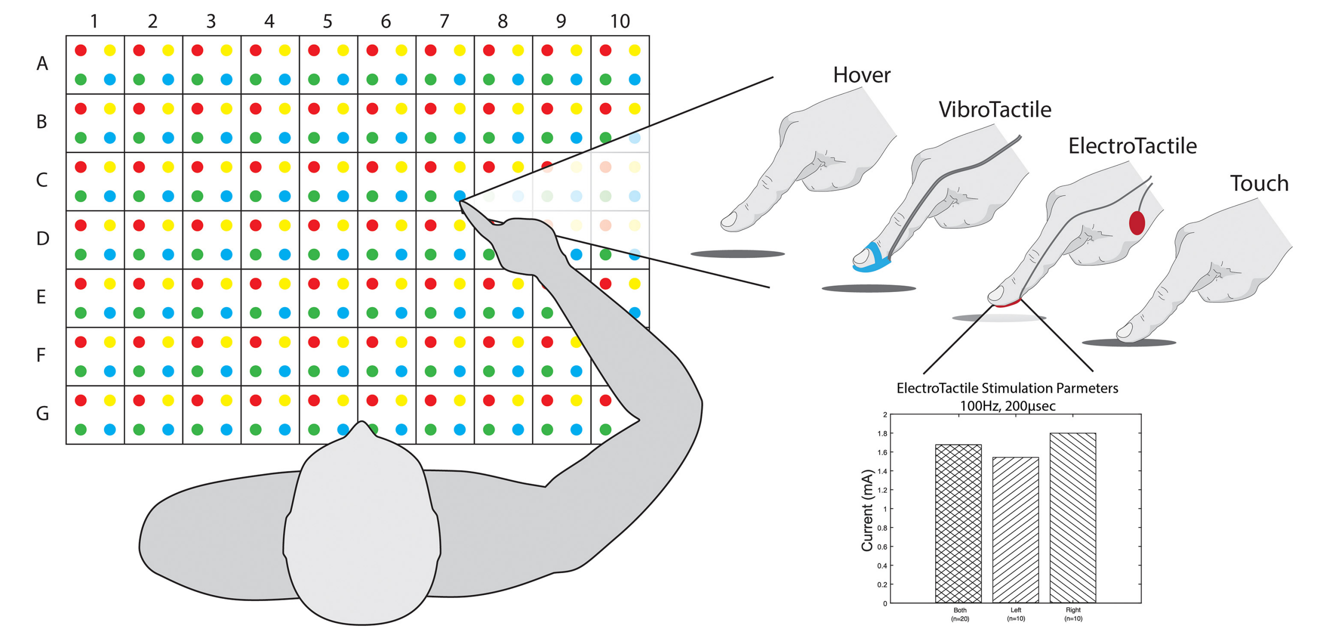

FIGURE 2 | Workspace and feedback. **(Left)** Subjects sit in front of a grid of dots with 2.5 cm spacing between them, creating a workspace 50 cm wide and 35 cm deep. Targets and responses are referred to via their numerical value, alphabetical letter, and color, e.g., A1Red. **(Right)** Subject interaction for each feedback mode. Vibrotactile feedback required a custom 3D printed piece to hold the vibration motor to the fingertip with a Velcro strap. Electrotactile feedback electrode placement is indicated on the fingertip and ground on the head of the radius. **(Inset)** Electrotactile parameters for subjects. Tolerable current levels were chosen by each subject with a maximum of 2 mA.

above the edge of the table's midline close to their chest. With the subject's eyes closed, the experimenter guided the subject's right hand to a randomly selected target, provided feedback for 5 s, and guided the hand back to the starting position. The subject then opened their eyes, and without moving their arm, reported the estimated target by alphanumeric value and color, e.g., "A1Red." The overall procedure was explained to the subject, and each subject was administered at least one practice trial, depending on the subject's self-reported confidence with respect to understanding the task. Trials were only aborted and repeated if the experimenter accidentally touched the subject's hand to the table in the process of approaching the target.

The task was randomly delivered as four separate blocks for each feedback mode: hover, touch, electrotactile, and vibrotactile (**Figure 2**). Hover consisted of the subject keeping their hand above the table and receiving no tactile feedback before being guided back to the starting position. Touch consisted of the experimenter moving the subject's hand to the target, then vertically lowering it to the table, allowing contact for 5 s and attempting to minimize any lateral or residual movement, vertically raising their hand, and then returning to the starting position. Vibrotactile feedback was delivered with a vibration motor in a 3D printed housing mounted to the finger with Velcro. Timing was controlled with an Arduino Uno microcontroller. Electrotactile stimulation was delivered via a Digitimer DS8R stimulator. Parameters of a biphasic, symmetrical pulse were set at 200 microsecond pulse width and subjective tolerable amplitudes. Pulse amplitude was determined for each subject, starting at 2 mA and lowered if needed until the subject reported the sensation as "tolerable but clear." This provided a strong stimulus rather than a "just noticeable" stimulus. Each pulse with triggered via a TekTronix function generator at 100 Hz, generating 500 pulses over 5 s (**Figure 2** Inset).

Analysis

Using a subject's estimations of the targets, the raw error magnitude and direction can be mapped across the sampled workspace. To obtain homogenous estimations across the entire workspace, the subjects' responses to all 75 targets are used to create raw error vectors for each condition of each subject. The raw response vectors are separated into separate cartesian components: the lateral X component and distal-proximal Y component. The X and Y error are independently modeled using separate 4th order polynomial regressions and then X-error and Y-error are evaluated across each potential alphanumeric-color target. This provides a calculated error that exhibits a smoothing effect and diminishes representation of actual variability, but previous studies have not indicated a strong discrepancy of error magnitude or direction estimations between raw and calculated errors (Rincon-Gonzalez et al., 2011). We maintained the same target set across feedback modes to enable direct comparisons between these models. The use of this model provides the ability to measure evenly across the workspace and compare error vectors that are non-zero. **Figure 3** illustrates this process for a single subject's raw and calculated error from two feedback conditions. The first two columns illustrate the error maps alone, and the third column overlays the two maps for visual comparison. Both shape and magnitude

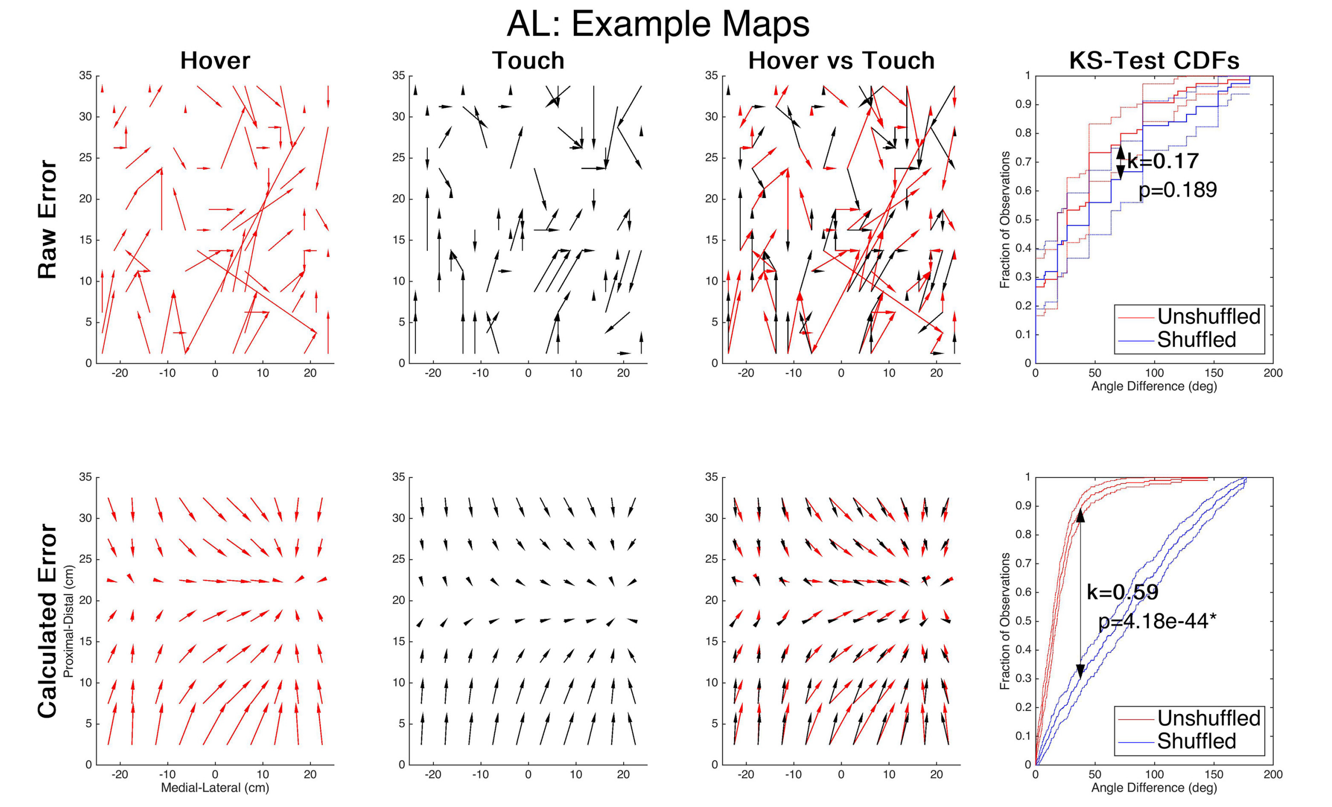

FIGURE 3 | Data processing example. Arrows show proprioceptive error magnitude and direction for the hover condition. Each tail is the target and each head is the response. The top row shows the raw error of actual responses to targets for each condition and the comparison of the two. The bottom row shows the modeled error of the same conditions averaged for each alphanumeric grid. The far right column demonstrates the K-S test statistical process, relying on the maximum span between the cumulative distributions of differences in shuffled/unshuffled error angles, denoted as "k" and accompanied by the *p*-value of the test.

need to be evaluated statistically, and all reported analyses were performed on each target's calculated, generated from the polynomial models.

Data within subjects and across subjects were determined to have a non-normal distribution using the Lilliefors test, so non-parametric analyses were implemented. To determine if the shape of the error map was maintained between conditions, we employed the Kolmogorov-Smirnov (K-S) test which is described thoroughly in Rincon-Gonzalez et al. (2011). This test non-parametrically compares the distribution of two variables and determines if they are sampled from an identical distribution. In this application, we used it to compare the distribution of shuffled and unshuffled angular differences between error vectors; comparing actual angular differences to a random distribution. Significance would indicate the actual angular differences are significantly small and therefore imply a consistent shape. The unshuffled distribution represents each target's error vectors' actual angular difference between two feedback modes. A shuffled distribution was built by finding the angular difference between one feedback mode's actual error vector and a randomly shuffled error vector for the second mode. If the unshuffled error vectors are similar, the angular difference is often small, creating a steep cumulative distribution function (CDF). Error maps with high variation in vector differences and a shuffled vector set would have CDFs that are more linear. Therefore, if the maximum difference between the CDFs of the shuffled and unshuffled sets is sufficiently large, then the error map shapes are significantly similar. An example of this is presented in the far-right column of **Figure 3** for both raw and calculated error. This analysis works much better for the calculated error rather than the raw error, as the latter can contain error vectors of zero magnitude which prevent the accurate assessment of angular difference. To evaluate difference of error magnitude between pairs of feedback modes, Wilcoxon rank-sum tests were performed on the mean vector magnitudes between an individual's estimations. To address the multiple comparisons between feedback conditions (6 total), we used $\alpha = 0.05/6$ as a Bonferroni correction for both Wilcoxon rank-sum tests and the K-S tests.

To explore condition effects more thoroughly, Friedman tests were implemented on feedback modes within handedness and handedness within feedback modes.

RESULTS

To evaluate the effect of sensory substitution on the map of proprioceptive error, the magnitude and shape of error were tested between feedback conditions. These experiments provided

TABLE 1 | Regression coefficients for polynomial fits.

	Subjects		Hover	Touch	Electro	Vibro		Subjects		Hover	Touch	Electro	Vibro
Right-handed	BL	X	0.97	0.97	0.95	0.96	Left-handed	JLR	X	0.96	0.94	0.94	0.97
		Y	0.94	0.95	0.94	0.96			Y	0.96	0.95	0.96	0.94
	GC	X	0.96	0.97	0.98	0.89		NW	X	0.97	0.99	0.98	0.98
		Y	0.98	0.97	0.97	0.96			Y	0.97	0.97	0.99	0.97
	HN	X	0.97	0.96	0.96	0.96		PKP	X	0.96	0.98	0.98	0.98
		Y	0.94	0.97	0.97	0.96			Y	0.96	0.97	0.98	0.97
	JR	X	0.94	0.94	0.94	0.96		WJ	X	0.97	0.97	0.98	0.97
		Y	0.97	0.94	0.95	0.96			Y	0.94	0.98	0.98	0.97
	KR	X	0.95	0.96	0.96	0.95		GL	X	0.97	0.96	0.95	0.97
		Y	0.97	0.94	0.97	0.98			Y	0.93	0.96	0.97	0.98
	ME	X	0.95	0.97	0.97	0.98		AI	X	0.97	0.95	0.86	0.91
		Y	0.96	0.98	0.97	0.97			Y	0.97	0.96	0.94	0.94
	NB	X	0.97	0.93	0.95	0.95		AL	X	0.91	0.98	0.97	0.94
		Y	0.97	0.96	0.91	0.96			Y	0.93	0.97	0.92	0.97
	PH	X	0.9	0.96	0.96	0.96		AT	X	0.86	0.96	0.96	0.96
		Y	0.95	0.95	0.97	0.94			Y	0.88	0.96	0.97	0.97
	RC	X	0.98	0.99	0.99	0.99		CH	X	0.96	0.97	0.95	0.97
		Y	0.96	0.99	0.99	0.98			Y	0.97	0.97	0.93	0.97
	SRD	X	0.96	0.98	0.98	0.95		PVG	X	0.96	0.97	0.98	0.96
		Y	0.95	0.96	0.96	0.98			Y	0.96	0.97	0.96	0.98

Modeled error for X and Y components of raw error vectors (target to response) for each subject in each condition.

raw error across 75 targets of the workspace (**Figure 3**, Top Row). The tests were then performed on 4th order polynomial models of each subjects' X and Y error, evaluated at each of the 280 target locations (**Figure 3**, Bottom Row and simplified to just the alphanumeric grid). R^2 coefficients of the 4th order polynomial fits were at minimum 0.86, averaged 0.96, and are displayed in **Table 1**. Using the resultant vectors, a Kolmogorov-Smirnov test compared the spatial structure between feedback conditions and a Wilcoxon rank-sum compared the magnitude of error between feedback conditions.

Figure 4 illustrates the error maps of each mode and the comparisons between each condition for a single subject, as well as that subject's statistical results. The visualization suggests that the spatial structure is similar across all modes and the significant K-S test results corroborate. **Table 2** outlines the statistical results of both tests with respective k values and change in mean error (ΔM). Comparing vector directions between feedback conditions (6 comparisons) for each subject (20 subjects) using the K-S test showed significantly similar spatial structures in 119/120 cases, with only one hover and vibrotactile comparison producing insignificant results. This case was a left-handed subject performing the task. Overall, sensory substitution does not appear to disrupt the spatial structure of proprioceptive error in this task.

Comparing error magnitude between feedback modes for each subject produces significant results in 96/120 tests. Specifically, Rincon-Gonzalez et al. showed that the touch condition had lower mean error than hover. We observed here a significant decrease in error in 7 out of 10 right-handed subjects, and 3 out of 7 left-handed subjects. We also carried out a Friedman test and a Kruskal-Wallis test, respectively, with feedback mode and handedness as primary factors. Both produced significant results: the test of differences between handedness rendered a Chi-square value of 109.75 ($p << 0.05$) and the test of differences between feedback mode rendered a Chi-square value of 117.75 ($p << 0.05$). Dunn-Sidak *post-hoc* tests produced no significant results in the feedback comparisons. To investigate further Friedman tests were performed across feedback mode within handedness, and Wilcoxan Ranksum tests across handedness within each feedback mode. For left-handed subjects, a test of differences between feedback mode rendered a Chi-square value of 78.19 ($p << 0.05$). For right-handed subjects, a test of differences between feedback mode rendered a Chi-square value of 268.84 ($p << 0.05$). Respectively, for the hover, electrotactile, vibrotactile, and touch conditions, respective Wilcoxon rank-sum test of differences between handedness rendered Z = 3.08 ($p << 0.05$), Z = -6.46 ($p << 0.05$), Z = 5.44 ($p << 0.05$), and Z = -12.14 ($p << 0.05$).

Trends of mean error and indications of *post-hoc* Dunn-Sidak tests' significance are provided in **Figure 5**. For the hover feedback mode, left-handed subjects demonstrate significantly less error than right-handed subjects while all other sensory feedback modes showed significantly more error for left-handed subjects. Also, in left-handed subjects, all sensory feedback modes produced higher mean error than the hover condition. Right-handed subjects produced opposing results: all feedback modes produced less mean error than the hover condition with the touch condition producing significantly less than the sensory substation modes. Thus, sensory substitution slightly improved error for right-handed subjects performing with their dominant hand, but not as much as actual touch. It also suggests that left-handed subjects performing a spatial task with their non-dominant hand are more accurate than right-handed subjects performing with their dominant hand with no feedback. Sensory feedback appears

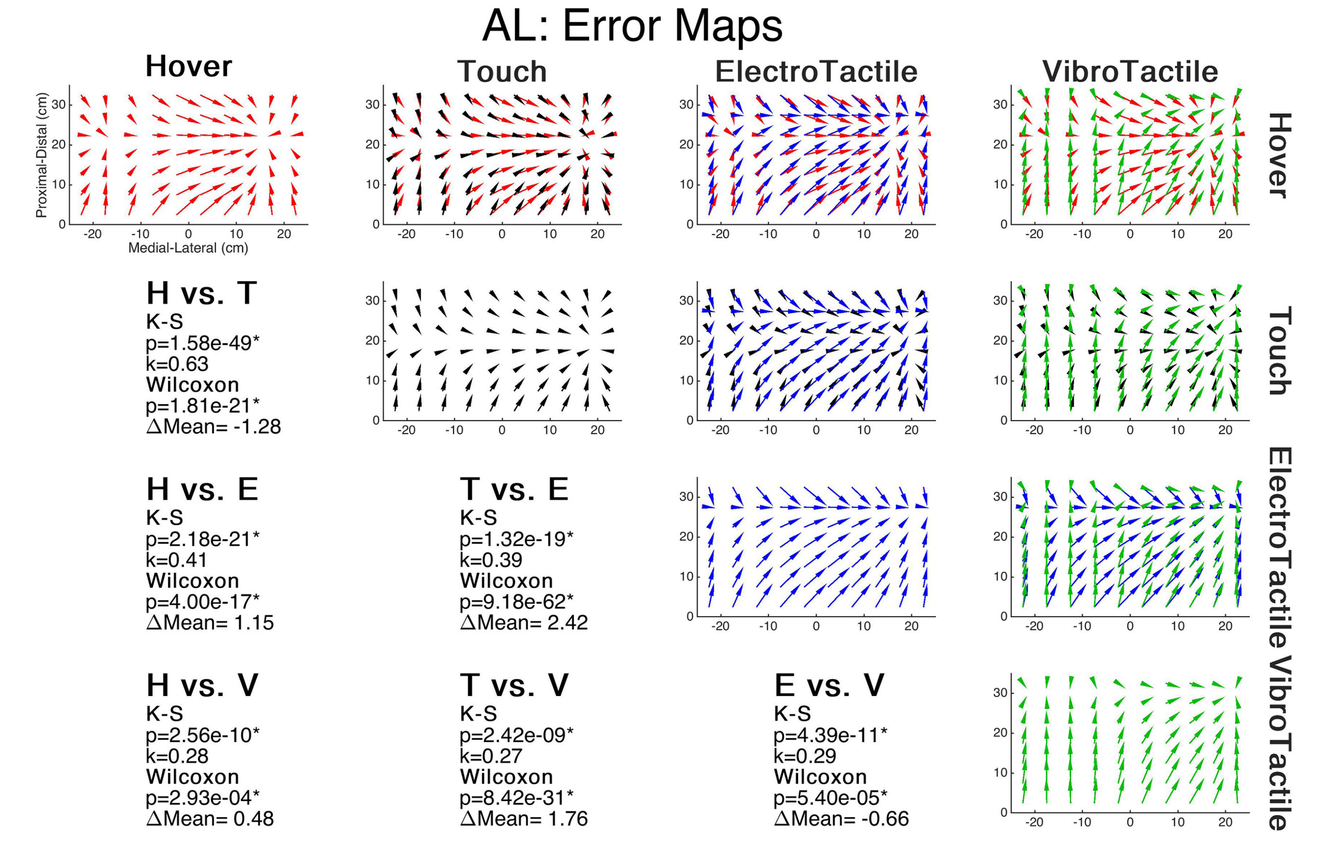

FIGURE 4 | Error maps comparisons. (Diagonal) Error maps of proprioceptive error direction for individual feedback conditions across the workspace for a single subject. (Upper Triangular) Each error map comparison between two feedback modes. (Lower Triangular) Each comparison's statistical results. K-S significance implies the maps possess statistically similar shapes. Wilcoxon rank-sum significance implies a difference in the error magnitudes, where positive ΔMean values indicate increased error in the latter mode.

to disrupt non-dominant hand location estimation strategies while bolstering dominant hand strategies.

DISCUSSION

For 99% of the comparisons of the error map shape, the introduction of artificial or natural tactile information did not provide a disruption, which indicates the synergistic multisensory integration of taction and proprioception and therefore supports the viable use of sensory substitution in terms of limited degradation to proprioceptive processing. Error maps were idiosyncratic and stable across conditions, confirming previous literature (Rincon-Gonzalez et al., 2011, 2012). This demonstrates that any multisensory integration that does occur does not alter the already established underlying mapping between sensory inputs and hand.

For error magnitude, handedness played an interesting role in the results. The task was completed with the right hand, so right-handed subjects performed it with their dominant hand and left-handed subjects performed with their non-dominant hand. Only the right-handed subjects demonstrated a significant reduction in error from the Hover condition to the Touch condition (**Figure 5**, bottom second from left). Left-handed subjects did not exhibit this improvement. However, left-handed subjects performed with less overall error than right-handed subjects (**Figure 5**, top right). This could be consonant with the hypothesis that the dominant hemisphere/limb system is used for trajectory/velocity control and the non-dominant system is used for positional control (Sainburg, 2005). Our experiment is fundamentally positional and it follows that the subjects performing with their non-dominant limb system would demonstrate better positional estimation.

Both vibrotactile and electrotactile sensory substitution modes result in error magnitudes that are statistically different from each other across handedness. For the right-handed subjects, the sensory substitution modes produce error that is significantly lower than the Hover condition and significantly higher than the Touch condition, evidencing multisensory integration but of lower quality than natural touch. However, the left-handed subject's positional error is increased during any sensory feedback condition. In this result, we observe antagonistic multisensory integration hindering the non-dominant positional estimation ability. As non-dominant limb system prioritize positional control, vibrational, or deterministic stimulation patterns may activate proprioceptive

TABLE 2 | Statistical results between conditions.

	Subjects	Hover vs. Touch	Hover vs. Electro	Hover vs. Vibro	Touch vs. Electro	Touch vs. Vibro	Electro vs. Vibro
Right-handed	BL	ΔM = 1.76 cm ($p < 0.05/6$)	ΔM = 0.51 cm ($p < 0.05/6$)	ΔM = 0.99 cm ($p < 0.05/6$)	ΔM = −1.25 cm ($p < 0.05/6$)	ΔM = −0.77 cm ($p < 0.05/6$)	ΔM = 0.48 cm ($p < 0.05/6$)
		k = 0.63 ($p < 0.05/6$)	k = 0.62 ($p < 0.05/6$)	k = 0.47 ($p < 0.05/6$)	k = 0.73 ($p < 0.05/6$)	k = 0.44 ($p < 0.05/6$)	k = 0.39 ($p < 0.05/6$)
	GC	ΔM = −1.6 cm ($p < 0.05/6$)	ΔM = 0.19 cm ($p = 0.33$)	ΔM = −0.45 cm ($p < 0.05/6$)	ΔM = 1.79 cm ($p < 0.05/6$)	ΔM = 1.14 cm ($p < 0.05/6$)	ΔM = −0.64 cm ($p < 0.05/6$)
		k = 0.33 ($p < 0.05/6$)	k = 0.23 ($p < 0.05/6$)	k = 0.34 ($p < 0.05/6$)	k = 0.37 ($p < 0.05/6$)	k = 0.42 ($p < 0.05/6$)	k = 0.34 ($p < 0.05/6$)
	HN	ΔM = −0.69 cm ($p < 0.05/6$)	ΔM = −1.81 cm ($p < 0.05/6$)	ΔM = −0.3 cm ($p = 0.12$)	ΔM = −1.12 cm ($p < 0.05/6$)	ΔM = 0.39 cm ($p = 0.15$)	ΔM = 1.51 cm ($p < 0.05/6$)
		k = 0.53 ($p < 0.05/6$)	k = 0.48 ($p < 0.05/6$)	k = 0.51 ($p < 0.05/6$)	k = 0.62 ($p < 0.05/6$)	k = 0.53 ($p < 0.05/6$)	k = 0.48 ($p < 0.05/6$)
	JR	ΔM = −0.43 cm ($p < 0.05/6$)	ΔM = 1.25 cm ($p < 0.05/6$)	ΔM = 0.1 cm ($p = 0.7$)	ΔM = 1.69 cm ($p < 0.05/6$)	ΔM = 0.53 cm ($p < 0.05/6$)	ΔM = −1.16 cm ($p < 0.05/6$)
		k = 0.2 ($p < 0.05/6$)	k = 0.2 ($p < 0.05/6$)	k = 0.17 ($p < 0.05/6$)	k = 0.25 ($p < 0.05/6$)	k = 0.55 ($p < 0.05/6$)	k = 0.29 ($p < 0.05/6$)
	KR	ΔM = −0.92 cm ($p < 0.05/6$)	ΔM = −1.64 cm ($p < 0.05/6$)	ΔM = −1.14 cm ($p < 0.05/6$)	ΔM = −0.72 cm ($p < 0.05/6$)	ΔM = −0.22 cm ($p = 0.02$)	ΔM = 0.5 cm ($p < 0.05/6$)
		k = 0.49 ($p < 0.05/6$)	k = 0.61 ($p < 0.05/6$)	k = 0.62 ($p < 0.05/6$)	k = 0.56 ($p < 0.05/6$)	k = 0.57 ($p < 0.05/6$)	k = 0.65 ($p < 0.05/6$)
	ME	ΔM = −1.67 cm ($p < 0.05/6$)	ΔM = 0.21 cm ($p < 0.05/6$)	ΔM = −0.75 cm ($p < 0.05/6$)	ΔM = 1.88 cm ($p < 0.05/6$)	ΔM = 0.92 cm ($p < 0.05/6$)	ΔM = −0.96 cm ($p < 0.05/6$)
		k = 0.5 ($p < 0.05/6$)	k = 0.45 ($p < 0.05/6$)	k = 0.34 ($p < 0.05/6$)	k = 0.33 ($p < 0.05/6$)	k = 0.34 ($p < 0.05/6$)	k = 0.38 ($p < 0.05/6$)
	NB	ΔM = 1.2 cm ($p < 0.05/6$)	ΔM = 1.16 cm ($p < 0.05/6$)	ΔM = 0.46 cm ($p = 0.18$)	ΔM = −0.04 cm ($p = 0.73$)	ΔM = −0.74 cm ($p < 0.05/6$)	ΔM = −0.7 cm ($p < 0.05/6$)
		k = 0.5 ($p < 0.05/6$)	k = 0.36 ($p < 0.05/6$)	k = 0.47 ($p < 0.05/6$)	k = 0.46 ($p < 0.05/6$)	k = 0.68 ($p < 0.05/6$)	k = 0.55 ($p < 0.05/6$)
	PH	ΔM = −3.22 cm ($p < 0.05/6$)	ΔM = −1.66 cm ($p < 0.05/6$)	ΔM = −1.59 cm ($p < 0.05/6$)	ΔM = 1.56 cm ($p < 0.05/6$)	ΔM = 1.62 cm ($p < 0.05/6$)	ΔM = 0.07 cm ($p = 0.8$)
		k = 0.47 ($p < 0.05/6$)	k = 0.66 ($p < 0.05/6$)	k = 0.58 ($p < 0.05/6$)	k = 0.43 ($p < 0.05/6$)	k = 0.37 ($p < 0.05/6$)	k = 0.77 ($p < 0.05/6$)
	RC	ΔM = −1.36 cm ($p < 0.05/6$)	ΔM = −1.21 cm ($p < 0.05/6$)	ΔM = −0.37 cm ($p < 0.05/6$)	ΔM = 0.15 cm ($p < 0.05/6$)	ΔM = 0.99 cm ($p < 0.05/6$)	ΔM = 0.84 cm ($p < 0.05/6$)
		k = 0.24 ($p < 0.05/6$)	k = 0.3 ($p < 0.05/6$)	k = 0.43 ($p < 0.05/6$)	k = 0.16 ($p < 0.05/6$)	k = 0.27 ($p < 0.05/6$)	k = 0.34 ($p < 0.05/6$)
	SRD	ΔM = 0.39 cm ($p < 0.05/6$)	ΔM = −0.2 cm ($p < 0.05/6$)	ΔM = 0.26 cm ($p = 0.04$)	ΔM = −0.59 cm ($p < 0.05/6$)	ΔM = −0.13 cm ($p < 0.05/6$)	ΔM = 0.46 cm ($p < 0.05/6$)
		k = 0.33 ($p < 0.05/6$)	k = 0.28 ($p < 0.05/6$)	k = 0.23 ($p < 0.05/6$)	k = 0.22 ($p < 0.05/6$)	k = 0.19 ($p < 0.05/6$)	k = 0.26 ($p < 0.05/6$)
Left-handed	JLR	ΔM = 0.23 cm ($p = 0.04$)	ΔM = −1.04 cm ($p < 0.05/6$)	ΔM = −1.06 cm ($p < 0.05/6$)	ΔM = −1.27 cm ($p < 0.05/6$)	ΔM = −1.28 cm ($p < 0.05/6$)	ΔM = −0.02 cm ($p = 0.9$)
		k = 0.64 ($p < 0.05/6$)	k = 0.46 ($p < 0.05/6$)	k = 0.39 ($p < 0.05/6$)	k = 0.62 ($p < 0.05/6$)	k = 0.5 ($p < 0.05/6$)	k = 0.56 ($p < 0.05/6$)
	NW	ΔM = 0.07 cm ($p = 0.01$)	ΔM = −0.54 cm ($p < 0.05/6$)	ΔM = 0.13 cm ($p = 0.14$)	ΔM = −0.61 cm ($p < 0.05/6$)	ΔM = 0.07 cm ($p = 0.41$)	ΔM = 0.68 cm ($p < 0.05/6$)
		k = 0.38 ($p < 0.05/6$)	k = 0.4 ($p < 0.05/6$)	k = 0.36 ($p < 0.05/6$)	k = 0.6 ($p < 0.05/6$)	k = 0.77 ($p < 0.05/6$)	k = 0.5 ($p < 0.05/6$)
	PKP	ΔM = −0.3 cm ($p < 0.05/6$)	ΔM = −0.86 cm ($p < 0.05/6$)	ΔM = −1.07 cm ($p < 0.05/6$)	ΔM = −0.55 cm ($p < 0.05/6$)	ΔM = −0.77 cm ($p < 0.05/6$)	ΔM = −0.21 cm ($p = 0.05$)
		k = 0.36 ($p < 0.05/6$)	k = 0.49 ($p < 0.05/6$)	k = 0.42 ($p < 0.05/6$)	k = 0.42 ($p < 0.05/6$)	k = 0.45 ($p < 0.05/6$)	k = 0.47 ($p < 0.05/6$)

(Continued)

TABLE 2 | Continued

Subjects	Hover vs. Touch	Hover vs. Electro	Hover vs. Vibro	Touch vs. Electro	Touch vs. Vibro	Electro vs. Vibro
WJ	$\Delta M = 1.25$ cm ($p < 0.05/6$)	$\Delta M = 0.14$ cm ($p = 0.06$)	$\Delta M = 1.35$ cm ($p < 0.05/6$)	$\Delta M = -1.12$ cm ($p < 0.05/6$)	$\Delta M = 0.1$ cm ($p = 0.53$)	$\Delta M = 1.22$ cm ($p < 0.05/6$)
	$k = 0.33$ ($p < 0.05/6$)	$k = 0.33$ ($p < 0.05/6$)	$k = 0.38$ ($p < 0.05/6$)	$k = 0.44$ ($p < 0.05/6$)	$k = 0.64$ ($p < 0.05/6$)	$k = 0.43$ ($p < 0.05/6$)
GL	$\Delta M = 1.35$ cm ($p < 0.05/6$)	$\Delta M = 2.02$ cm ($p < 0.05/6$)	$\Delta M = 2.68$ cm ($p < 0.05/6$)	$\Delta M = 0.67$ cm ($p < 0.05/6$)	$\Delta M = 1.32$ cm ($p < 0.05/6$)	$\Delta M = 0.66$ cm ($p = 0.02$)
	$k = 0.58$ ($p < 0.05/6$)	$k = 0.56$ ($p < 0.05/6$)	$k = 0.41$ ($p < 0.05/6$)	$k = 0.68$ ($p < 0.05/6$)	$k = 0.49$ ($p < 0.05/6$)	$k = 0.52$ ($p < 0.05/6$)
AI	$\Delta M = 1.71$ cm ($p < 0.05/6$)	$\Delta M = 0.56$ cm ($p < 0.05/6$)	$\Delta M = 0.71$ cm ($p < 0.05/6$)	$\Delta M = -1.16$ cm ($p < 0.05/6$)	$\Delta M = -1.01$ cm ($p < 0.05/6$)	$\Delta M = 0.15$ cm ($p = 0.01$)
	$k = 0.35$ ($p < 0.05/6$)	$k = 0.3$ ($p < 0.05/6$)	$k = 0.39$ ($p < 0.05/6$)	$k = 0.34$ ($p < 0.05/6$)	$k = 0.28$ ($p < 0.05/6$)	$k = 0.47$ ($p < 0.05/6$)
AL	$\Delta M = -1.28$ cm ($p < 0.05/6$)	$\Delta M = 1.15$ cm ($p < 0.05/6$)	$\Delta M = 0.48$ cm ($p < 0.05/6$)	$\Delta M = 2.42$ cm ($p < 0.05/6$)	$\Delta M = 1.76$ cm ($p < 0.05/6$)	$\Delta M = -0.66$ cm ($p < 0.05/6$)
	$k = 0.63$ ($p < 0.05/6$)	$k = 0.42$ ($p < 0.05/6$)	$k = 0.57$ ($p < 0.05/6$)	$k = 0.31$ ($p < 0.05/6$)	$k = 0.5$ ($p < 0.05/6$)	$k = 0.43$ ($p < 0.05/6$)
AT	$\Delta M = -0.07$ cm ($p = 0.11$)	$\Delta M = 1.18$ cm ($p < 0.05/6$)	$\Delta M = -0.54$ cm ($p < 0.05/6$)	$\Delta M = 1.26$ cm ($p < 0.05/6$)	$\Delta M = -0.47$ cm ($p < 0.05/6$)	$\Delta M = -1.72$ cm ($p < 0.05/6$)
	$k = 0.23$ ($p < 0.05/6$)	$k = 0.12$ ($p = 0.04$)	$k = 0.09$ ($p = 0.17$)	$k = 0.2$ ($p < 0.05/6$)	$k = 0.36$ ($p < 0.05/6$)	$k = 0.18$ ($p < 0.05/6$)
CH	$\Delta M = -1.33$ cm ($p < 0.05/6$)	$\Delta M = 0.39$ cm ($p = 0.07$)	$\Delta M = 0.16$ cm ($p = 0.29$)	$\Delta M = 1.73$ cm ($p < 0.05/6$)	$\Delta M = 1.49$ cm ($p < 0.05/6$)	$\Delta M = -0.23$ cm ($p = 0.74$)
	$k = 0.5$ ($p < 0.05/6$)	$k = 0.25$ ($p < 0.05/6$)	$k = 0.4$ ($p < 0.05/6$)	$k = 0.3$ ($p < 0.05/6$)	$k = 0.42$ ($p < 0.05/6$)	$k = 0.41$ ($p < 0.05/6$)
PVG	$\Delta M = 0.54$ cm ($p < 0.05/6$)	$\Delta M = 0.61$ cm ($p < 0.05/6$)	$\Delta M = 1.01$ cm ($p < 0.05/6$)	$\Delta M = 0.06$ cm ($p = 0.52$)	$\Delta M = 0.46$ cm ($p = 0.01$)	$\Delta M = 0.4$ cm ($p = 0.01$)
	$k = 0.63$ ($p < 0.05/6$)	$k = 0.42$ ($p < 0.05/6$)	$k = 0.57$ ($p < 0.05/6$)	$k = 0.31$ ($p < 0.05/6$)	$k = 0.5$ ($p < 0.05/6$)	$k = 0.43$ ($p < 0.05/6$)

Difference in means and Wilcoxon rank-sum tests significance in parentheses on top. K-S test k value and significance on bottom. A negative ΔM value implies the latter has decreased error. Any non-significant comparisons are indicated in gray. Used alpha of 0.05/6 for multiple comparison corrections.

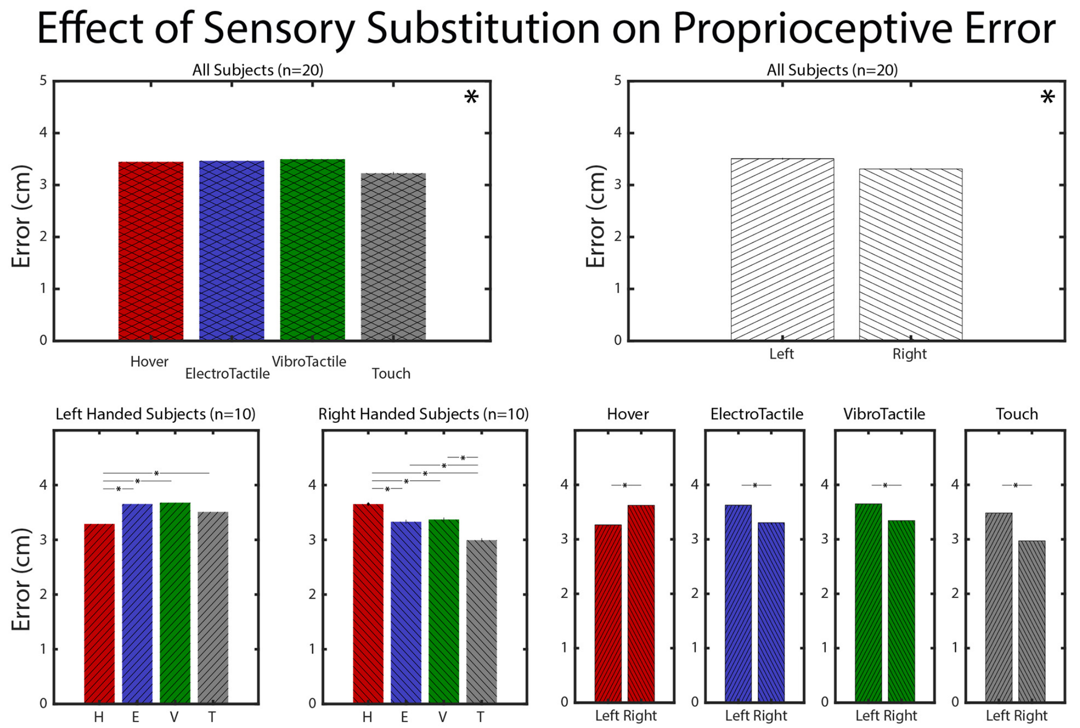

FIGURE 5 | Mean error comparisons. Proprioceptive estimation error separated by handedness and averaged across all subjects or subjects by handedness (* indicates significance for the appropriate test).

receptors via tissue transduction and confound the system in a way for which the dominant limb system can account. In this vein, successfully multisensory integration of taction and proprioception appears to rely on the interaction of task context (positional vs. velocity) and taction mode (natural vs. artificial). Investigation into this relationship with Semmes-Weinstein filaments is immediately prudent, to utilize tactile stimulation that can be perceived with minimal joint or proprioceptive activation.

While error maps are stable across all investigated feedback modalities, sensory substitution fails to achieve the same multisensory integration as normal touch: error is not reduced to the same level for dominant hand cases and error is increased for non-dominant hand cases. The overall limitation is likely due to familiarity with the stimulation percept and lack of training to use it practically. The handedness discrepancy is likely from existing properties of the proprioceptive system. We know that tactile sensory substitution can help with proprioceptive movements (Bark et al., 2015) but it fails to replace proprioceptive positional estimation (Hasson and Manczurowsky, 2015). As the non-dominant hand prioritizes positional control, the unfamiliarity of the sensation appears to have a more profound and deleterious effect on the subjects' ability to estimate position. Finally, our results show that the effect of tactile stimulation on proprioceptive mapping is not simply dependent on unstructured tactile information from the fingertip: actual contact with a stable substrate seems to provide the best cue to enhancing proprioceptive estimation.

CONCLUSION

In this study, we examined the role of multiple feedback modalities on multisensory integration of tactile and proprioceptive information. By reconstructing the end-point estimation error across a two-dimensional workspace, we were able to statistically compare error magnitude and error map shape. We were also able to investigate the role handedness had on the multisensory integration of the multiple feedback modes, which provided an unexpected insight into proprioceptive prioritization. Vibrotactile and electrotactile sensory substitution does not disrupt estimation strategies across the workspace. For the dominant hand, this feedback does provide significant improvements in positional estimation error, but not to levels seen with multisensory integration of normal touch. Non-dominant hand positional error was significantly exacerbated even though normal touch beneficially integrates.

Successful multisensory integration of touch and proprioception appears to be a function of taction mode. It is unknown if the limitation is perceptual due to non-familiar or non-practical sensations, neurophysiological due to excessive mechanoreceptor/nerve recruitment from mechanical or electrical transduction, or if normal multisensory integration requires the utilization of arm and digit joint forces. These results also suggests that sensory substitution may hinder positional ability in practical application, such as prosthetics, during non-dominant tasks even if it does not hinder overall estimation strategy. If prostheses or other haptic environments integrate sensory feedback, it is imperative that such feedback not produce a worse result than the absence of any feedback. This should be addressed in the design, assignment, and training of feedback so that the users are aware of the limitation.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Arizona State University Institutional Review Board. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

All authors contributed to experimental design, experimental execution, data analysis, and drafting the manuscript.

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