WHEN THE BODY FEELS LIKE MINE: CONSTRUCTING AND DECONSTRUCTING THE SENSE OF BODY OWNERSHIP THROUGH THE LIFESPAN

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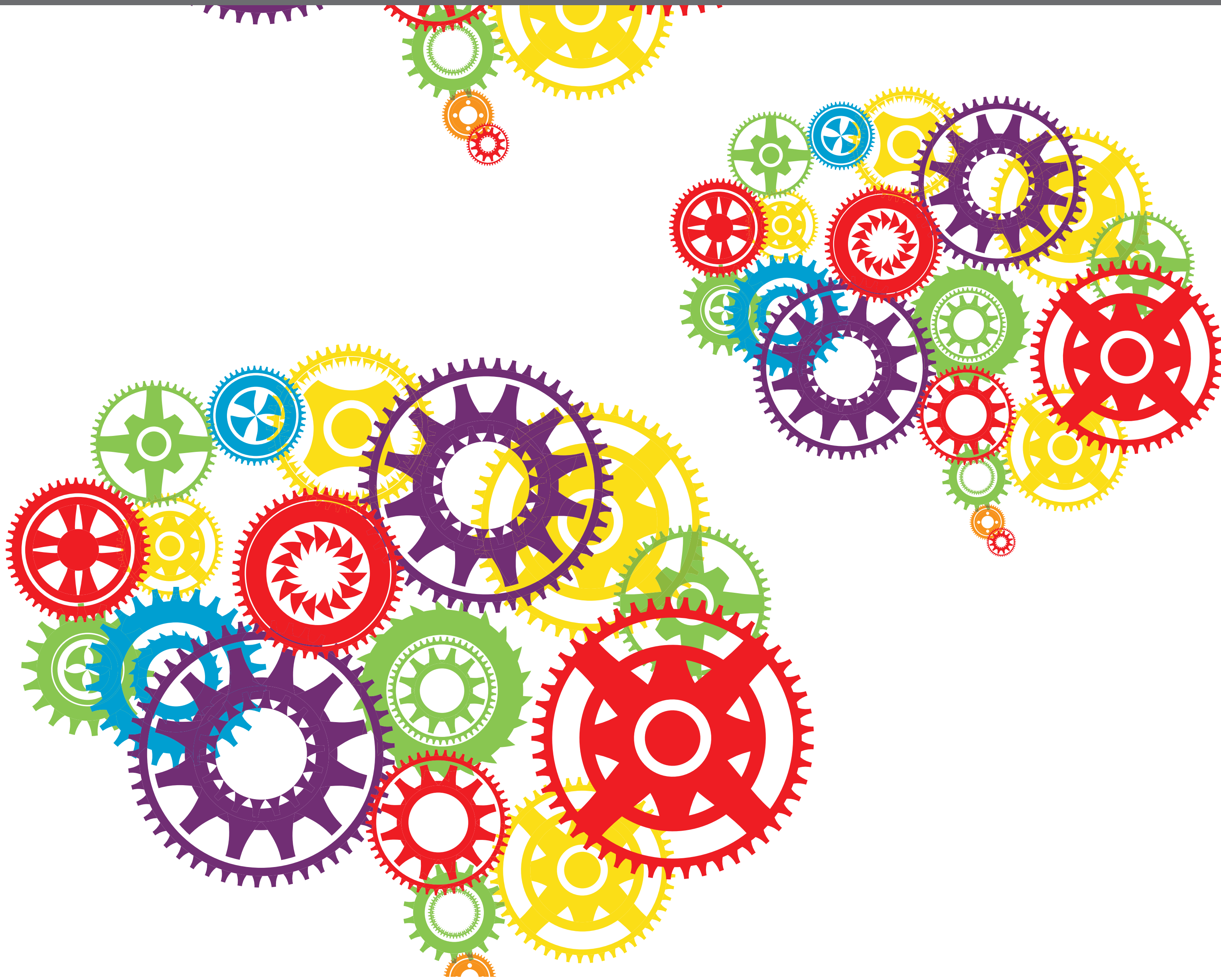

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WHEN THE BODY FEELS LIKE MINE: CONSTRUCTING AND DECONSTRUCTING THE SENSE OF BODY OWNERSHIP THROUGH THE LIFESPAN

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EDITORIAL
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Editorial: When the Body Feels Like Mine: Constructing and Deconstructing the Sense of Body Ownership Through the Lifespan

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Editorial on the Research Topic

When the Body Feels Like Mine: Constructing and Deconstructing the Sense of Body Ownership Through the Lifespan

Bodily self-awareness is a multidimensional construct defined as the feeling that conscious experiences are bound to the self as a unitary entity (Berlucchi and Aglioti, 2010; Blanke et al., 2015; Salvato et al., 2020). A fundamental aspect of bodily self-awareness is the sense of body ownership, described as the awareness of one's body as belonging to oneself and the feeling that a given body part belongs to one's own body (Tsakiris, 2010; de Vignemont, 2011). Even though we all have a body and we usually do not question its very existence, the way in which we build and maintain a coherent sense of body ownership is not fully understood. The last two decades have seen an exponential increase in trying to elucidate its underpinning mechanisms and important studies have significantly advanced the field (see Ehrsson, 2020 for a review). For example, it has been proposed that the integration of exteroceptive, interoceptive, and proprioceptive signals may play a fundamental role in giving rise to the feeling that our body belongs to ourselves (e.g., Park et al., 2016; Crucianelli et al., 2018; Salvato et al., 2020). Nevertheless, several questions remain to be answered. The present Research Topic aimed to better characterize how a coherent sense of body ownership emerges, changes, it is maintained and/or updated throughout the life span and in the case of disorders of body ownership. As such, our Research Topic provides a state-of-the-art overview of the current investigations and topics on the sense of body ownership. It combines interdisciplinary findings from experimental and developmental psychology, neuropsychology, neurology, and cognitive neuroscience, and covers the relation between the sense of body ownership, body awareness, and various cognitive functions in the motor and social domain. We welcomed submissions on the topic ranging from birth to aging, in healthy and pathological conditions, from behavioral, neurophysiological, neuroimaging, and philosophical points of view, as well as more recent virtual reality and technology-oriented research on body ownership.

NOVEL EXPERIMENTAL SET-UPS TO INVESTIGATE BODY OWNERSHIP

In healthy populations, body ownership is mainly assessed and manipulated by means of multisensory illusion paradigms (mainly visual-tactile), which allow to temporary alter the feeling of ownership over a body part or the entire body (e.g., *Rubber Hand Illusion,* Botvinick and Cohen, 1998; Tsakiris and Haggard, 2005, *Full Body Illusion,* Ehrsson, 2007; Lenggenhager et al., 2007, and its *virtual reality* equivalent, Slater, 2009). In this context, a few articles in the present collection used modified versions of these classical bodily illusion methods, which we believe could path the way for future studies aiming at further characterizing body ownership. de Silva et al. provided new evidence on the efficacy of a modified version of the Rubber Hand Illusion (RHI) paradigm (Botvinick and Cohen, 1998), namely the Parasagittal-Mirror-RHI paradigm. This proof-of-concept study combines the use of a parasagittal mirror and synchronous stroking of both a prosthetic hand (viewed in the mirror) and the participant's hand, with a manipulation of the distance between the hands. de Silva et al. showed that the Parasagittal-Mirror-RHI was successful in inducing the illusion of body ownership and the strength of the experience was closely linked to the illusory distance between the rubber hand (reflected in the mirror) and the participant's own hand rather than the actual distance between the two. The result of this study provides important insight into the role of spatial distance of the hands in the way we recognize a body part as our own.

The work by Crivelli et al. offered another novel way to investigate body part ownership by means of the Implicit Association Test (IAT, Greenwald et al., 2003). Participants were asked to complete an IAT of the dominant (vs. non-dominant) hand to the self. There was a linear correlation between the strength of the implicit association of the dominant hand with the self, and such effect increased as a function of hand preference. By implication, this study suggests that the illusion of body ownership might be more effective if applied on the non-dominant hand, toward which healthy individuals have a weaker feeling of ownership. Indeed, their results provided insight into the magnitude of the sense of ownership for one of the two hands, which varies according to the use that the subject makes of the hand in everyday life. The stronger ownership toward the dominant hand could be linked to the fact that such hand plays a more crucial role in motor behavior, and it might interact more extensively with the environment.

BEHAVIORAL, COGNITIVE, AND AFFECTIVE CONSEQUENCES OF BODY OWNERSHIP'S MANIPULATIONS

A growing body of evidence has shown that manipulating the sense of body ownership by means of visuo-tactile paradigms can also induce specific behavioral and physiological changes, such as thermoregulatory and somatosensory processes (e.g., Salomon et al., 2013; Romano et al., 2014; Ricci et al., 2019; Crivelli et al., 2021). Along this line, Ricci et al. showed that transient manipulations of the sense of ownership may alter tactile awareness. During the experiment, healthy participants had to complete a Tactile Quadrant Stimulation (TQS) test while they were exposed to the mirror box, whereby their right hand was reflected and the left one was hidden from view. Results showed that participants reported phantom touch sensation on the hidden left hand, an effect that had previously been observed in patients following stroke. Thus, this study further corroborates the idea that the sense of body ownership can modulate tactile perception, and it provides novel knowledge on the uni- and bilateral representations of touch.

Another study pushed this idea a step further by showing that behavioral changes following manipulations of body ownership might be more profound than previously thought. Clausen et al. demonstrated how body ownership manipulation using an illusory auditive paradigm (*Footsteps Illusion*, Tajadura-Jiménez et al., 2015) may give rise to changes in implicit self-gender associations and explicit self-gender group identification. Across two experiments, Clausen et al. manipulated participants' footstep sounds in real time to resemble more feminine or masculine footsteps during walking. They tested how these sounds changed participants' self-concept and the relation to social groups for cisgender females and cisgender males. Their results showed that females felt more feminine and closer to the group of women after walking with feminine sounding footsteps. Similarly, males felt more feminine after walking with feminine sounding footsteps and associated themselves relatively stronger with the "female" attribute. Thus, auditory-induced body illusions can temporally alter gender identity as well as self-concept and social group identification.

In another study, Burin and Kawashima conducted a randomized controlled trial exposing healthy older participants to illusory sense of body ownership and agency over a moving virtual body. Participants completed two virtual reality high-intensity intermittent exercise sessions, either in a first- or third-person perspective, and they completed cognitive tasks before, in between, and after these two experimental sessions. The results showed that participants observing a virtual body in a first-person perspective performing 20 min of virtual high-intensity intermittent exercise improved their executive functions, and an increase in prefrontal cortex activity was observed following the intervention, as compared to participants performing the sessions in a third-person perspective. As such, this study corroborates the impact of the virtual full-body illusion and its physiological consequences on the elderly, and they further suggest that a longer exposure to those illusions might be necessary to observe significant improvement in cognitive performance.

DEVELOPMENTAL STUDIES ON BODY OWNERSHIP AND MULTISENSORY INTEGRATION

The ability to recognize our body as our own arises from complex multisensory integration processes (Blanke, 2012; Ehrsson, 2020), which have been shown to emerge in the early stages of human development (e.g., Filippetti et al., 2013). Along this line, Ratcliffe et al. investigated the relative contributions of visual and proprioceptive inputs on the development of body localization in primary school-aged children. A mediated reality device called MIRAGE was used to explore how the brain weighs visual and proprioceptive information in a hand localization task, whereby children were asked to estimate the position of their index finger after viewing congruent or incongruent visuo-proprioceptive information regarding hand position. Younger children were more accurate in the hand localization task as compared to older children, suggesting that they relied more on proprioceptive inputs and less on visual information. Thus, the results demonstrate that the integration between different sensory inputs starts early in infancy and it optimizes through development, with the bias toward visual information increasing with age.

The contribution to the present Research Topic by Della Longa et al. specifically focused on the difference between pre-term and full-term children in the development of body ownership. The authors investigated whether the deprivation of parent-infant bodily contact in the neonatal period, such as in the case of preterm birth, bears long-term negative consequences for the development of bodily self-awareness. Children completed a RHI, while having EEG continuously recorded, and they performed a pre and post pointing task as well as filling in a questionnaire. Della Longa et al. showed that preterm children present less susceptibility to the RHI, as compared to full-term children, suggesting an atypical integration of multisensory bodily signals. Thus, this study provides an important insight into our understanding of the emergence of bodily self-awareness in pre-term and full-term children, and it corroborates the idea that tactile contact in the first stages of life might play a crucial contribution to the development of a healthy sense of self (e.g., Cascio et al., 2019; Crucianelli and Filippetti, 2020).

BODY OWNERSHIP AND THE MOTOR SYSTEM

Previous research indicated that the sense of body ownership is also linked to the motor aspect of the self (for a review, see Seghezzi et al., 2019), as highlighted in the review paper by Liesner et al. The Authors integrated evidence from perception-action interactions, multisensory integration, and developmental psychology to discuss how the sense of body ownership is flexibly updated throughout lifespan. Specifically, a description and mechanistic explanation of "active ownership" is provided, i.e., how humans construct a sense of ownership over the effects of their actions. Liesner et al. suggested that the overlap (or conflict) of interoceptive and exteroceptive sensations is the key factor shaping both active and passive body ownership, and they call for future, more integrative research, encompassing the fields of ideomotor action control, perception and action, and the crucial importance of comparing children in different age groups.

Yizhar et al. used a virtual reality environment to investigate the relationship between sensory and motor cues within a RHI paradigm. Across two experiments, participants viewed their hands switched and mirrored, so that when they moved their hand, they would see the incongruent virtual hand moving. Despite this, participants reported strong body ownership sensation over the virtual hands and the perceived level of agency over hand movement mediated the anatomical congruency effect. Yizhar et al. demonstrated that goal direct agency override plausibility constraints during the RHI paradigm, thus challenging early findings on the importance of the canonical position of the rubber hand during the visual-tactile illusion.

De Coster et al. offers a yet new perspective on the relationship between body ownership and action. This study investigated own-perceived body matching in a more ecological manner as compared to previous studies, namely by focusing on body movement dynamics and clothing cues. Participants were asked to match their own body with a 3D-generated avatar, which was manipulated based on movement dynamics, body size, and fitted clothes. De Coster et al. showed that the accuracy in self-recognition is not significantly influenced by movement dynamics nor fitted clothes. However, confidence about dress fit was higher for dynamic avatars. These findings provide insight for research exploring (own-) body perception and bodily self-awareness and can have implications for future clinical studies with populations characterized by disorders of body representation, such as anorexia nervosa and body dysmorphic disorder.

DISORDERS OF BODY OWNERSHIP

We believe that our Research Topic provides some insight into the underlying mechanisms of disorders of body ownership, which may be present also in the absence of a brain lesion. This is the case of Body Integrity Dysphoria (BID), a poorly understood neuropsychiatric disease (Sedda, 2011; Brugger et al., 2013), associated with a persistent urge to amputate one of their healthy limbs. Individuals with BID manifest a puzzling behavioral dissociation. They describe a profound feeling of limb disownership, while they rationally acknowledge the physical presence and biological ownership of body parts (Romano et al., 2015; Saetta et al., 2020; Gandola et al., 2021; Salvato et al., 2022). Addressing this topic, Chakraborty et al. reviewed and discussed current treatment options available for BID, which have proven largely ineffective. Thus, they suggested a novel approach to target and potentially treat people with BID using Brain-Computer Interface (BCI) and neurofeedback. In their mini-review, Chakraborty et al. provided some practical approaches to implicitly promote re-ownership of the limb and engender more positive associations to body representation using BCI, which can target altered patters of brain activity without impairing the anatomical structure and functionality of the individual. This paper is particularly timely in highlighting the urgent need for more effective form of treatment for BID, a clinical condition that can lead to significant distress and life-long suffering.

CONCLUSION AND CLOSING REMARKS

In conclusion, the evidence produced by this collection of papers provides new knowledge on the way we build, update, and maintain a coherent sense of ownership throughout the lifespan, which is a crucial aspect of our physical and mental wellbeing. As such, it is now clear that to achieve a better understanding of the complexity of the topic of body ownership, we must embrace a multidisciplinary approach. All the contributions to the present Research Topic touched upon different and equally important topics, ranging from perception and action (e.g., touch, sense of agency, and movement dynamics), social cognition (e.g., gender identity and group identification), to developmental and aging psychology, using behavioral, virtual, and neuroimaging methods.

The ample breadth of the contributions allowed this issue to target the multiple dimensions of body ownership. On the one hand, some studies have investigated the factors that contribute to the feeling of recognizing our body as our own; on the other hand, other studies have discussed the behavioral, cognitive, and social aspects that are influenced when manipulating the sense of body ownership. Taken together, we believe that the work here presented in the form of both empirical papers and reviews significantly advances the field of research in body ownership and can stimulate further debate and future research to achieve an even better understanding of how our brain constructs the sense of self and makes sense of the reality around us.

Moving forward, research priorities in this fascinating field are numerous and include, for example, considering a method to assess the sense of body ownership in healthy participants at baseline, without inducing body ownership illusions. Another critical issue to address is understanding the role of different physiological components in the emergence of the sense of ownership, such as respiration, heartbeat, and thermoregulation. Finally, we also believe that this field of research should prioritize the study of pathological ownership in brain-damaged patients; such neuropsychological approach will allow us to build and eventually test theoretical models and infer neuroscientific principles on the construction of the sense of the self. This is important also for developing novel treatments for disorders of body representation, which could apply some of the methods here discussed.

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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Repeated Exposure to Illusory Sense of Body Ownership and Agency Over a Moving Virtual Body Improves Executive Functioning and Increases Prefrontal Cortex Activity in the Elderly

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We previously showed that the illusory sense of ownership and agency over a moving body in immersive virtual reality (displayed in a first-person perspective) can trigger subjective and physiological reactions on the real subject's body and, therefore, an acute improvement of cognitive functions after a single session of high-intensity intermittent exercise performed exclusively by one's own virtual body, similar to what happens when we actually do physical activity. As well as confirming previous results, here, we aimed at finding in the elderly an increased improvement after a longer virtual training with similar characteristics. Forty-two healthy older subjects (28 females, average age = 71.71 years) completed a parallel-group randomized controlled trial (RCT; UMIN000039843, umin.ac.jp) including an adapted version of the virtual training previously used: while sitting, participants observed the virtual body in a first-person perspective (1PP) or a third-person perspective (3PP) performing 20 min of virtual high-intensity intermittent exercise (vHIE; the avatar switched between fast and slow walking every 2 min). This was repeated twice a week for 6 weeks. During the vHIE, we measured the heart rate and administered questionnaires to evaluate illusory body ownership and agency. Before the beginning of the intervention, immediately after the first session of vHIE, and at the end of the entire intervention, we evaluated the cognitive performance at the Stroop task with online recording of the hemodynamic activity over the left dorsolateral prefrontal cortex. While we confirm previous results regarding the virtual illusion and its physiological effects, we did not find significant cognitive or neural improvement immediately after the first vHIE session. As a novelty, in the 1PP group only, we detected a significant decrease in the response time of the Stroop task in the post-intervention assessment compared to its baseline; coherently, we found an increased activation on left dorsolateral prefrontal cortex (lDLPFC) after the entire intervention. While the current results strengthen the impact of the virtual full-body illusion and its physiological consequences on the elderly as well, they might have stronger and more established body representations. Perhaps, a longer and increased exposure to those illusions is necessary to initiate the cascade of events that culminates to an improved cognitive performance.

Keywords: immersive virtual reality, sense of body ownership, sense of agency, executive functions, Stroop task, functional near-infrared spectroscopy, dorsolateral prefrontal cortex, virtual intervention

INTRODUCTION

The relationship between the sense of body ownership (i.e., the conscious subjective feeling of owning one's own body) (Gallagher, 2000) and the sense of agency (i.e., the experience of controlling one's motor acts and, through them, the external events) (Haggard, 2017) is intricate. Despite several theories and experimental efforts having been attempted over time, they can be organized into three main factions: (1) those who support the "additive model," where agency entails the sense of body ownership, so they are strongly connected, but the sense of agency includes additional components (Tsakiris et al., 2006; Longo and Haggard, 2009; Kalckert and Ehrsson, 2014; Ma and Hommel, 2015; Pia et al., 2016); (2) those who, in contrast, support the "independence model," where body ownership and agency are separate experiences with different neural basis (Farrer and Frith, 2002; Schwartz et al., 2005; Tsakiris et al., 2010); and (3) the more recent supporters of the "interactive model," where body ownership and agency are partially connected at the level of sensory-related signals and shared neural network, but they can be treated as separate experiences at the level of additional specific processes (Pyasik et al., 2018; Seghezzi et al., 2019). Even comparing studies that involve the same type of measurement, there are frequently controversial results (see, for example, Tsakiris et al., 2010 and Seghezzi et al., 2019 for brain imaging data or Kalckert and Ehrsson, 2012 and Dummer et al., 2009 for behavioral data).

However, in most daily life activities, we do not perceive any discrepancies or mismatches. On the other hand, experimental situations have demonstrated how these two components can be deconstructed (also independently of each other) and reconstructed over an entity different from the actual own body by exploiting the same multisensory integration process that leads to the assimilation of the minimal self (Tsakiris, 2010): in the rubber hand illusion (RHI) (Botvinick and Cohen, 1998), the sense of body ownership is deconstructed (Moseley et al., 2008, 2012; Burin et al., 2017; Pfister et al., 2020) and reconstructed over a prosthetic hand that is simultaneously touched (and seen) with the real subject's hand (not seen) by integrating body-related afferent signals (Pyasik et al., 2018, 2019).

Despite the RHI procedure having been revised in several different ways (Ehrsson, 2007; Kalckert and Ehrsson, 2012; Burin et al., 2017), it has been outdated by its full-body version in immersive virtual reality (IVR), where the entire body can be displayed and the illusion can be triggered by the sole visual stimulation (Maselli and Slater, 2013; Kokkinara et al., 2016; Slater, 2018; Burin et al., 2019a): through an IVR visor, the virtual body (also called avatar) can be entirely displayed and such environment allows the control of several variables (somatic features of the avatar, spatial location, movement control, etc.) (Kilteni et al., 2012; Banakou et al., 2013, 2016; Peck et al., 2013). Crucially, the virtual body can be shown in a first-person perspective, being spatially coincident with the real one, overlapping it (if the person wearing the visor looks down to where his/her body is supposed to be, he/she sees the virtual body) and immediately creating the illusion of ownership, without the necessity of additional stimulations (Kokkinara et al., 2016; Burin et al., 2019a; Neyret et al., 2020). Different with respect to the RHI, the avatar in IVR can replicate in real-time complex movements through a tracking system (Banakou and Slater, 2014). However, it can also reproduce animated movements (such as walking or running) (Kokkinara et al., 2016), which can be attributed to one's motor intention, possibly thanks to *a posteriori* reconstruction of the sense of agency (meaning "this virtual body is mine–the virtual body is moving–those movements are mine") (Burin et al., 2019a).

Recent studies have shown that the illusory feeling of ownership and agency over the virtual body creates the necessary conditions to induce effects on the physiological (Martini et al., 2013; Kokkinara et al., 2016; Fossataro et al., 2020) or even components higher than the mere perceptual level, such as social (Peck et al., 2013; Banakou et al., 2018), neural (Seinfeld et al., 2021), or cognitive functions: concerning the latter, in our previous study, we demonstrated on young healthy participants acute improvement of cognitive (executive) functions after a high-intensity intermittent exercise performed exclusively by the considered-as-own virtual body (Burin et al., 2019c, 2020). We argued that, despite the participants being completely still, the feeling of ownership and agency over the virtual body (only if displayed in a first-person perspective) (Kokkinara et al., 2016) induced a cascade of events (from the physiological activation of the heart rate to the increased neural activity over task-related areas), culminating in the improved cognitive performance immediately after the virtual exercise, comparable to what happens after a similar training performed by one's own physical body (Hyodo et al., 2016; Kujach et al., 2017). These results have potential clinical applications, such as improvement of bodily and cognitive functions for those who cannot perform physical activity.

Abbreviations: RHI, rubber hand illusion; IVR, immersive virtual reality; vHIE, virtual high-intensity intermittent exercise; 1PP, first-person perspective; 3PP, third-person perspective; lDLPFC, left dorsolateral prefrontal cortex; HR, heart rate; TDMS, Two-Dimensional Mood Scale; fNIRS, functional near-infrared spectroscopy; O_2Hb, oxygenated hemoglobin; HHb, deoxygenated hemoglobin; RT, response time; ER, error rate.

While the beneficial effects of a physical (or virtual, as in this case) training seem to be more defined in young participants, it is still quite unclear whether the same phenomenon can be observed in the elderly as well for several reasons: from the perspective of multisensory illusions, such as the RHI, the elderly can experience it, subjectively and objectively, but they report different levels of strength of the illusion, probably because of an altered sense of body ownership (Kuehn et al., 2018; Zeller and Hullin, 2018; Riemer et al., 2019). Also, from the behavioral and cortical activation points of view, the differences between young and old people are not entirely clear: a very recent study described that, after mild-intensity physical activity, the young as well as the elderly showed an acute (30 min after the training) improvement of overall inhibitory functions, specifically at the Stroop task, even though they might show some differences (Fujihara et al., 2021). Clearly, whether the same training is also effective if performed virtually (as with young participants) is unknown. Lastly, despite the elderly representing the typical control group for neurological patients (most of them are, in fact, elderly), it is quite complicated for them to perform this kind of high-intensity exercise (it might, for example, enhance the risk of falls).

Consequently, questions remain open: does this virtual exercise benefit a different population, such as the elderly? Are there differences between the acute and long-term impacts of this virtual exercise?

In the present study, in order to answer these questions, we adapted the same virtual training (Burin et al., 2019c, 2020) to test its efficacy on a sample of 42 physically and neurologically healthy elderly (over 60 years old) and to compare the acute and long-term impacts on cognitive, physiological, and neural functions. We conducted a parallel-group randomized controlled trial (RCT) composed of a 6-week (twice a week) IVR intervention, each session including 20 min of virtual high-intensity intermittent exercise (vHIE), alternating the avatar between fast walking and slowly walking every 2 min: while the participants were sitting still, they observed the virtual body, either in a first-person perspective (1PP, the experimental group) or a third-person perspective (3PP, the control group), performing the virtual exercise. We measured the heart rate and administered questionnaires during the virtual training to evaluate the presence of the full-body illusion on a physiological and subjective level. We assessed cognitive performance with the Stroop task [with the online recording of hemodynamic activity over the left dorsolateral prefrontal cortex (lDLPFC) with a functional near-infrared spectroscopy (fNIRS) device] at three time points: before the beginning of the intervention (as baseline assessment), immediately after the first session of virtual training (as short-term assessment), and at the end of the entire intervention (as long-term assessment). We also recorded mood changes (with the Two-Dimensional Mood test) before and after each virtual session.

We hypothesized the following: (1) to replicate previous findings on body ownership/agency and physiological effect in the elderly population—meaning the 1PP group experiences ownership and agency over the avatar, which leads to increased heart rate coherently with the virtual movements, while the 3PP group does not; (2) to replicate previous findings on acute cognitive benefits—meaning the cognitive performance is improved immediately after the first session of virtual training in 1PP combined with an increased activity over the lDLPFC, confirming the acute cognitive benefits of this training also on the elderly; and (3) to find an increased cognitive improvement after the 6-week training in the 1PP group of elderly and not in the 3PP group.

MATERIALS AND METHODS

The protocol of this parallel-group RCT, developed according to CONSORT guidelines (**Figure 1**) and carried out in accordance with the Declaration of Helsinki, was registered to the University Hospital Medical Information Network (UMIN) Clinical Trial Registry (UMIN000039843) on March 18, 2020 and approved by the Ethics Committee of the Tohoku University Graduate School of Medicine (application no. 2019-1-956, final approval April 9, 2020). As soon as the participants visited the laboratory for the first session, in addition to a verbal explanation of the entire experimental procedure, each of them signed the information sheet and the informed consent form before the initiation of the study, agreeing to the conditions of their participation. The raw data that support the findings of this study are available upon request to the corresponding author.

Participants

We recruited the participants through an advertisement published in a local newspaper (Sendai, Japan), so they were Japanese nationals and native Japanese speakers. A total of 54 people were first screened *via* phone call: we excluded under 60 years old, those who had a history of neurological, psychiatric, or motor disorders, and color blindness, and we asked to refrain from participating those who easily experience motion sickness or dizziness. Eight of them did not meet the inclusion criteria or did not accept to the experiment's conditions; therefore, they were excluded. We initially recruited and allocated 46 subjects. While the RCT was ongoing, three participants dropped out for no explicit reason (one of them was in the experimental group) and one dropped out because of motion sickness (this subject was part of the experimental group).

Forty subjects entered and completed the entire RCT and were included in the analysis (28 females; age: average = 71.71 years, SD = 5.71 years; education: average = 13.85 years, SD = 2.24 years). In the Edinburgh Handedness Inventory, they all resulted right handed (average = 96.21, SD = 9.09). In the Physical Activity Questionnaire (IPAQ—Short Form), they all resulted with a score from "moderate" to "high" physical activity level, indicating their general health and engagement in physical activity (the subjects who scored "moderate" were 13 in the 1PP group and 14 in the 3PP group).

After enrollment, the participants were then randomly allocated to one of two study arms: the first-person perspective group (hereinafter, 1PP group), the experimental one, and the third-person perspective group (hereinafter, 3PP group), the control one. Group assignment occurred using a simple randomization 1 (experimental):1 (control) ratio, with the

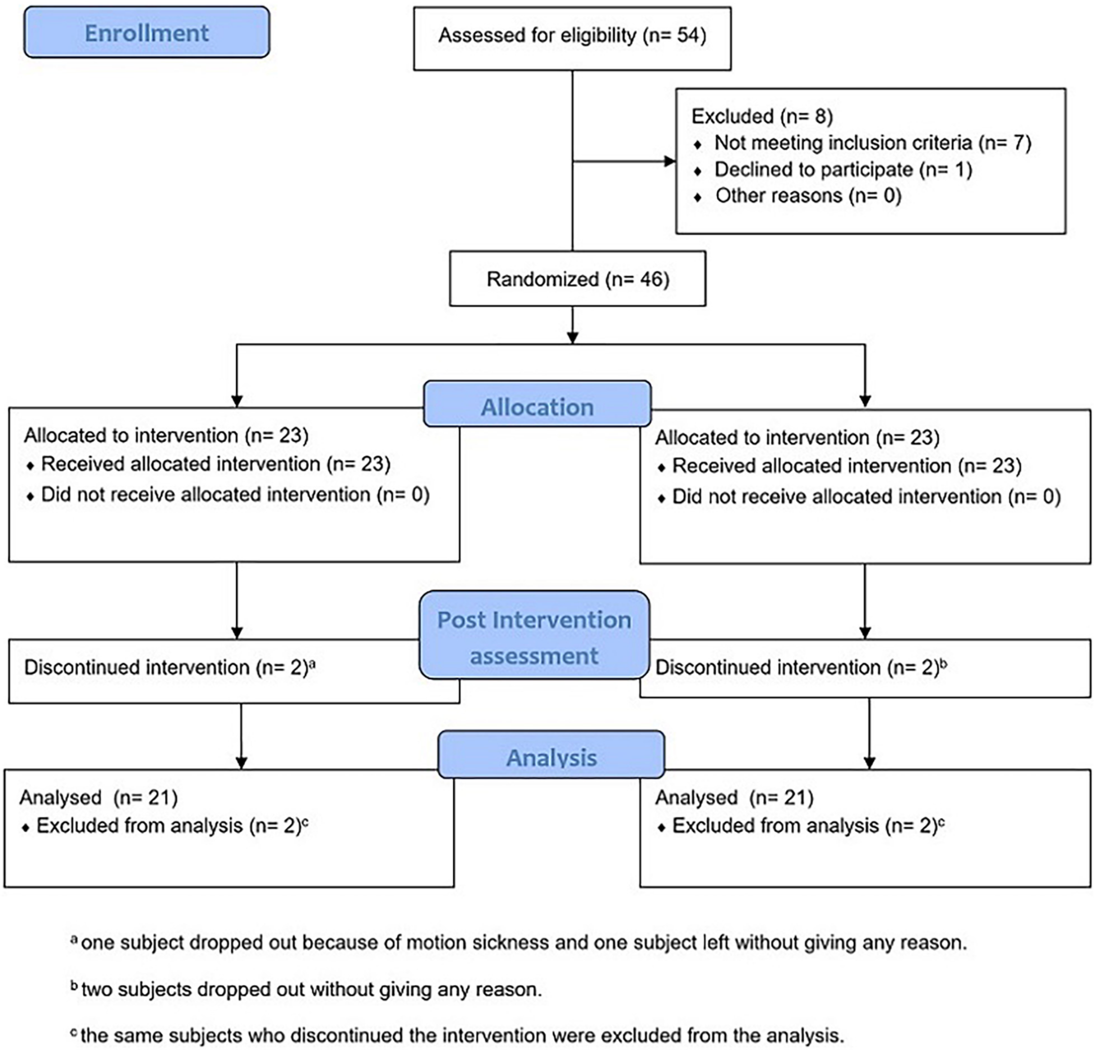

FIGURE 1 | CONSORT flow diagram of the present registered clinical trial (UMIN000039843).

allocation of participants to each arm based on order of entry into the study (Summers et al., 2018).

The demographic composition of the groups is as follow: in the 1PP group, there are 21 subjects (11 females; age: average = 70.57 years, SD = 6.51 years; education: average = 14.25, SD = 2.46); in the 3PP group, there are also 21 subjects (17 females; age: average = 72.86 years, SD = 4.65 years; education: average = 13.45 years, SD = 1.95 years). The *t* test comparing the age and education of the two groups resulted not significant (age: $p = 0.19$; education: $p = 0.26$). A chi-square test of independence showed that there was a significant difference between gender and group [$\chi^2(1,42) = 3.85$, $p = 0.04$; Yates-corrected $\chi^2 = 2.68$, $p = 0.10$]. Despite this, we proceeded with the 1:1 ratio group assignment since we did not have any assumptions related to the main outcome of the study regarding gender.

The sample size was estimated using G*Power 3.1 with *a priori* power analysis for an *F* test with between–within interactions: considering the Stroop task's response time as the main outcome, we set a small to moderate effect size [$f(V) = 0.4$] (Byun et al., 2014; Monteiro-Junior et al., 2017a; Burin et al., 2020), so we calculated a total sample size of 52 subjects (with the α error probability set at 0.05 and power set at 0.8). We were able to recruit 46 subjects.

Procedure

The RCT protocol was composed of 12 separate sessions (**Figure 2**). We invited participants to visit the laboratory twice a week (for example, every Monday and Thursday or every Tuesday and Friday, compatible with their availability) for consequent weeks, without interruption, to maintain as constant as possible the duration and timing of the intervention (Mirelman et al., 2016; Monteiro-Junior et al., 2017b): the volunteers carried on the actual sessions on average 3.54 days (SD = 0.25 days) between each other; this resulted in an average of 38.31 days (SD = 2.34 days) between the first and the last session.

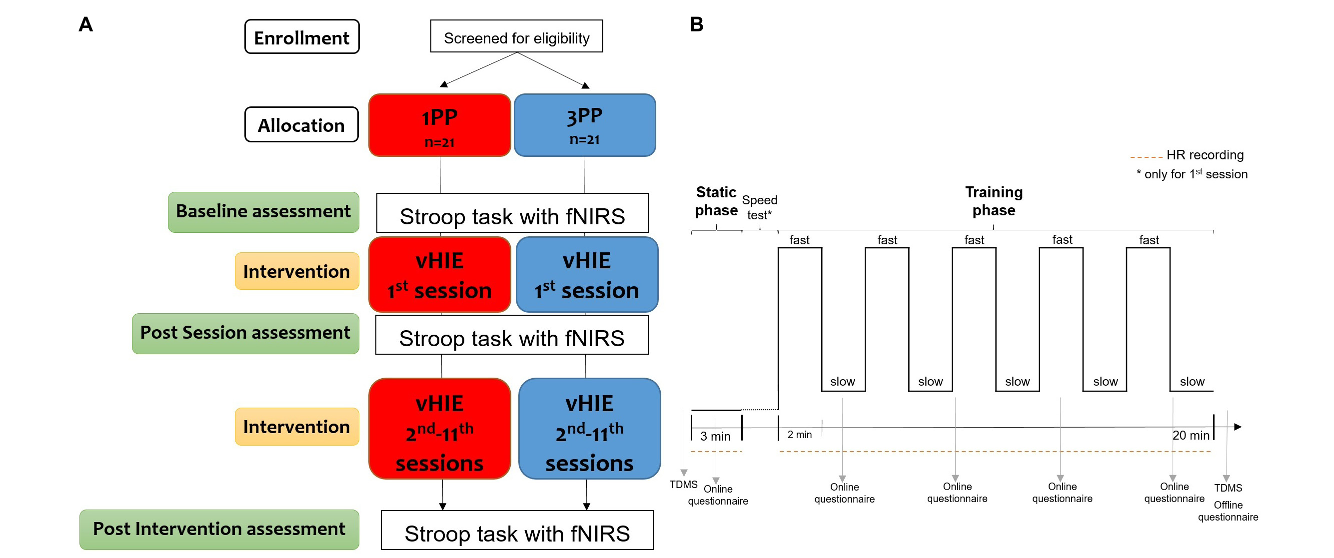

FIGURE 2 | Schematic procedure of the randomized controlled trial (RCT) **(A)** with the timeline and measurements for each session of the virtual high-intensity intermittent exercise (vHIE) intervention **(B)**. After recruitment, the subjects were verbally screened, according to the inclusion criteria for this study, and then allocated to one of two groups [first-person (1PP) or third-person (3PP) perspectives]. During the first session only (which lasted approximately 1 h), all participants read and signed the information sheet and consent form, and they received an additional verbal explanation of the entire RCT procedure, giving them the possibility to ask questions. They also filled out the Edinburgh Handedness Inventory and the International Physical Activity Questionnaire (IPAQ—Short form) for handedness and level of physical activity, respectively. As baseline assessment, they all underwent the color–word matching Stroop task during the recording of cortical hemodynamic changes with a functional near-infrared spectroscopy (fNIRS) device over the left dorsolateral prefrontal cortex (lDLPFC). Then, the intervention started **(B)**: all participants completed the Two-Dimensional Mood Scale (TDMS) including the two subscales for pleasure and arousal. After that, they performed for the first time the vHIE (with the online recording of the heart rate and subjective questionnaire about sense of ownership and agency) in the 1PP or 3PP, according to the group allocation. Immediately after that, they filled out a questionnaire about their experience and they repeated the TDMS. As post-session assessment, they all underwent again the Stroop task with fNIRS recording **(A)**. The procedures of the sessions from the second to the 11th were the same (each lasted about 30 min): according to the group allocation, participants experienced the vHIE in the 1PP or the 3PP, with the online recording of the heart rate and questionnaires during and right after the vHIE part. All subjects repeated the TDMS before and after the vHIE for each session **(B)**. As post-intervention assessment, during the 12th session (which lasted about 15 min), all subjects repeated the Stroop task with the fNIRS recording **(A)**.

Virtual High-Intensity Intermittent Exercise

The IVR setup used in this study was the same as that already tested in Burin et al. (2020), with the exceptions that, here, the RCT is a parallel-group design and the same intervention is repeated for 11 sessions for 20 min each (Mirelman et al., 2016; Monteiro-Junior et al., 2017b).

During the vHIE part of each session, the participants were instructed to sit and not to move their bodies, with their feet resting on the ground and their arms relaxed along the body side. However, they were allowed to move their neck and rotate their head in order to always look at the virtual body (**Figure 3**). Through the Oculus Rift visor[1], they saw a virtual environment, modeled in Unity3D, composed of a simple open space with a green floor (simulating a meadow) and a natural-like bright sky. The gender-matched life-sized humanoid standing bodies were downloaded from the Microsoft Rocketbox Avatar public library (Gonzalez-Franco et al., 2020).

The intervention performed by the two groups was the same, except for the crucial difference made by the visual perspective: in the 1PP group, the virtual body was displayed in a first-person perspective, coherently with the real one, spatially overlapping it (**Figure 3A**), known to be the crucial condition to induce a sense of ownership and to create the virtual full-body illusion (Kokkinara et al., 2016; Burin et al., 2019a, 2020; Neyret et al., 2020). In the 3PP group, the virtual body was located about 1.5 m to the left of the actual participant's position, resembling another person (**Figure 3B**) and not inducing the same illusion mentioned in the 1PP group (Pavone et al., 2016; Gonzalez-Liencres et al., 2020).

The vHIE part was repeated for all sessions, except for the last one (where subjects did only the post-intervention assessment), with the same characteristics (**Figure 2B**): for the first 3 min, the virtual body is displayed standing, either in 1PP or 3PP, but it does not move (hereinafter, static phase) in order to familiarize with the environment, to eventually control for dizziness or sickness due to the virtual display and to induce the illusion of a sense of ownership thanks to the perspective, considering that it may take a few seconds/minutes for the subjective perception, as it happens with other multisensory illusions (Burin et al., 2018). For the following 20 min (hereinafter, training phase), the virtual body in both conditions (1PP and 3PP) alternates 2 min of fast walking (also called fast phase) and 2 min of slow walking (also called slow phase) (Kokkinara et al., 2016; Kujach et al., 2017), while the participant is sitting still. Right after the static phase of the first session only, the participants were asked to choose a speed for the fast walking animation that would be appropriate

[1] https://www.oculus.com/

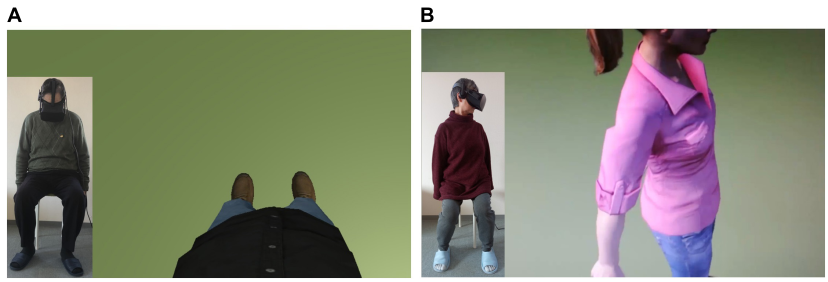

FIGURE 3 | Virtual bodies in the virtual scenario. **(A)** The male virtual body displayed in a first-person perspective (1PP) from the same perspective of the participant (in the *bottom left corner*, the male participant is sitting and looking down toward himself, where his virtual body is). **(B)** The female virtual body displayed in a third-person perspective (3PP) from the perspective of the participant (in *the corner*, the female participant is sitting and looking to the left side at the virtual body).

for them among four options (1: 3.30 m/s, 2: 4 m/s, 3: 4.30 m/s, and 4: 5 m/s), while the speed for the slow walking animation was the same for all subjects (0.5 m/s). Then, the chosen speed for the fast walking parts was kept constant for the following sessions for each subject. As previously done (Burin et al., 2020), this procedure ensured (especially in the experimental group) that the fast walking animation was subjectively reported as considerably fast (in order to show a detectable physiological activation), but not too much to be impossible to perform (in order to not break the ownership and agency illusion).

We decided that the duration of each training phase was 20 min based on a previous report (Monteiro-Junior et al., 2017b), but also for safety reasons: because it is not a medical device but is considered an entertainment system, there are no international safety guidelines on the use of IVR devices. Based on previous studies and the experience of the researchers, we decided to keep the duration of the vHIE part no longer than 30 min (Hamilton et al., 2021).

For the entire duration of the vHIE part of the session, we repeatedly asked the participants to immediately report any feeling of discomfort, nausea, sickness, etc. As previously described, one subject (belonging to the 1PP group) reported nausea during his/her fourth session; consequently, the intervention was interrupted (his/her data were discarded and not included in the analysis reported here).

Heart rate

For the entire duration of the vHIE part of each session (composed of the static and training phases) and for both groups, we recorded the heart rate (HR): the increased physiological activation, even in static conditions, might be a measurable reflection of the anticipation or preparation of the body to move, as it happens with motor imagery studies (Wegner and Wheatley, 1999), or a direct effect of the sense of agency over a moving body performing a physical task that requires physiological activation (Kokkinara et al., 2016; Burin et al., 2020). In addition, the recording of the HR in this study was necessary to validate the actual presence of the virtual illusion (especially in the 1PP group) with an objective measurement, in addition to the subjective component (see Section "Online Questionnaire on Sense of Body Ownership and Agency"), and to check the effectiveness of the training itself. As previously done (Burin et al., 2020), we used a Polar H10 (Polar Electro, Kempele, Finland; polar.com), a very common heart rate monitor used by athletes, connected *via* Bluetooth to a smartphone where an *ad hoc* application collects the recorded data (flow.polar.com). The HR monitor was pinned to an elastic strip worn around the chest, before the beginning of the vHIE part every session, positioning it as close as possible to the heart.

Online questionnaire on sense of body ownership and agency

The questionnaires administered in this study are the same as that previously used in Burin et al. (2020). During the static and training phases of the vHIE for each session, we administered an online questionnaire in order to check the effectiveness of the virtual illusion from a subjective perspective, referring specifically to the illusory sense of body ownership and agency over the virtual body. The online questionnaire was verbally administered by the researchers and the subjects had to report their level of agreement with the questionnaire's statements on a 1–7 Likert scale (1 = meaning "totally disagree" and 7 = meaning "totally agree"). The questionnaire included four statements (from s1 to s4 in **Table 1**), two of them about the sense of body ownership and two about the sense of agency (for each, one is a "real statement" that checks for the actual presence of the illusion, while the other is a "control statement") (**Table 1**). The same statements were repeated in a random order at five time points: at 1 min and 30 s after the beginning of the static phase and at 3, 8, 13, and 18 min after the beginning of the training phase, for every single session. This repetition throughout the session was necessary to eventually check for differences in the fluctuation of the illusion (especially in the 1PP group) and potential changes between the fast (minutes 8 and 13 of the training phase) and slow (minutes 3 and 18 of the training phase) phases.

Offline questionnaire on sense of ownership and agency

Right after the vHIE part of each session, the participants were asked to complete another questionnaire with more detailed statements about subjective feelings of movements, motor control, and physical effort. This questionnaire was self-administered. As mentioned before, the statements here are the same as those of Burin et al. (2020), adapted from Kokkinara et al. (2016) and Burin et al. (2019a) (see **Table 2**).

TABLE 1 | Online subjective questionnaire verbally administered during the virtual high-intensity intermittent exercise (vHIE) for each session and group.

Online questionnaire				1PP group: average ± SE	3PP group: average ± SE	*p* value
Static phase	s1	Sense of body ownership	*I feel as if I am looking at my own body.*	4.69 ± 0.39	2.04 ± 0.32	< 0.01*
	s2	Sense of body ownership control	*I feel as if the virtual body belongs to another person.*	3.40 ± 0.40	6.08 ± 0.29	< 0.01*
	s3	Sense of agency	*The virtual body moves just as I want, as if I am controlling it.*	3.63 ± 0.36	1.89 ± 0.31	< 0.01*
	s4	Sense of agency control	*I feel as if the virtual body is controlling my will.*	2.30 ± 0.26	1.48 ± 0.17	0.57
Training phase	s1	Sense of body ownership	*I feel as if I am looking at my own body.*	4.74 ± 0.41	2.01 ± 0.34	< 0.01*
	s2	Sense of body ownership control	*I feel as if the virtual body belongs to another person.*	3.37 ± 0.42	6.13 ± 0.31	< 0.01*
	s3	Sense of agency	*The virtual body moves just as I want, as if I am controlling it.*	3.69 ± 0.37	1.88 ± 0.31	< 0.01*
	s4	Sense of agency control	*I feel as if the virtual body is controlling my will.*	2.29 ± 0.29	1.49 ± 0.17	0.81

*The columns, from left to right, indicate respectively the phase during which the questionnaire was administered, the statement number (for example, s1), the underlying domains (not disclosed to subjects) and the actual statements (in italic). The results for the first-person perspective (1PP) and third-person perspective (3PP) groups are expressed as average ± standard error. The data in the table are expressed on the 1–7 Likert scale (not ipsatized data) and each statement is averaged across all the sessions of the intervention. *Significant p values comparing groups.*

We decided to repeat the questionnaires for each session to control for potential effects of time (meaning, the illusion's strength might be different between sessions).

Two-dimensional mood scale

Before and after the vHIE part for each session, the participants completed the Two-Dimensional Mood Scale (TDMS) to record mood state changes that might affect physiological responses (e.g., the heart rate). TDMS includes two subscales: pleasure and arousal (Sakairi et al., 2013). The participants rated their current psychological state using a six-point Likert scale from 0 = "Not at all" to 5 = "Extremely."

Baseline, Post-session, and Post-intervention Assessments

The baseline assessment coincided with the beginning of the first session, while the post-session assessment was performed after the first repetition of the vHIE part. Lastly, the post-intervention assessment coincides with the very end of the entire vHIE intervention, so it was performed during the last (12th) session, an average of 3.35 days (SD = 1.99 days) after the last repetition of the vHIE part (**Figure 2A**).

The baseline assessment ensured evaluating the starting level abilities for each person and checking the actual presence of the typical Stroop effect in the sample; then, the comparison with post-session and post-intervention evaluates the short-term and the long-term effects of the vHIE intervention. The assessment was the same for all of the participants: we used the Stroop task to test executive functions, with the online recording of cortical hemodynamic changes over lDLPFC.

Stroop task

Like we did in Burin et al. (2020), the Stroop task used was developed in E-prime 2.0 and was administered and recorded automatically from a laptop. It includes 30 trials presented in random order. For each single trial, two words are displayed on the PC monitor, one above the other: for the 10 neutral trials, the upper row consists of XXXX printed in red, white, blue, brown, or yellow ink, and the lower row shows the words "RED," "WHITE," "BLUE," "BROWN," or "YELLOW" printed in black. For the 10 congruent trials, the upper row contains the same words printed coherently in the same color (e.g., RED written in red), and the lower row shows the same words printed in black. For the 10 incongruent trials (the ones that produce cognitive interference between the color word and the color name, i.e., Stroop interference), the word in the upper row is printed in an incongruent color (e.g., RED written in yellow). All words were written in Japanese hiragana (except for XXXX). The lower row is presented 100 ms later than the upper row to achieve sequential visual attention. Between each trial, an inter-stimulus fixation cross is shown for a random interval between 9 and 13 s to avoid prediction (Hyodo et al., 2012; Byun et al., 2014; Kujach et al., 2017). The words remain on the screen for 3 s, independently of the subject's answer. Subjects were instructed to decide whether the color of the upper word (or XXXX) corresponded to the color name of the lower word by pressing button 1 on the keypad to give a "yes" or button 2 a "no" response with their right forefingers. Fifty percent of the presented stimuli were correct (the correct answer is "yes").

Functional near-infrared spectroscopy

While performing the Stroop task during the baseline, post-session, and post-training assessments, the participants wore a wearable fNIRS optical topography system (WOT-HS, Hitachi Corporation and NeU Corporation, Japan) managed by its software (Hitachi Solutions, Inc.). This system is the same as that used in the previous study (Burin et al., 2020): the 35 capsules of this device compress near-infrared emitting or high-sensitivity receiving sensors, organized in three lines (the top and the bottom lines alternate an emitting and a receiving sensor, while the central line comprises receivers only), creating a system

TABLE 2 | Offline subjective questionnaire self-administered immediately after the virtual high-intensity intermittent exercise (vHIE) part for each session in both groups.

Offline questionnaire			1PP group: average ± SE	3PP group: average ± SE	*p* value
s5	Located	*I felt as if my body was located where I saw the virtual body to be.*	4.37 ± 0.33	2.49 ± 0.40	0.02*
s6	Sense of ownership	*I felt that the virtual body was my own body.*	4.15 ± 0.39	2.27 ± 0.37	0.01*
s7	Standing	*I felt that I was standing upright.*	3.98 ± 0.39	2.37 ± 0.31	0.16
s8	My movements	*I felt that the leg movements of the virtual body were my movements.*	4.21 ± 0.39	2.41 ± 0.39	0.02*
s9	Sense of agency	*I felt that the leg movements of the virtual body were caused by my movements.*	3.59 ± 0.30	2.49 ± 0.29	0.23
s10	Sense of ownership control	*I felt that the virtual body belonged to someone else.*	3.69 ± 0.32	4.82 ± 0.35	< 0.01*
s11	Effort	*I felt I had to give extra physical effort when the virtual body was walking faster.*	3.75 ± 0.34	2.12 ± 0.25	0.04*
s12	Vection	*I felt that I was moving through space rather than the world moving past me.*	4.72 ± 0.36	2.58 ± 0.38	0.01*
s13	Walking	*I felt that I was walking.*	4.13 ± 0.33	2.45 ± 0.37	0.04*
s14	Dragged	*I felt that I was being dragged.*	1.79 ± 0.16	1.56 ± 0.17	< 0.01*
s15	Sliding	*I felt that I was sliding.*	2.04 ± 0.19	1.69 ± 0.18	< 0.01*

*The columns, from left to right, indicate respectively the statement number (for example, s5, continuing from previous ones), the underlying domains (not disclosed to subjects) and the actual statements (in italic). The results for the first-person perspective (1PP) and third-person perspective (3PP) groups are expressed as average ± standard error. The data in the table are expressed on the 1–7 Likert scale (not ipsatized data) and each statement is averaged across all the sessions of the intervention. *Significant p values comparing groups.*

of 34 channels over the lateral and anterior prefrontal cortex. The device was positioned on the forehead by centering the specific mark on the bottom line of probes at the frontopolar zone (FPZ; 10% of the distance between the nasion and inion), according to the international 10–20 system (Klem et al., 1999).

Various previous studies have stressed the importance of the prefrontal cortex (PFC) and specifically the dorsolateral prefrontal cortex (DLPFC) in the context of the executive performance (MacDonald et al., 2000; Hoshi et al., 2001). More specifically, because of the significance of the lDLPFC in relation to the executive performance examined, thanks to the Stroop task (Yanagisawa et al., 2010; Hyodo et al., 2012, 2016), and the similarity between the previously used tasks and the present one (Kujach et al., 2017; Burin et al., 2020), we focused the analysis on lDLPFC. To monitor the cortical hemodynamic changes in the lDLPFC, we recorded the concentrations of oxygenated hemoglobin (O_2Hb) and deoxygenated hemoglobin (HHb), expressed in units of millimolar.millimeter (Watanabe et al., 1995), by applying two short-distance wavelengths of near-infrared light (850 and 730 nm).

Statistical Analysis

For all analyses, distribution was assessed using a Shapiro–Wilk test for normality and, accordingly, parametric or non-parametric analyses were conducted. The significance level was set at $p < 0.05$. *Post hoc* analysis was conducted with Duncan's test. All displayed values are average ± standard error (SE). When necessary, we performed a retrospective power analysis (between-group effect sizes using G-Power) with specified effect sizes: Cohen's d was used for parametric comparisons, while for non-parametric eta squared (η^2) was used (with α error probability set at 0.05).

Heart Rate Data

The software recorded the HR data as the instantaneous heart rate changes (expressed in beats per minute, as in Kokkinara et al., 2016; Burin et al., 2020) at 1 Hz frequency (Malik, 1996) during the static (3 min) and the training (20 min) phases of each session. At first, we excluded from the individual raw data outliers or artifacts, defined as data with values ± 20% or greater with respect to the adjacent one (Ribeiro et al., 2018). For each session, the HR recordings (23 min in total) were divided into the corresponding phases of the vHIE part, i.e., static (one segment, corresponding to the first 3 min), fast walking (five segments of 2 min each), and slow walking (other five segments of 2 min each, temporally alternated between fast walking and slow walking) phases. For each segment accordingly obtained, we discarded the first 30 s of recordings: this procedure ensured considering in the analysis the actual HR variability directly imputable to the IVR stimulation, considering that HR is a slow physiological measurement that requires time to adapt to external events (Wang et al., 2018). Finally, for each subject, we averaged the obtained segments corresponding to the same phase (static, fast walking, and slow walking). Lastly, we subtracted the obtained data for static (HRst) from the data of fast walking (HRf) and slow walking (HRs), resulting in dHRf (= HRf - HRst) and dHRs (= HRs - HRst) for each group.

Since data were not normally distributed, we ran a Mann–Whitney *U* test comparing the two groups.

Online Questionnaire Data

The four online questionnaire statements (from s1 to s4; see **Table 1**) have been repeated in a random order during each session at five time points (during the static phase at 1 min 30 s and during training at 3, 8, 13, and 18 min). The obtained raw data from each statement underwent an intra-individual ipsatization procedure (Cattell, 1944): this is a quite common procedure (also called "standardization per person") that applies to subjective measurements (such as questionnaires), and it allows neutralizing potential response biases in a response set. The ipsatization was done as follows: every raw value was first subtracted by the mean rating of the subject responses in all questions and conditions and then divided by the standard deviation of the responses in all questions and conditions (Romano et al., 2014; Burin et al., 2015), obtaining *z*-scores ± SE. Although the analysis was performed with *z*-scores, in **Table 1**, we reported the non-ipsatized data (average ± SE) in order to have a more precise reference of the answers on the 1–7 Likert scale.

In test *W*, the data resulted as non-normally distributed, so we ran a Mann–Whitney *U* test comparing each statement separately (separating also the static and training phases) between groups.

Offline Questionnaire Data

The 11 statements of the offline questionnaire (from s5 to s15; see **Table 2**) were repeated right after the end of the vHIE part of each session. As for the online ones, the answers to the offline questionnaire were ipsatized (Pia et al., 2015), but in **Table 2**, we reported non-ipsatized data. The data resulted as non-normally distributed, so we ran a Mann–Whitney *U* test comparing each statement (from s5 to s15) by groups (1PP and 3PP).

TDMS Data

According to the TDMS guidelines, we calculated pleasure and arousal levels separately (Sakairi et al., 2013). We ran a 11 × 2 × 2 ANOVA with factors session (corresponding to the 11 sessions), time (pre and post each session), and group (1PP and 3PP) for each pleasure and arousal data.

Stroop Task's RT and ER Data

We recorded as outcomes the response time (RT, in milliseconds), as the difference between the display of the upper row stimulus and the subject having given an answer, and the error rate (ER, in percentage of error; missed trials or answered over the time limit are considered errors).

Concerning the RT measurements of the Stroop task (main outcome of this study), we first compared the ones recorded during the baseline assessments. In test *W*, all RT data resulted as normally distributed, so we ran a 2 × 2 repeated measures ANOVA with factors condition (neutral and congruent) and group (1PP and 3PP). The Stroop task's crucial outcome is the so-called Stroop interference, which is assumed to actually characterize the cognitive process underlying the task itself, defined as the average of incongruent trials - average of neutral trials (Zysset et al., 2001). Hence, the 2 × 3 repeated measures ANOVA with between factor group (1PP and 3PP) and within factor time of assessment (baseline, post-session, and post-intervention).

Concerning the ER measurements (expressed in percent of error) of the Stroop task, we first controlled again whether there was the typical Stroop interference effect in the sample. In this case, we ran a Wilcoxon matched pair test to compare the ER results during the baseline assessment for all subjects (independently of group assignment). Mainly, we compared with Mann–Whitney *U* test the ER between groups (1PP and 3PP) and the time of assessment (baseline, post-session, and post-intervention).

fNIRS Data

The optical fNIRS data of the O_2Hb and HHb signals (sampling rate at 10 Hz) were analyzed according to the modified Beer–Lambert law (Delpy et al., 1988). After processing each channel singularly (see Burin et al., 2019c for details), we focused on channels 23, 25, and 26, which are associated with the target area, lDLPFC (**Figure 4A**). Because of the time difference between the fNIRS signals of participants' responses, we selected for each trial the averaged changes in the concentrations of O_2Hb and HHb 2 s before the onset task as a "rest," during the "task" (lasting for 3 s), and 10 s after the onset task as "vascular response" (Schroeter et al., 2002). In an event-related design, we matched each trial's signal with the corresponding Stroop task conditions and averaged them. As for the Stroop task results, we considered here the Stroop interference (incongruent–neutral condition).

O_2Hb and HHb (expressed in millimolar.millimeter) were analyzed separately by means of a 2 × 3 ANOVA, with group (1PP and 3PP) as the categorical factor and time of assessment (baseline, post-session, and post-training) as the within-subjects factor.

Correlations Analysis

Lastly, we checked for correlations among the above-mentioned variables. Because of the elevated number of independent correlations, we also applied a false discovery rate (FDR) procedure with $\alpha = 0.05$ (Benjamini and Hochberg, 1995), so we displayed the FDR-adjusted *p* value for each correlation.

At first, we tested for correlations during the vHIE part, i.e., HR and data of the online questionnaire. Considering each statement separately (from s1 to s4), we compared the HR results from the training (fast walking and slow walking phases) with Spearman's correlation; then, we ran the same analysis for the correlations between HR and the offline questionnaire. Secondly, we correlated the data collected during the assessments, i.e., Stroop task's RT and ER with O_2Hb signal, with Pearson's correlation. Lastly, we correlated the measurements during the vHIE (HR and questionnaires) with the measurements during the assessments (RT and ER of Stroop interference and the O_2Hb signal) with Spearman's correlation.

RESULTS

To test hypothesis 1 about the subjective and physiological effects of the illusory virtual body on the real one (see Section

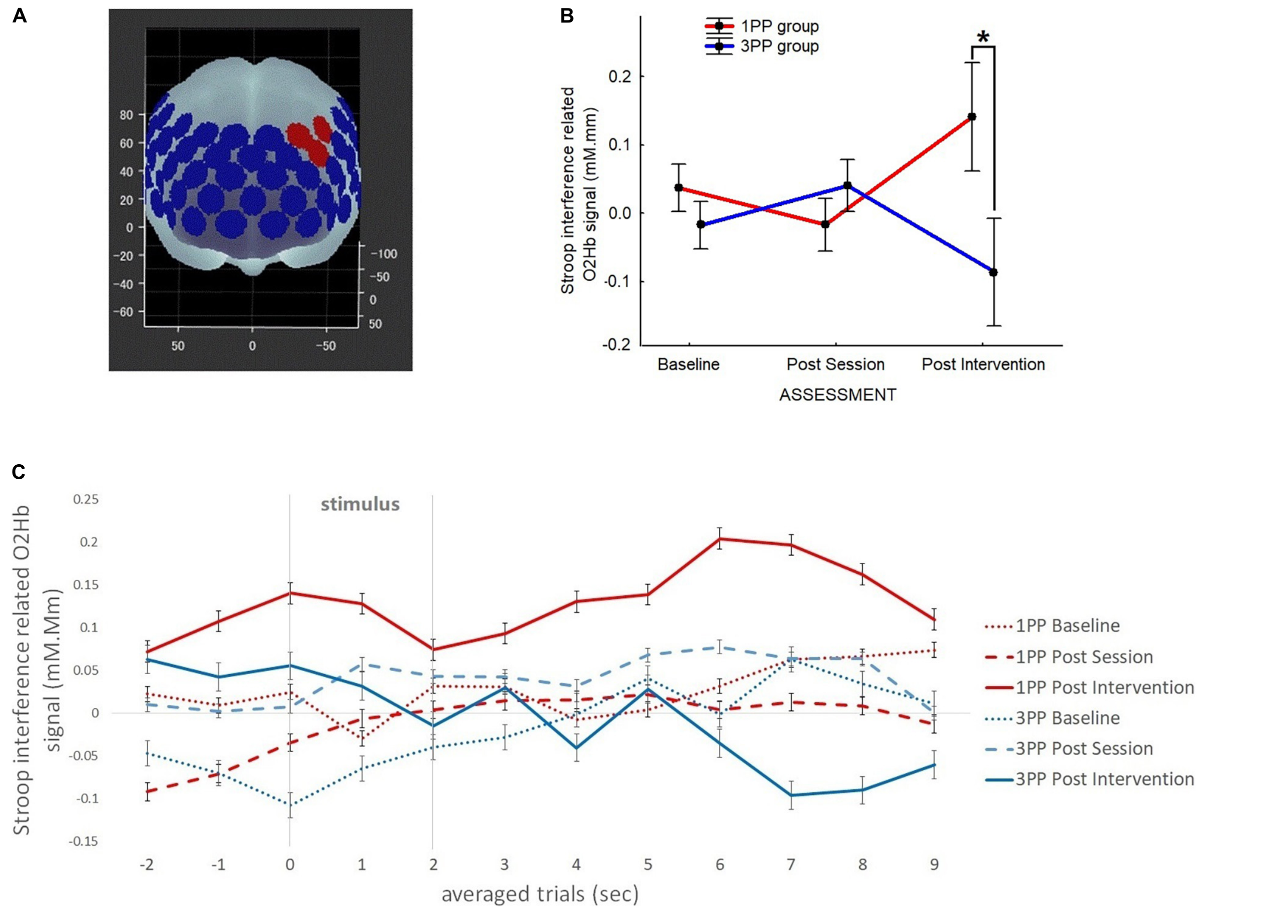

FIGURE 4 | Line plots of the functional near-infrared spectroscopy (fNIRS) Stroop interference-related results over the left dorsolateral prefrontal cortex (lDLPFC) for the oxygenated hemoglobin (O_2Hb) signal. **(A)** Representation of the fNIRS device's channels over the prefrontal cortex: *red spots* (representing channels 23, 25, and 26) are the ones considered for the analysis of the lDLPFC (channel 23: x = -30, y = 33, z = 51; channel 25: x = -47, y = 16, z = 50; channel 26: x = -43, y = 34, z = 39). **(B)** Results of the Stroop interference-related activation of the O_2HB signal (in millimolar.millimeter) across the three assessment time points: baseline, post-session, and post-intervention. *Asterisk* highlights the significant differences ($p < 0.05$). *Red line* refers to the results of the first-person perspective (1PP) group, while *blue line* refers to the third-person perspective (3PP) group. *Vertical black bars* denote plus/minus standard errors. **(C)** fNIRS data (O_2HB signal only) associated with Stroop interference activation showing the timeline of the averaged trials per group and assessment. *Red lines* refer to the results in the 1PP group, while *blue lines* refer to those of the 3PP group. *Dotted lines* show results recorded during the baseline assessment, *dashed lines* refer to post-session, and *solid lines* are for post-intervention assessment. The X-axis displays the time in seconds for every trial of the Stroop task: 2 s before the stimulus display, the stimulus is displayed (from 0 to 2 s) and the next 7 s (where there is an increased peak around 6–8 s in the 1PP post-intervention line). *Vertical black bars* denote plus/minus standard errors.

"Introduction"), we analyzed first the data from the online and offline questionnaires and the heart rate data. Then, to test hypotheses 2 and 3, we proceeded with the main analysis of the Stroop test, fNIRS, and TDMS measurements across the three assessment time points. Lastly, we ran correlations among them.

Heart Rate

Considering that we did not find differences in time, i.e., the main effect of session, or in the interaction with group, we averaged the results across sessions for each subject.

In the Mann–Whitney U test comparing the two groups dHRf was significantly ($p < 0.01$, 2*1-sided exact $p < 0.01$, adjusted $z = 5.27$) higher in the 1PP (9.53 ± 0.57) with respect to the 3PP (-1.44 ± 0.57) group. The dHRs did not result significantly different in the group comparison (1PP: -0.99 ± 0.45; 3PP: -1.47 ± 0.449) (**Figure 5**). The retrospective power analysis resulted in power = 0.95, $\eta^2 = 0.80$.

As previously mentioned, the participants were allowed to choose a speed for the fast walking phase animation appropriate for them: 41 subjects chose speed 1 (3.30 m/s) and only one subject (in the 1PP group) chose speed 2 (4 m/s).

Online Questionnaire on Sense of Body Ownership and Agency

Firstly, we checked eventual differences between sessions (meaning that ratings to the same statement do not change across the time of the intervention) and also in the repetitions of the statements in the training phase (meaning that ratings

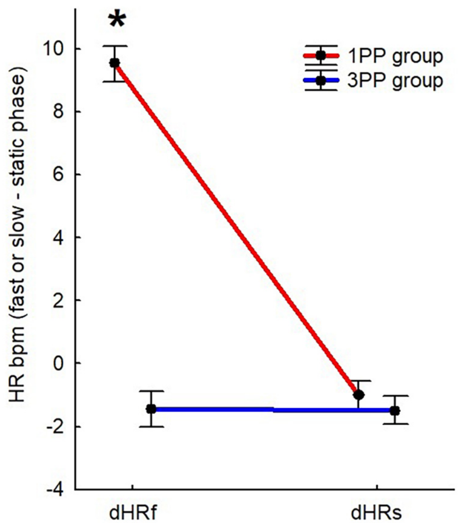

FIGURE 5 | Line plots of the heart rate (HR) results (expressed in beats per minute). *Red line* represents the results of the first-person perspective (1PP) group and *blue line* is for the results of the third-person perspective (3PP) group. *Left part of the graph* shows the results of HR during the fast phase (dHRf) of the virtual high-intensity intermittent exercise (vHIE) across sessions and the *right one* concerns the slow phase (dHRs). For both, the results shown here are obtained by subtracting the corresponding static phase. Significant differences ($p < 0.05$) are highlighted with *asterisk*. *Vertical black* bars denote plus/minus standard errors.

to the same statement do not change across the time of the same session). We found no relevant differences between sessions or within the sessions, so we averaged for each subject each statement separately across sessions for the static phase and also across repetitions in the same session for the training phase (see **Supplementary Material**).

In the Mann–Whitney *U* test comparing groups, in the static phase, s1 (about sense of body ownership) was significantly different ($p < 0.01$, 2*1-sided exact $p < 0.01$, adjusted $z = 3.81$) between the 1PP group (2.87 ± 0.33) and the 3PP group (0.75 ± 0.33), with 1PP higher than the control group. The same pattern was found for s3, the statement about sense of agency ($p < 0.01$, 2*1-sided exact $p < 0.01$, adjusted $z = 2.88$), with ratings in the 1PP group (1.84 ± 0.31) higher than those of 3PP (0.59 ± 0.31). In contrast, s2, the control statement on body ownership, showed the opposite pattern: in 1PP (1.44 ± 0.44), s2 was significantly lower ($p < 0.01$, 2*1-sided exact $p < 0.01$, adjusted $z = -4.29$) than that in the 3PP group (4.74 ± 0.44). Lastly, s4, the control statement about agency, did not differ between groups (**Figure 6A**).

In the training phase, it seems that the pattern of ratings in the static phase is maintained. s1, about sense of body ownership, was significantly ($p < 0.01$, 2*1-sided exact $p < 0.01$, adjusted $z = 3.68$) higher in the 1PP group (2.91 ± 0.36) than in the 3PP group (0.72 ± 0.36)., The same goes for s3, the statement about sense of agency ($p < 0.01$, 2*1-sided exact $p < 0.01$, adjusted $z = 2.95$), which was, again, higher in the 1PP group (1.90 ± 0.32) than in the control group (0.59 ± 0.32). The control statement s2, the statement on body ownership, was significantly ($p < 0.01$, 2*1-sided exact $p < 0.01$, adjusted $z = -4.21$) lower in the 1PP group (1.43 ± 0.45) than in 3PP (4.79 ± 0.45) (**Figure 6B**). Again, s4, the control statement about agency, did not differ between groups. The retrospective power analysis resulted in power = 0.85, $\eta^2 = 0.73$.

Despite the above-mentioned significances, if we consider the non-ipsatized data (see **Table 1**), in the 1PP group, s1 (statement about body ownership) during the static phase was rated 4.69/7 and during the training phase was rated 4.74/7, meaning close to "I slightly agree." s3 (about sense of agency) in the static phase was rated 3.63/7 and in the training phase was 3.69/7, meaning close to "I don't know" (corresponding to 4/7). If we consider the groups separately and compare the statements (with Wilcoxon test), in the 1PP group, s1 (about sense of body ownership) during the static and also the training phase was not significantly different from its control (s2), while s3 (about sense of agency) was significantly higher (static: $p < 0.01$, $z = 2.69$; training: $p < 0.01$, $z = 2.66$) than s4 (its control statement) in static (2.30/7) and training (2.29/7).

Offline Questionnaire on Sense of Body Ownership and Agency

Firstly, we needed to check whether there was an effect of the session (meaning that ratings to the same statement do not change across the time of the intervention): we found no main effect of sessions or interaction with statement or group, so we proceeded by averaging the answers to the same statement across sessions.

In the Mann–Whitney *U* test comparing between groups, s5, about sense of being located where the virtual body was, was significantly different ($p = 0.01$, 2*1-sided exact $p = 0.02$, adjusted $z = 2.35$) and higher in the 1PP group (2.08 ± 0.32) with respect to the 3PP group (0.92 ± 0.27). The same pattern was found for s6, about sense of body ownership ($p = 0.01$, 2*1-sided exact $p = 0.01$, adjusted $z = 2.52$; 1PP: 2.01 ± 0.36; 3PP: 0.70 ± 0.24); s8, about the ownership of the virtual movements ($p = 0.02$, 2*1-sided exact $p = 0.02$, adjusted $z = 2.20$; 1PP: 1.97 ± 0.37; 3PP: 0.85 ± 0.27); s11, about sense of effort ($p = 0.03$, 2*1-sided exact $p = 0.04$, adjusted $z = 2.07$; 1PP: 1.55 ± 0.31; 3PP: 0.60 ± 0.18); s12, concerning the feeling of the movement of the body in the space, or vection ($p = 0.01$, 2*1-sided exact $p = 0.01$, adjusted $z = 2.47$; 1PP: 2.36 ± 0.344; 3PP: 1.01 ± 0.28); and s13, about the feeling of walking ($p = 0.04$, 2*1-sided exact $p = 0.04$, adjusted $z = 2.05$; 1PP: 1.78 ± 0.30; 3PP: 0.89 ± 0.25). The opposite pattern was shown in s10, the control statement about sense of body ownership, where ratings in the 1PP group (1.10 ± 0.37) were significantly lower ($p < 0.01$, 2*1-sided exact $p < 0.01$, adjusted $z = -3.01$) than those in the 3PP group (3.24 ± 0.47); s14, regarding the feeling of being dragged ($p < 0.01$, 2*1-sided exact $p < 0.01$, adjusted $z = -3.33$; 1PP: -0.44 ± 0.10; 3PP: 0.05 ± 0.10); and s15, about the feeling of sliding ($p < 0.01$, 2*1-sided exact $p < 0.01$, adjusted $z = -2.70$; 1PP: -0.17 ± 0.13; 3PP: 0.18 ± 0.10). Note that the raw data of s14 (about being dragged) and s15 (about sliding) seem to have the 1PP higher than the 3PP group, but after the ipsatization process, the pattern was inverted.

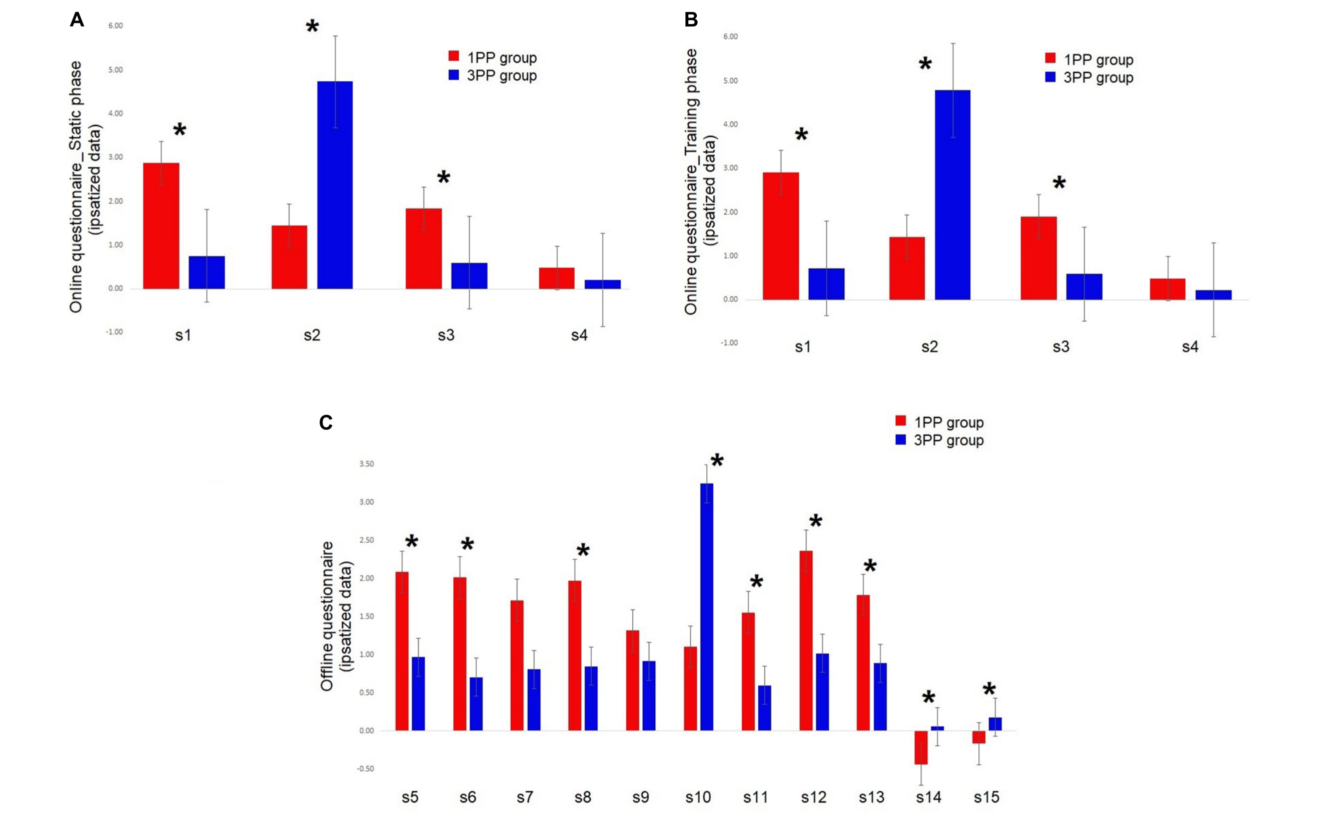

FIGURE 6 | Histograms of the online and offline questionnaires about sense of body ownership and agency results (ipsatized data used in the analysis). **(A)** Results of the online questionnaire (from s1 to s4) during the static phase. **(B)** Results of the online questionnaire (from s1 to s4) during the training phase (averaged between repetitions). **(C)** Results of the offline questionnaire (from s5 to s15). All the displayed data represent the average scores between sessions. *Red bars* represent the results of the first-person perspective (1PP) group and *blue bars* the results of the third-person perspective (3PP) group. Significant differences ($p < 0.05$) are highlighted with *asterisk*. *Vertical black bars* denote plus/minus standard error.

S7 (about standing) and s9 (about sense of agency) did not differ between groups (**Figure 6C**). The retrospective power analysis resulted in power = 0.80, $\eta^2 = 0.72$.

Two-Dimensional Mood Scale

For pleasure, we found no effect of interaction or main effect of time, meaning that the pleasure level did not change before and after each session, so it did not affect the physiological recording. We found though a main effect of session [$F(10, 300) = 12.31$, $p < 0.01$], showing a decline in the level of pleasure, but independently of the group or before/after the session itself. Consequently, we averaged the results for pleasure for pre- and post-sessions, and we confirmed that there are no significant differences.

As for arousal, we found a comparable pattern: although there was no effect of interaction, there was a main effect of session [$F(10, 300) = 28.27$, $p < 0.01$], again showing a decline in the pleasure levels as the intervention continued. We found no differences in time or group, combining the pre and post results for all sessions. In summary, no changes in mood (pleasure and arousal specifically) were detected comparing the two groups before or after each session, so they unlikely affected the physiological recordings.

Stroop Task's RT and ER

Regarding the RT measurements, in 2 × 2 ANOVA to compare the data recorded during the baseline assessment, the interaction between factors [$F(1, 40) = 6.13$, $p = 0.02$] and also the main factor condition [$F(1, 40) = 95.31$, $p < 0.01$] were significant, with RT in the neutral condition (1,548.22 ± 45.96 ms) inferior to that in the incongruent condition (1,933.42 ± 52.25 ms). The main factor group was not significant. Therefore, we can conclude that, independently of group assignment, on average, all subjects showed the typical Stroop interference, before beginning the RCT.

In the 2 × 3 ANOVA to compare the Stroop interference between groups and time of assessment, we found that the effect of interaction was significant [$F(2, 80) = 5.24$, $p < 0.01$]. At *post hoc* comparison, the Stroop interference in the 1PP group during the post-intervention assessment (270.20 ± 41.78) was significantly lower ($p = 0.01$) than that at baseline (437.80 ± 50.58), but not different with respect to the post-session assessment (345.07 ± 50.36). Although they clearly have opposite patterns (**Figure 7A**), it is worth noticing that there were no differences between groups at the assessments, except at baselines ($p = 0.02$; 1PP: 437.80 ± 50.58; 3PP: 260.59 ± 50.58). In the 3PP group, no differences were detected. The retrospective power analysis resulted in power = 0.80, dz = 0.25.

Regarding the ER measurements, in the Wilcoxon test to compare the data collected during the baseline assessment, the comparison between neutral (1.82 ± 0.39) and incongruent (15.79 ± 1.41) resulted significant ($p < 0.01$, $z = 5.44$), with the incongruent higher than the neutral, therefore showing the typical Stroop interference also for the ER. If we eventually compare between groups with the Mann–Whitney *U* test, we confirm that there was no difference.

In the Mann–Whitney *U* test to compare between groups and time of assessment, ER (incongruent–neutral) was significantly different ($p = 0.04$, 2*1-sided exact $p = 0.04$, adjusted $z = -2.06$) between groups at baseline (1PP: 12.17 ± 1.71; 3PP: 16.51 ± 1.80), but not at post-session or at post-intervention (**Figure 7B**).

fNIRS Data

While we did not find any significant difference in HHb, we found a significant effect of group × condition interaction [$F(2, 64) = 3.32$, $p = 0.04$] for O_2Hb in the 2 × 3 ANOVA. At *post hoc* (Duncan's test), the only significant difference was between post-intervention comparing groups ($p = 0.01$), showing an increased activation in the 1PP (0.14 ± 0.08) with respect to the 3PP (−0.09 ± 0.08) group (**Figure 4B**). The retrospective power analysis resulted in power = 0.90, dz = 0.40.

There was no difference in activation comparing the baselines of the two groups. Different with respect to predictions and the previous results, we did not find any difference in post-session activation but, as mentioned before, only at post-training assessment. This result seems to be coherent with the Stroop task results of RT. Interestingly, plotting the O_2Hb results by trial (showing the timing of activation with respect to the Stroop task stimulus), there was clearly an increased activity in post-intervention, 6–8 s after displaying the visual stimulus (**Figure 4C**).

Correlations

In Spearman's correlation (to test for correlations between measurements during the vHIE), we found that the HR during the fast walking phase positively correlated with s1 [$r = 0.42$, $t(N - 2) = 2.94$, $p = 0.01$, FDR-adjusted $p = 0.01$], s3 [$r = 0.41$, $t(N - 2) = 2.85$, $p = 0.01$, FDR adjusted $p = 0.01$], and s4 [$r = 0.49$, $t(N - 2) = 3.55$, $p < 0.01$, FDR-adjusted $p < 0.01$]. A negative correlation was found for s2 [$r = -0.43$, $t(N - 2) = -3.01$, $p < 0.01$, FDR-adjusted $p = 0.01$]. We found no significant correlations between HR and the subjective ratings in the slow walking phase or between the HR and the questionnaire during the static phase.

Concerning the correlation between HR and the offline questionnaire's results, we found positive significant correlations between HR during the fast walking phase and s5 [$r = 0.38$, $t(N - 2) = 2.66$, $p = 0.01$, FDR-adjusted $p = 0.02$], s6 [$r = 0.44$, $t(N - 2) = 3.10$, $p < 0.01$, FDR-adjusted $p = 0.01$], s7 [$r = 0.38$, $t(N - 2) = 2.61$, $p = 0.01$, FDR-adjusted $p = 0.01$], s8 [$r = 0.39$, $t(N - 2) = 2.70$, $p = 0.01$, FDR-adjusted $p = 0.02$], s11 [$r = 0.42$, $t(N - 2) = 2.96$, $p = 0.01$, FDR-adjusted $p = 0.01$], s12 [$r = 0.44$, $t(N - 2) = 3.09$, $p < 0.01$, FDR-adjusted $p = 0.01$], s13 [$r = 0.47$, $t(N - 2) = 3.40$, $p < 0.01$, FDR-adjusted $p = 0.01$], s14 [$r = 0.38$, $t(N - 2) = 2.63$, $p = 0.01$, FDR-adjusted $p = 0.01$], and s15 [$r = 0.38$, $t(N - 2) = 2.58$, $p = 0.01$, FDR-adjusted $p = 0.01$]. s9 and s10 did

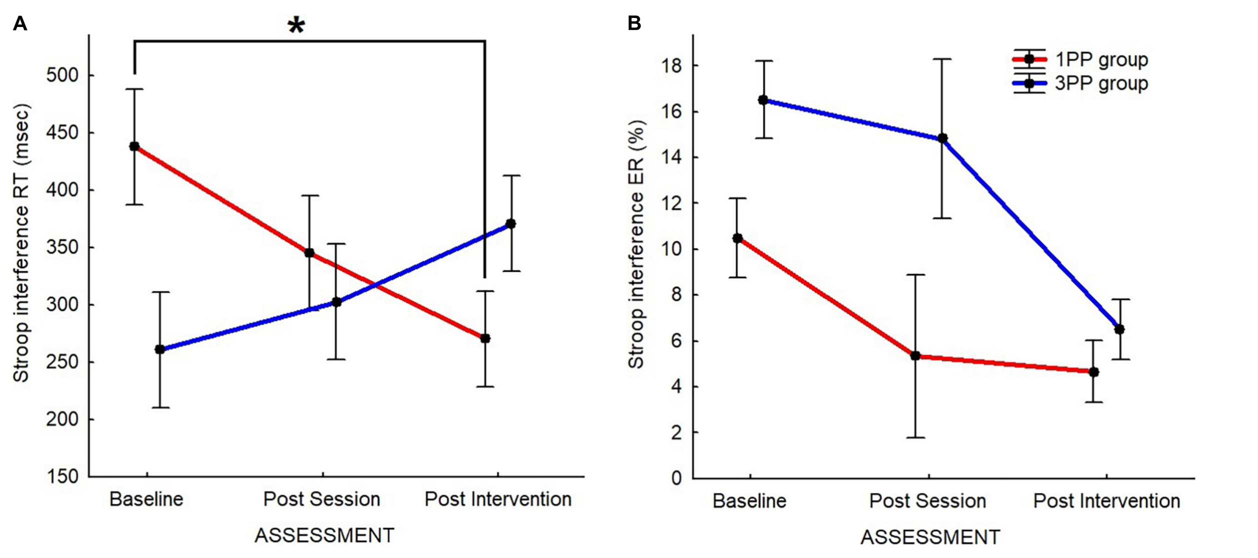

FIGURE 7 | Line plots of the Stroop interference (incongruent–neutral condition) results for the Stroop task's response time (RT) **(A)** and error rate (ER) **(B)**. For both, *red line* represents the results of the first-person perspective (1PP) group and *blue line* the results of the third-person perspective (3PP) group. Stroop interference results for response time (in milliseconds) **(A)** and error rate (in percent of error) **(B)** across the three assessment time points: baseline, post-session, and post-intervention. Significant difference ($p < 0.05$) is highlighted with *asterisk*. *Vertical black bars* denote plus/minus standard errors.

not correlate with HR, and we found no correlations between statements and the HR during the slow walking phase, as it happened for the online questionnaire.

In Pearson's correlation (to test for correlations between measurements during the assessment), we found a significant negative correlation between RT Stroop interference and O_2Hb signal during the baseline assessment (r = -0.39, p = 0.02, FDR-adjusted p = 0.04) and a significant positive correlation during the post-session assessment (r = 0.37, p = 0.03, FDR-adjusted p = 0.03), but we did not find significant correlations during the post-intervention assessment. As for ER, we did not find correlations with the O_2Hb data.

In Spearman's correlation (to test for correlations between measurements during the vHIE and measurements during the assessment), after the FDR adjustment, only the correlations between s9 and the O_2Hb signal in the post-intervention assessment resulted significant [$r = 0.31$, $t(N - 2) = 2.03$, $p = 0.04$, FDR-adjusted $p = 0.04$].

DISCUSSION

The present study not only aimed at confirming previous results about the cognitive benefits of virtual training (Burin et al., 2020) but also intended to provide new knowledge concerning the long-term effects of this intervention on the elderly population. Here, we proposed a vHIE intervention, with similar characteristics to that in Burin et al. (2020) and Burin et al. (2019c): with the participants sitting still, the virtual body alternated sequences of fast and slow walking while we measured the heart rate and questionnaires during the virtual training and Stroop task and the cortical activity at different time points during the intervention. The main differences with respect to our previous study are the target sample and the timing of the intervention: in this case, we recruited a sample of over 60-year-old participants (organized into two groups, 1PP and 3PP, according to the visual perspective of the virtual body), and we modified the intervention itself in order to repeat the vHIE for 6 weeks, twice a week, for 20 min each session (instead of the 8 min for one session in the previous study). Coherently, we repeated the cognitive assessments before the beginning of the intervention, right after the first session, and at the end of the entire intervention. We will discuss the present findings starting from the initial hypothesis made in Section "Introduction."

Findings on Body Ownership, Agency, and Physiological Effect During the vHIE (Hypothesis 1) Are Confirmed in the Elderly Across the Long-Term Intervention

In the present study, we confirm, thanks to the questionnaires' results, that the full-body illusion can cause a sense of body ownership over the virtual body, but only when the avatar is displayed coherently with the participants' perspective (i.e., in the 1PP). Here, we confirm that the visual perspective seems to be the necessary condition for the ownership illusion to arise (Kokkinara et al., 2016; Burin et al., 2020; Neyret et al., 2020), while other stimulations, such as tactile, might contribute to increase it (Maselli and Slater, 2013), but are not as determinant as the visual channel.

We also confirm here that, despite the discrepancy between the real (no actions) and virtual (fast and slow walking) actions, the sense of agency over the virtual movements is, to some extent, preserved. The possibility to transfer the sense of agency to an agent other than our own body is not entirely a novelty: revisited versions of the rubber hand illusion involving movements proved how the sense of ownership over a fake hand (induced by visuotactile stimulation) can be so consistent to persist if it moves, inducing the sense of agency over the embodied movement (Kalckert and Ehrsson, 2012, Kalckert and Ehrsson, 2014; Burin et al., 2017). The full-body illusion replicates and strengthens this result by involving the entire body and allowing the overlap of the real and the physical body (Ehrsson, 2007; Slater, 2018), thanks to technologies such as IVR. In this context, while the sense of ownership is maintained, it is possible to manipulate several aspects related to the sense of agency. For example, the same illusion is effective even when there is a discrepancy between the intended and the executed movements: within certain spatial or temporal constrains (Burin et al., 2019a), the seen/executed movements can differ from the intended ones, without disrupting the sense of agency or even increasing it (Aoyagi et al., 2019).

Different with respect to the previous studies, here, the real person's body is still and no instructions were given about any movements (Kokkinara et al., 2016; Burin et al., 2020), so there is no motor intention created. Therefore, there is no direct contrast in the neurocognitive comparator model, which compares the predicted action and the executed one (Frith et al., 2000). It is worth noticing that for the 1PP group, the recorded answers to the questionnaire's statements related to the sense of agency are, on average, between 4/7 ("I don't know") and 5/7 ("I slightly agree"), but still higher than those of the 3PP group or with respect to the control statements: possibly, in a situation of uncertainty, where the virtual body in the 1PP is considered as one's own (see answers to sense of body ownership statements in **Tables 1**, **2**) and it is moving, people tend to attribute the agency of the seen movements to themselves, driven by the increased sense of ownership over the avatar (Burin et al., 2017, 2020). The absence of a motor plan might have positively contributed to this phenomenon because the seen movements (performed by one's own virtual body) do not directly contrast the plan itself, but they can somehow integrate and be justified by the increased sense of body ownership ("this is my body–my body is moving–I am moving"). In this case, what happens might be an *a posteriori* reconstruction of the motor intention, based on the sense of body ownership, while normally it is a forward process, starting with the intention itself.

These levels of sense of subjective body ownership and agency might be sufficient to determine consequent reactions on a physiological level, i.e., increasing the heart rate coherently with the virtual movements, despite the participant being completely still. Even though this phenomenon has been observed in previous studies (Moseley et al., 2008; Kokkinara et al., 2016; Matamala-Gomez et al., 2020), here, the virtual movements alternate sequences of fast and slow walking (2 min each) instead of having a constant animation at the same speed with a final rush, which makes the physiological reaction even more reliable. The correlations between the heart rate results during the fast walking phase and the sense of body ownership and agency during the vHIE indicate that the more one feels the virtual body and the virtual movements as one's own, the more the heart rate increases when the avatar is fast walking, confirming the link between the subjective experience of the illusion and the physiological reaction.

It also proves, once again, that the IVR illusion is extremely effective: in fact, the physiological response to the HIE seems to be somehow comparable to what happens during the same training performed in real life (Kujach et al., 2017), even though the heart rate during the fast walking phase of the vHIE shows peaks much lower than its real version.

Curiously, ratings of the online and offline questionnaires seem to be quite similar in the sample of elderly in this study and that in our previous study with young participants (Burin et al., 2020). Despite some argued differences in the sense of body ownership (Riemer et al., 2019) or in the potential strength of the multisensory illusion in the two populations (Marotta et al., 2018; Serino et al., 2018; Hide et al., 2021), the virtual illusion is quite effective independently of age (Palomo et al., 2018). The same illusion in the elderly is constant across the long-term study since there are no differences between sessions of the intervention in both groups. Independently of the experimental procedures, there might be a certain level of individuality, personality traits, or undetected components that establish the singular adherence to the multisensory illusion (Marotta et al., 2016; Burin et al., 2019b).

Previous Findings on Acute Cognitive and Neural Benefits of the vHIE (Hypothesis 2) Are Not Replicated in the Elderly

In the previous study with vHIE on young participants, the main outcome resulted from diminished response time at the Stroop task immediately after one session of virtual training in the 1PP condition (Burin et al., 2020). Here, right after the first session of vHIE in the 1PP group, we did not find the same effect replicated in the senior sample. This result is further set by the absence of an increased activation over the lDLPFC, as described by the fNIRS results. Nonetheless, we observed a clear trend from the baseline (before the beginning of the intervention) to the post-session assessment, where the response time at the Stroop task clearly decreased in the experimental group only.

This is the first attempt to compare the short- and long-term cognitive effects of a training performed virtually, to the best of our knowledge. While several studies have confirmed the potential effects of long-term interventions with different types of training, from exergames to brain trainings (Wollesen et al., 2020), little is known about the acute effects of virtual motor trainings on the elderly. A previous study with non-immersive virtual reality measuring different outcomes, including executive functions, went in a similar direction with respect to the current result: institutionalized elderly people did not show an improvement after a single session of exergames (Monteiro-Junior et al., 2017b).

Our previous study's only direct comparison is where young people showed an acute improvement in cognitive functions right after 8 min of vHIE in the 1PP condition. Perhaps, the crucial difference here is the population itself: it is quite established that body representations are updated less quickly and efficiently with age because of the deteriorated sensory modalities (Poliakoff et al., 2006; Kuehn et al., 2018), showing, for example, a bias in proprioceptive judgment (Riemer et al., 2019), which may cause falls and reduced manual dexterity. Even in the context of multisensory illusions, they seem to have difficulties in merging sensory cues coming from different sources (Hay et al., 1996; Graham et al., 2014; Kállai et al., 2017). Someone argued that adolescents and young adults need to have a more flexible self-perception with respect to the elderly since their appearance change more quickly (Tajadura-Jiménez et al., 2012), while someone else supported the associative learning theory based on the fact that the elderly have a longer experience of spatiotemporal matching sensory experiences, which in turn makes the probability of an uncertain situation, such as an experimentally induced multisensory illusion, *a priori* less likely to happen (Armel and Ramachandran, 2003; de Vignemont, 2010). Despite these possible explanations, the rubber hand illusion and other variations can be effectively induced in the elderly, as we have shown in this study, with underlying processes comparable to those in the younger population. It has been demonstrated that older adults perceive their own hand as closer to their own body with respect to younger adults before any kind of visuotactile stimulation; however, this proprioceptive bias does not correlate with the behavioral (i.e., the proprioceptive drift) and subjective measurements (i.e., questionnaire), but the strength of the illusion is persistent in a comparable manner to young people (Riemer et al., 2019). For these reasons, it might be possible that the full-body illusion (despite being present and persistent), but especially its consequences on cognitive and neural functions, requires more time to adapt in such an established representation of body and movements, while young adults are more prone to modifications of their relatively flexible system. Considering we did not perform assessments other than the post-session and post-intervention, we cannot argue here about the exact timing when the cognitive performance actually improves, i.e., which is the minimum amount of time necessary for a training, such as this one, to be effective on a cognitive and neural level. Also, since we did not run a follow-up measurement, we cannot argue about the stability of this effect. This might be an issue to be further studied.

Increased Cognitive and Neural Improvement After the Entire Intervention (Hypothesis 3) Are Reported as Long-Term Effects of the vHIE Performed by One's Own Virtual Body

As the main outcome of the study, we found a decreased response time at the Stroop task in the assessment after the 6-week intervention with respect to the baseline in the 1PP group only.

This result is doubly confirmed by the fNIRS results, where an increased activity over the lDLPFC (generally considered as part of the underlying neural network of the Stroop task) was detected, again only after the entire intervention, in the 1PP group. Interestingly, the two results significantly correlate, i.e., a shorter response time in the Stroop task corresponds to an increased neural activation on the lDLPFC. The strength of the illusion (in terms of sense of body ownership and agency over the moving virtual body in 1PP) and its repetitions across the intervention triggered the alterations in the body and movement representation of the elderly participants, necessary to induce first the physiological reaction and then the high-level cognitive response, supported by the neural activation. As argued in Burin et al. (2020), we believe that the chain of events that culminates with the improved behavioral output starts with the manipulation of sense of body ownership and agency, thanks to the virtual illusion (Slater, 2009), which has been proven to be very effective in several previous studies on a subjective (Maselli et al., 2016), motor (Burin et al., 2019a), physiological (Kokkinara et al., 2016; Martens et al., 2019; Matamala-Gomez et al., 2020), or even social (Maister et al., 2015; Bedder et al., 2019) level. In this case, we focused the effectiveness of the illusion on the subjective and physiological responses as we found especially higher ratings to the online questionnaire during the vHIE training in the 1PP, but also an increased heart rate while the virtual body in the 1PP was fast walking (also, the two measurements correlate, i.e., the increased heart rate corresponds to higher ratings to s1 and s3, statements for ownership and agency, respectively). These two data, combined in consideration of all sessions, confirm the success of the illusion itself and constitute the first and necessary "building block" for the illusion to arise (Maselli and Slater, 2013) and to determine its consequent effects. Comparable to what happens after a real physical activity (Byun et al., 2014; Kujach et al., 2017), here, we crucially found an improvement in the cognitive task, specifically at the response time.

From a neurobiological perspective, it has been described that intermittent acute physical exercises, with various intensities, trigger the release of noradrenaline, dopamine, and acetylcholine from the nuclei, possibly triggered, in turn, by the increased general physiological activation of the organism (e.g., heart rate) (Lambourne and Tomporowski, 2010; Dietrich and Audiffren, 2011). These nuclei are structurally and functionally connected to the hippocampus and prefrontal cortex (Arnsten, 2011). The latter is critically involved in executive functions and specifically to those involved in the Stroop task (MacDonald et al., 2000) and related to physical activity (Yanagisawa et al., 2010; Byun et al., 2014; Kujach et al., 2017). Here, we confirm these results by showing an increased activation with a coincident timeline with respect to the task itself (i.e., in **Figure 6**, there clearly is a peak at 6–8 s after the stimulus onset, proving its connection with the task). Inhibitory control, which is one of the key functions in the execution of the Stroop task, seems to be critical to selecting or discarding unrelated information that can interfere with the completion of a specific goal, and it seems to decline with age (Friedman and Miyake, 2004). Although, a recent study proved how overall inhibitory control at the Stroop task can be improved after an acute training even in aged people (Fujihara et al., 2021). Because of the behavioral and neural results of the present study, this neurobiological explanation might be a potential interpretation; unfortunately, as it happened in the previous study with young subjects, we did not find any significant differences in the TDMS, and specifically in the arousal subscale. This might be explained by the overall heart rate activation, which was significantly higher during the running phase, but never really high, and surely not as it happens with real physical exercise. It is possible that the virtual illusion created the conditions for the physiological activation, but that activation was not enough to be reflected in a subjective increase of the arousal level. Even though the ratio of the heart rate increase during the 1PP training is way lower with respect to what happens in real physical activity, we assume that the subjective illusion and its physiological activation on the real person's body was enough to determine the cognitive outcome, which was sustained and mediated by the neural activation over the lDLPFC. As previously argued, it also seems that the repetition of the training was fundamental for the elderly since we did not find the same effect in the acute but only in the long-term intervention.

In summary, we believe that comparable processes happen after a "real" physical exercise and after a virtual one, except that, in the latter, the actual execution of movements is replaced by the virtual body: the illusion is so strong that the general bodily arousal (even though it is not subjectively perceived) might be enough to determine the release of neurotransmitters, comparable to what happens after a training with one's own body. As explained in the first subsection of Section "Discussion," we consider the sense of body ownership and agency over the avatar in the 1PP themselves. Their consequences on the real body are a crucial key component to connecting the perceptual level of the virtual illusion with the higher functions. In contrast with previous studies (Kujach et al., 2017), we cannot argue that the generic arousal activation supplies to that role because we did not find any significance of the TDMS. Other studies with combinations of exergames (such as the Kinect) and physical exercise, in some cases on the elderly with mild cognitive impairments, argue that the improved neural efficiency acts as an intermediate between the improvement of bodily and global cognitive functions (Ansai et al., 2017; Bacha et al., 2018; Morita et al., 2018; Liao et al., 2019, 2020; Wollesen et al., 2020), which might be in line with our results. Nevertheless, they clearly exploit "real" physical activity, actually performed by the physical body, or they test VR games acting specifically on certain cognitive functions, perhaps in combination with physical exercises: the novelty of our study lies in the manipulation of the sense of body ownership and agency over the virtual body, which is the only agent performing the training, while the real body is still. Despite this contradiction, the illusory feelings toward the avatar show consequences on different and higher functions, such as the cognitive one, after the long-term intervention.

Limitations

We mentioned that the main outcome of this study is the response time of the Stroop task, although the other behavioral component is represented by the accuracy (i.e., percentage of error). We did not find any significant difference between assessments for the latter, but only a difference in the baseline between groups. It shows a pattern similar to the response time, decreasing after post-session and post-intervention assessments, but not significantly. This is consistent with the results shown by young participants (Burin et al., 2020), where it was possibly due to a contingency or a repetition effect (Hazeltine and Mordkoff, 2014), which seems to be specific for the error rate and not for speed.

A similar issue was with regard to the baseline assessments: for the error rate, as for the response time, we found a difference between groups, meaning that the two groups do not start from the same baseline level concerning the Stroop task. Possibly for this same reason, we did not find a significant difference in RT in the post-intervention assessment between groups, but a significant interaction and a significant difference in the 1PP group with respect to its baseline. Nonetheless, they show opposite patterns, and the main outcome of the response time correlates with the fNIRS data, the other measurement assessed during the Stroop task. Although the group allocation was done before the baseline assessment, it is possible that the selected participants started from different levels of speed.

The scores concerning the sense of agency statements in both online and offline questionnaires are between 3 and 4/7, around the middle point of the Likert scale, meaning uncertainty. In the online questionnaire, there is still a significant difference between groups (with 1PP higher than 3PP), but in the offline questionnaire, at s9, there is no difference between groups. These results are quite comparable to those in younger participants. As previously argued, it might be possible that this feeling of uncertainty about the explicit sense of agency is enough to attribute to oneself the seen movements, or at least show their physiological counterpart. It would be possible to further increase the sense of agency over the moving virtual body by including additional stimulations, such as vibrotactile feedbacks in correspondence to the walking–fast walking animation.

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 Ethics Committee of the Tohoku University Graduate School of Medicine. The patients/participants provided their written informed consent to participate in this study. Written informed consent was obtained from the individual(s) for the publication of any potentially identifiable images or data included in this article.

AUTHOR CONTRIBUTIONS

DB and RK conceptualized the study. DB developed and RK approved the methodology. DB implemented the software, organized the investigation and the database, performed the formal analysis, and provided the financial resources. RK was responsible for supervision. DB wrote the first draft of the manuscript. DB and RK edited and reviewed the manuscript. All authors contributed to the manuscript revision, read, 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/fnhum.2021.674326/full#supplementary-material

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REVIEW
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How Action Shapes Body Ownership Momentarily and Throughout the Lifespan

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Objects which a human agent controls by efferent activities (such as real or virtual tools) can be perceived by the agent as belonging to his or her body. This suggests that what an agent counts as "body" is plastic, depending on what she or he controls. Yet there are possible limitations for such momentary plasticity. One of these limitations is that sensations stemming from the body (e.g., proprioception) and sensations stemming from objects outside the body (e.g., vision) are not integrated if they do not sufficiently "match". What "matches" and what does not is conceivably determined by long–term experience with the perceptual changes that body movements typically produce. Children have accumulated less sensorimotor experience than adults have. Consequently, they express higher flexibility to integrate body-internal and body-external signals, independent of their "match" as suggested by rubber hand illusion studies. However, children's motor performance in tool use is more affected by mismatching body-internal and body-external action effects than that of adults, possibly because of less developed means to overcome such mismatches. We review research on perception-action interactions, multisensory integration, and developmental psychology to build bridges between these research fields. By doing so, we account for the flexibility of the sense of body ownership for actively controlled events and its development through ontogeny. This gives us the opportunity to validate the suggested mechanisms for generating ownership by investigating their effects in still developing and incomplete stages in children. We suggest testable predictions for future studies investigating both body ownership and motor skills throughout the lifespan.

Keywords: body ownership, attentional reweighting, children, haptic neglect, ideomotor theory, ontogeny, perception and action

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INTRODUCTION

What counts as a person's body? When looking at other living agents, most of them appear to have a more or less clearly circumscribed body, which is separated from other objects and other agents. Thus, the body of other agents is an object that can be distinguished from other objects by all the perceptual means that apply to separating objects from each other (such as figure-ground segmentation and gestalt factors of perception).

Yet, when agents perceive their own body, the matter of affairs seems to become more complicated. Of course, an agent's body is a distinct object, like all other objects, and can thus be separated from other objects by the same means as mentioned before. But what makes it unique? How is the biological body experienced as not just another object in the environment, but as being "owned" by oneself? The crucial factors seem to relate to interoception[1], which can be passively experienced or actively generated, as discussed in the following.

"Passive" Coincide of Interoceptive and Exteroceptive Signals

An agent's body provides sensory signals that are accessible to only the agent herself. These are interoceptive signals, which result in tactile, proprioceptive, and kinesthetic perception. Thus, interoceptive signals are unique in the sense that only one object in the perceptual world generates such signals, namely the object that is called own "body", whereas other objects do not. For example, agents can see that two objects touch each other so as they can see that an object touches the own body. Yet, only the own body generates the experience of touch. Interoceptive signals thus provide a very strong and unambiguous cue of ownership. The special role of interoceptive signals is also underlined by the existence of neuronal pathways and brain regions like the insular, anterior cingulate, or somatosensory cortex which are specialized in processing these interoceptive signals (Critchley et al., 2004; Craig, 2009).

However, an organism can perceive exteroceptive signals as well, i.e., signals that originate from locations other than that of the sensors which encode them (e.g., light reflected by an object creating a visual sensation) and also for these specific neuronal pathways exist (e.g., visual cortex: Grill-Spector and Malach, 2004; auditory cortex: Romani et al., 1982; Belin et al., 2000). Obviously, we see parts of our body (such as our hands) quite often, and other agents can also see them. If a body limb is touched, the agent feels and sees that touch so both interoceptive and exteroceptive perceptual information is available. Interestingly, visual changes that are accompanied by corresponding tactile changes are judged as belonging to the agent herself. This is the basic idea behind the rubber hand illusion and its various versions (e.g., Botvinick and Cohen, 1998; Armel and Ramachandran, 2003; Sanchez-Vives et al., 2010; Kalckert and Ehrsson, 2012; Ma and Hommel, 2015a,b; Cardinali et al., 2021). In the original experiment by Botvinick and Cohen (1998), participants received brush strokes on their occluded hand while simultaneously watching a fake hand in front of them being stroked synchronously or asynchronously with their real hand. While participants had the illusory experience that the artificial hand was part of their own body in the synchronous condition, this was not the case or to a much lesser extent in the asynchronous condition. That the system ascribes ownership to such artificial objects like fake hands comes across in different ways. First, people report experiencing ownership when being asked (e.g., Dummer et al., 2009; Rohde et al., 2011; Kalckert and Ehrsson, 2012; Ma and Hommel, 2013, 2015b; Liesner et al., 2020a). Second, the felt position of a touched body part moves towards the object that is seen to be touched (proprioceptive drift; e.g., Dummer et al., 2009; Rohde et al., 2011; Kalckert and Ehrsson, 2012; Liesner et al., 2020b). Third, there are neural (Ehrsson et al., 2004; Makin et al., 2008) and several physiological responses to these manipulations such as a temperature decrease of the stimulated body part (e.g., Moseley et al., 2008; Hohwy and Paton, 2010; van Stralen et al., 2014) and increased skin conductance responses when the observed external object is threatened (e.g., Armel and Ramachandran, 2003; Ma and Hommel, 2013, 2015a).

Following this ground-breaking observation it has been suggested that the human perceptual system is biased towards ascribing body ownership to essentially any object that generates exteroceptive signals (e.g., Gallagher, 2000; Verschoor and Hommel, 2017), providing they sufficiently coincide in a spatial-temporal manner with interoceptive signals (e.g., Botvinick and Cohen, 1998; Suzuki et al., 2013; Kalckert and Ehrsson, 2014; Tajadura-Jiménez and Tsakiris, 2014; Ma and Hommel, 2015a,b). This relatively "unselective" approach has however been criticized recently, the reasons for which we will discuss throughout this article.

Constraints of Passive Ownership and Developmental Factors

The experience of ownership in passive agents is constrained in various ways. As said before a sufficient spatial and temporal coincidence of exteroceptive and interoceptive signals is necessary. In fact, the comparison between synchronous and asynchronous stimulation has become a kind of gold standard to indicate ownership experience (Botvinick and Cohen, 1998; Ehrsson et al., 2004; Tsakiris and Haggard, 2005; for a critical assessment see Kalckert et al., 2019a).

Physical resemblance (i.e., "corporeality") of the seen body part to the own body seems important as well. By and large, the less similar an object is to an agent's body parts, the lower is experienced ownership (Tsakiris et al., 2010; Guterstam et al., 2013). Here it is important to critically evaluate the synchronous-asynchronous index mentioned before. For example, it might well be that people report more experienced ownership in the former than latter condition with all kinds of objects they see. Yet, the absolute level of the body ownership experience with non-corporeal objects is often way below what people report with a body-similar rubber hand (e.g., Kalckert et al., 2019a) and it is unclear from which level of reported experience on an "authentic" feeling of bodiliness should be assumed (see Liesner et al., 2020b, for similar arguments). Therefore, besides investigating difference scores, researchers should carefully take into account the absolute level of ownership measures and critically evaluate which conclusions can and cannot be drawn from their measures. This especially applies to explicit ratings of ownership which might be prone to demand effects (Orne, 1962) since participants might feel "committed" to respond differently

[1] Regarding the inconsistent use of the term "interoception" in the literature, we want to state here what we refer to by this term: Unlike other authors we do not constrain interoception to the perceptual signals generated only inside the body (e.g., by visceral organs; Craig, 2009; Tsakiris, 2017), but we subsume all perceptual signals under this term which are generated either on or within the biological body like, for example, also tactile signals or proprioception.

to different manipulations. Additionally, for highly corporeal objects some level of ownership experience has been reported even in the absence of any stroking, though lower compared to conditions with stroking, suggesting that the experience is elicited easily with these objects (Rohde et al., 2011; Samad et al., 2015). Despite quantitative changes, even the qualitative aspect of ownership might change with more or less corporeal objects which are stroked or actively controlled. For example, while even in the most realistic settings using the rubber hand illusion, most participants still explicitly "know" that the seen rubber hand is not actually part of their body, they nevertheless have the experience that they feel the brush stroke on the rubber hand and report that it feels like it would be their own hand (e.g., Botvinick and Cohen, 1998). However, while even with non-corporeal objects (e.g., wooden blocks, balloons, cursors), several measures (e.g., proprioceptive drift, skin conductance response) might still suggest the presence of the illusion, it is much less likely that participants report to "feel" the stroke on the artificial object, let alone rationally accept it as part of their own body (e.g., Ma and Hommel, 2015a; Kalckert et al., 2019a; Liesner et al., 2020b). In fact, it has been suggested by most studies that illusory (explicit) ownership cannot be experienced for non-corporeal objects at all (e.g., Tsakiris and Haggard, 2005; Tsakiris et al., 2010; Guterstam et al., 2013; Kalckert et al., 2019a). There are a few noticeable studies from recent years which question this constraint which we will discuss in the section "Does Active Ownership Depend on Immediate Control Experience?" (e.g., Liepelt et al., 2017; Cardinali et al., 2021). Full-body illusions (e.g., Slater et al., 2010), a paradigm in which a complete virtual body is looked at by the participant which either receives (a)synchronous tactile stimulation with the participant or is (a)synchronously controlled by the participant, might provide the opposite end of a corporeal-to-non-corporeal continuum. While grounding on the same mechanisms of visuotactile or visuomotor matching as the rubber hand illusion, it has been shown that the more realistic a virtual body looks, the less additional multisensory stimulation is needed to induce an ownership illusion (Maselli and Slater, 2013; Kilteni et al., 2015; O'Kane and Ehrsson, 2021).

In the same vein, it seems as if a biologically plausible position of the external object is necessary (e.g., Ehrsson et al., 2004) to experience ownership over it. Ownership over the (stroked) body-external object decreases with increasing distance to the participant's real limb until it vanishes completely (e.g., Lloyd, 2007; Kalckert et al., 2019b).

From a developmental perspective, it would be interesting to study whether the requirement of visual and/or anatomical resemblance is a matter of own visual experience of body parts, or perhaps more or less innate. This question is particularly pertinent for certain versions of ownership "illusions" like the impression that a seen face is the own face when being concurrently touched (enfacement illusion; e.g., Tajadura-Jiménez et al., 2012). The visual experience of the own face is, in any case, limited to technically supported instances like mirrors. Additionally, at a young age where such instances have not occurred that often, children might be even more limited regarding a visual representation of their own face. In line with this, Brownell et al. (2010) demonstrated that children below 2.5 years of age have considerable problems in identifying their own corresponding body parts when asked to match them with the body parts of an observed person which the authors interpreted as evidence for a less developed representation of the own body in these children. Consequently, the limited visual experience with their own face in young children might facilitate the "embodiment" of other faces, as there is not yet a visual standard that runs counter to this perceptual interpretation (Filippetti and Tsakiris, 2018). It has been suggested that such a standard for a "robust" face representation is only acquired by extensive visual experience with a face and that even highly familiar faces might still gradually differ from each other regarding the robustness of such a representation (Tong and Nakayama, 1999; Caharel et al., 2002). Multiple studies have shown that the right temporoparietal junction is of high relevance for recognizing one's own face providing a possible neural basis for such a robust face representation (e.g., Decety and Lamm, 2007; Heinisch et al., 2011; Zeugin et al., 2020). However, while these findings and arguments suggest that the limited visual experience with one's own face might facilitate ownership experiences in the enfacement illusion, this should only lead to gradual differences in ownership experiences so that the basic mechanisms discussed in this review which are mainly based on observations from the rubber hand illusion should also account for other body ownership illusions like the enfacement or full-body illusion (e.g., Slater et al., 2010; Maselli and Slater, 2013).

Likewise, it is important to study whether the requirement of "coincidence" of interoceptive and exteroceptive signals is innate or a matter of experience. In other words, must an agent have experienced that a certain touch typically goes along with a visually accessible object to ascribe ownership to that visual object? Some interesting insights on this might be taken from studies investigating mirror-self-recognition which suggest that, especially at an early age, immediate current visuomotor matching might play an important role in the ability to pass self-recognition tests such as the mark task (e.g., Merleau-Ponty, 1982; Mitchell, 1993). It has however been criticized that these studies might not represent "actual" understanding of the visual representation of oneself in the mirror. Instead, young children might just be highly sensitive for visuomotor synchronies and therefore simply notice the matching contingencies between sensorimotor and visual perceptions when moving in front of a mirror, without necessarily "understanding" that they see themselves in the mirror (Mitchell, 1993). The notion of children's high sensitivity for visuomotor synchronies is also supported by various studies demonstrating that children already show differentiation between synchronously and asynchronously presented visual and tactile stimulation within the first year of life (Bahrick and Watson, 1985; Zmyj et al., 2011; Filippetti et al., 2013, 2015 though see Maister et al., 2020 for possible limitations to this). This should then also account for the child's own body, which is supported by a study from Bigelow (1981) demonstrating that children in their second year of life recognize themselves earlier in conditions in which synchronous movement feedback is provided (e.g., a mirror) than in conditions without movements (e.g., a photograph). Supporting our previous suggestion that embodiment of external objects might be very flexible in children and that this flexibility should decrease with accumulating knowledge about "typical" multisensory or sensorimotor experiences, it has also been shown that the rubber hand illusion effect in children as compared to adults, is larger (Cowie et al., 2016) or less constrained to synchronous conditions or to the application of stroking at all (Cowie et al., 2013; Nava et al., 2017). This high sensitivity for visuomotor matching and flexible and less restrained inference of ownership might be extremely important for children in order to learn a consistent body model through actively generating sensory signals.

There is however also a very different way of interpreting the previously mentioned findings on children's sensitivity for synchronous and asynchronous visual and tactile stimulation (Bahrick and Watson, 1985; Zmyj et al., 2011; Filippetti et al., 2013, 2015). Tsakiris (2010) suggested a multi-step model of body-ownership in which incoming sensory information is first tested against a fixed body model before a potential multisensory contingency is detected and a sense of (body) ownership is inferred. This assumes a more or less innate body model independent from the learning experience, whose neural basis might be located in the temporoparietal junction (Tsakiris et al., 2008). According to Tsakiris (2010), the findings that (passive) ownership often cannot be elicited with non-corporeal objects or objects in an anatomically implausible position provide evidence for such a fixed body model (Ehrsson et al., 2004; Tsakiris and Haggard, 2005; Lloyd, 2007; Tsakiris et al., 2010; Guterstam et al., 2013; Kalckert et al., 2019a,b). Besides, Morgan and Rochat (1997) observed that already 3-month olds could distinguish between mirrored and unmirrored real-time videos of their own moving legs. However, even at 3 months of age children have already gained considerable sensorimotor experience, and also other (ir)regularities limiting ownership might just as well be learned based on experience. Nevertheless, the two accounts might not be that incommensurable after all since even fetuses presumably already collect some sensorimotor experience *in utero* so that an innate body model might be based on such prenatal experiences as well.

"Active" Generation of Coinciding Interoceptive and Exteroceptive Signals and "Active Ownership"

Ownership can also originate from an agent's efferent activity (e.g., Sanchez-Vives et al., 2010; Kalckert and Ehrsson, 2012). In these cases, the agent creates the sort of interoceptive-exteroceptive coincidence that generates ownership experience herself. For example, if hand muscles are contracted this comes with proprioceptive and visual experiences at the same time. As with passive stimulation discussed in the preceding paragraph, ownership by self-stimulation goes beyond objects that resemble typical body parts. Everyday experience and scientific studies suggest that all kinds of objects an agent actively controls by body movements, such as tools (e.g., Maravita et al., 2002; Weser et al., 2017), sports gadgets or virtual objects (e.g., Ma and Hommel, 2015a,b; Kirsch et al., 2016; Liesner et al., 2020a,b) can be experienced by the agent as belonging to her body to some degree as indicated by neural, physiological, explicit and implicit behavioral measures.

Despite the coincidence of interoceptive and exteroceptive signals, a very important factor shaping "active" ownership experience is that perceptual changes that occur after efferent activity were predicted or anticipated prior to these efferent activities. In other words, the perceptual changes caused by motor activity must be controllable, to create an experience of agency (Haggard, 2017). This sort of active ownership experience can thus be called "ownership by agency". In fact, it has been proposed that the controllability of perceptual events is the key, if not the only, factor for ascribing ownership to these events (Verschoor and Hommel, 2017, "self by doing approach"). In a nutshell, this approach claims that every perceptual change that is foreseeably caused by efferent activity counts as body suggesting a bottom-up approach of ownership where perceptual input is simply integrated with any motor activity producing it (e.g., Botvinick and Cohen, 1998; Armel and Ramachandran, 2003; Ma and Hommel, 2015a). This is a very optimistic approach regarding the extension of ownership to external events since it does not only suggest that a sense of ownership is triggered by control experience over perceptual changes, but also that any such control experience should lead to the ascription of ownership to the manipulated object. If it was correct, there was neither room for a distinction between the sense of agency and sense of ownership nor for a special role of interoceptive effects of motor activities for generating ownership experience, provided exteroceptive effects are sufficiently predictable. Agents with absence or loss of interoception provide an interesting testbed for this proposal (e.g., Gallagher and Cole, 1995). Furthermore, according to this reasoning, an agent should also not be able anymore to distinguish between different components of an action like a body effector, a tool, or an object in the environment that is acted upon. For example, when using a hammer to put a nail into a wall, perceptual input from the hand (proprioceptive, tactile), the hammer (visual), and the nail (visual) are all equally predictable and controllable, but does this mean that they are also ascribed ownership equally? We believe that this is too far-fetched since again, differences between interoception and exteroception need to be accounted for.

Constraints of Active Ownership

One constraining factor regarding active ownership is the anatomical resemblance. As with passive stimulation methods, most studies investigating ownership for corporeal objects showed larger illusion effects as compared to non-corporeal objects (e.g., Tsakiris and Haggard, 2005; Tsakiris et al., 2010; Guterstam et al., 2013; Kalckert et al., 2019a). However, this difference seems to be smaller for active ownership than for passive ownership (Ma and Hommel, 2015b; Liepelt et al., 2017; Zopf et al., 2018). While a sense of ownership is very limited for non-corporeal objects with passive stimulation (Tsakiris and Haggard, 2005; Tsakiris et al., 2010; Guterstam et al., 2013; Kalckert et al., 2019a), it might still be possible with active movements. However, this seems to be restricted to implicit measures such as proprioceptive drift (Liesner et al., 2020b).

Additionally, similar to passive ownership illusions, active ownership illusions have been shown to be disrupted by temporal asynchrony between interoceptive and exteroceptive sensations (Dummer et al., 2009; Kalckert and Ehrsson, 2012, 2014; Ma and Hommel, 2013, 2015a,b) and increasing distances between the biological body and the body-external object (Liesner et al., 2020b).

There is however another important constraint in active ownership, which relates to the processes of generating efferent activities in the first place. While actively operated tools can be ascribed ownership, this does not occur, if the spatial discrepancy between felt and seen movements exceeds a certain level, despite identical levels of (complete) predictability (Liesner et al., 2020a,b). In the studies by Liesner et al. (2020a,b), participants moved a cursor on a computer screen by spatially compatible or incompatible hand movements, i.e., by hand movements in the same or opposite direction. Subjective ownership ratings were higher in the compatible than in the incompatible condition, and only with compatible tool movements was proprioceptive drift significantly different from a non-control baseline condition (Liesner et al., 2020b). Interestingly, the sense of agency seems to be affected similarly by such discrepancies between interoceptive and exteroceptive signals (e.g., Ebert and Wegner, 2010; Liesner et al., 2020a), supporting the idea that the experience of agency and ownership are correlated in these situations and that the sense of agency could be a factor underlying the experience of active ownership. But why should spatial discrepancy have such detrimental effects on the sense of agency and ownership despite an identical objective level of predictability? There is ample evidence that human agents generate motor activities by recollecting the perceptual changes these motor activities produce according to previous experience (e.g., Elsner and Hommel, 2001; Kunde, 2001; Liesner et al., 2020a). This is the so-called *ideomotor approach* to action control (e.g., Koch et al., 2004; Shin et al., 2010; Waszak et al., 2012; Hommel, 2013). In the case of incompatible hand and object movements, the anticipated perceptual changes are interfering because the anticipated inverted movements of hand and object contradict the common experience that objects controlled by one's hand should move in the same direction as the hand. This interference, which is already present at movement planning, thus seems to disrupt the integration of interoceptive and exteroceptive sensations in terms of ownership experience as well.

Human agents amass a lot of experience with the interoceptive (e.g., proprioceptive, kinesthetic) effects of their motor activities, except in rare cases of loss of body-related perception which will be discussed later (section "Development of Active Ownership"). James (1981) called these effects "resident" as they almost insurmountably accompany bodily movements and thus "reside" within or on the body. So in neurotypical agents, interoceptive signals are not only unique in the sense, that just one object in the world can generate that experience. They are also unique in the sense, that they are very closely linked to the agent's efferent activities, conceivably much closer than any other possible exteroceptive effect of motor activities, both, in terms of spatial proximity and ubiquity. As explained above, efferent activities mostly produce interoceptive as well as exteroceptive effects, and agents can access motor patterns based on both. Thus, we can feel and see a hand moving and can generate that movement by imaging the visual or proprioceptive effects of doing so (Pfister, 2019). Which of these effect codes are eventually engaged is a matter of instruction (Memelink and Hommel, 2013; Mocke et al., 2020). It is also a matter of the compatibility between interoceptive and exteroceptive effects. If agents aim at certain exteroceptive effects which, however, go along with spatially incompatible interoceptive effects, such as when operating tools that move in directions opposite to the operating hand, this typically comes with performance costs (Kunde, 2001; Kunde et al., 2007; Müsseler and Skottke, 2011; Kunde et al., 2012; Wirth et al., 2015; Liesner et al., 2020a,b). Agents aim to overcome such performance costs by downregulating the less task-relevant effect component during action generation (Fourneret and Jeannerod, 1998; Knoblich and Kircher, 2004; Sülzenbrück and Heuer, 2009; Liesner and Kunde, 2020; Liesner et al., 2020b) which in tool use are interoceptive representations. This downregulation of interoceptive codes in tool use has been named "haptic neglect" (Heuer and Rapp, 2012) and can be understood as an attentional shift away from sensory signals emerging from the body and towards sensations emerging from the controlled tool. It is tempting to assume that it is exactly this downregulation of interoceptive codes in situations of discrepant interoceptive and exteroceptive action effects that prevents the integration of temporally contingent visual and interoceptive signals from the same action, which is key to ascribe ownership to visual objects (Gallagher, 2000; Tsakiris, 2017, see section "Linking Action Control and Active Ownership"). This idea has to be tested empirically though.

Does Active Ownership Depend on Immediate Control Experience?

The previously discussed studies have revealed the pivotal role of active control for the illusion of ownership for non-corporeal objects. It is however unclear whether the experience of ownership for these objects is limited to the narrow temporal windows in which this active control is experienced or outlasts the duration of immediate control over the object. In a recent study, Pfister et al. (2020) investigated this topic in an active rubber hand illusion in which they linked the tapping of participants' index fingers to the movements of a rubber hand. After 2 min of tapping, participants were asked to stop and simply look at the rubber hand for another 2 min. The authors collected subjective ownership ratings for the rubber hand both after the 2 min of tapping and the 2 min of looking at the rubber hand. Subjective ownership significantly decreased in the 2 min after participants had stopped tapping, but even after the 2 min of inactive observation, subjective ratings were still relatively high (around 5 on a 0–10 scale). Taking a cautious interpretation of absolute values of ownership into account, this study provides the first evidence that even after discontinuation of matching interoceptive and exteroceptive sensations, ownership can be experienced to some (reduced) degree. This suggests that not only present but also past agency experience with an object can shape ownership experience. In a more radical approach, Liepelt et al. (2017) used the passive rubber hand illusion paradigm and compared conditions in which the rubber hand was stroked with conditions in which the participants' cell phones or a computer mouse were stroked (a)synchronously with the participants' hands to investigate how the past experience of agency with these objects shapes possible ownership experience in the absence of immediate, current control experience and thus in the absence of immediate sensorimotor matching between interoception and exteroception. The authors found significant differences between synchronous and asynchronous stroking conditions for all tested objects, both regarding subjective ownership ratings and regarding proprioceptive drift, even though these effects were larger for the rubber hand than for the mouse and cell phone. Interestingly, the effects for the latter objects were however larger than for an additionally used wooden block (Liepelt et al., 2017, Experiment 2), an object with supposedly no experience of control over. These results suggest that in addition to concrete and recent sensory matching of interoceptive and exteroceptive signals when controlling an external object, also more complex and long–term experience of action control over external (non-corporeal) objects can lead to the feeling of ownership over these objects.

A related open question is whether mere knowledge of controllability of an object is sufficient to experience ownership over this object independently of any direct control experience. Such situations can, for example, occur with different kinds of tools which people basically know how to use but have not done so before. Cardinali et al. (2021) tested this idea by also adapting the passive rubber hand illusion, but this time using a mechanical gripper instead of a rubber hand and a balloon as a control object. While neither object resembles body parts, the illusion was elicited in terms of proprioceptive drift, subjective ratings, and skin conductance response for the gripper but not the balloon (Experiments 1 and 3) even without previous use of the gripper (Experiment 2). These results suggest that mere knowledge of sensory correlations between the body and object movements can trigger ownership experiences for external objects, possibly by means of activated action plans (see Kirsch and Kunde, 2019).

Knowledge of tool use can originate from observation (e.g., Want and Harris, 2002; Flynn, 2008; Paulus et al., 2011). This is usually explained by the observer forming associations between the observed tool changes and the actions of the observed person triggering these changes (Paulus, 2012, 2014). Thus, by observing other people's actions, humans can learn the correlations between exteroceptive and expected interoceptive sensory effects of these actions. While we are currently not aware of any studies investigating whether knowledge about the controllability of objects gained from such observation can support the feeling of ownership when later confronted with the object oneself, this might certainly be an interesting question for future research.

A further open question regarding the influence of movements on ownership illusions is whether active control and agency or a pure match between interoceptive and exteroceptive signals that come with actively moving is the driving factor behind the ownership experiences. A way to disentangle these possible influences might be to investigate the impact of passively moving a bodily effector which triggers movement effects in an artificial object. Participants undergoing such an approach would essentially lack the processes of planning and generating these movements themselves and presumably also the experience of agency since they would not actually be "controlling" the external effector in this situation. In the rubber hand illusion, it has been demonstrated that active control is necessary for the sense of agency, but not for the sense of ownership (Kalckert and Ehrsson, 2012, 2014). Kalckert and Ehrsson (2012, 2014) compared the effects of actively controlling a rubber hand and the effects of passive "control" over the rubber hand (the experimenter moved the participant's real hand and the rubber hand). While ownership over the rubber hand was elicited in both conditions (although smaller in the passive condition), a sense of agency only resulted in the active condition. It is not clear, however, how these findings would translate to non-corporeal objects such as tools and how they would interact with the other factors we have discussed. Especially the situation of incompatible interoceptive and exteroceptive perceptions would be interesting to study in this context since there could be no interference stemming from movement planning anymore. Research on *sensory attenuation* suggests that events are perceived differently when they are effects of one's own action compared to when the same events are presented without such a previous action (e.g., Voss et al., 2008; Desantis et al., 2012; Brown et al., 2013; Hughes et al., 2013) which is why it is often also used as a measure for a sense of agency (e.g., Braun et al., 2018). However, it is up until now debated whether this effect is based on mechanisms related to the action itself or rather to more general prediction processes (e.g., Kaiser and Schütz-Bosbach, 2018; Klaffehn et al., 2019). Self-induction of interoceptive and exteroceptive changes might not be necessary for a sense of ownership, providing that the input is sufficiently predictable. Interestingly, temporal binding which is often regarded as an implicit measure for the sense of agency (*intentional binding* e.g., Haggard, 2017), does not differ between active or passive finger movements if appropriate control conditions are considered (Kirsch et al., 2019). So measures of the sense of ownership might produce similar results.

Finally, past control experience may play a role in the formation and maintenance of a sense of ownership in clinical cases of paralysis caused by, for example, spinal cord injury. In these patients, afferent and efferent signals cannot be processed beyond the location of the injury which almost always leads to a loss of the ability to generate motor actions and often also limited processing of sensory input from the affected body parts (Lenggenhager et al., 2012; Lucci and Pazzaglia, 2015). However, processing of these signals had been intact in many of these patients for a long time before the incidence, posing the question of how these past experiences can still shape the sense of ownership of the affected limbs. Pozeg et al. (2017) compared paraplegic patients and healthy controls when applying a passive full-body illusion and a passive virtual leg illusion. While they found no group differences in the full-body illusion, experienced ownership for the virtual leg was significantly lower in patients than in controls. Moreover, ownership measures in patients were negatively correlated with the time since the onset of the condition. Even though the illusion in this study was induced by passive stimulation, these results suggest that the "possibility" to act, and previous sensorimotor experience support the formation of the sense of ownership, specifically for the affected limb. Additionally, attempts to re-establish sensorimotor functions in spinal cord injury patients by physiotherapy or passive motor stimulation have beneficial effects on other body-related cognitive processes such as the processing of peripersonal space or body positions (e.g., Scandola et al., 2019, 2020). Given the overlap between these processes and the sense of body ownership, it would be interesting to see whether body ownership could also be strengthened by applying such external motor stimulation similar to active control experience. Besides motor restrictions, spinal cord injuries often come with painful experiences from the paralyzed body parts (van Gorp et al., 2015). Interestingly, some of these painful sensations have also been shown to be reduced by the application of ownership illusion methods to the affected limbs, possibly because the experience of ownership over an artificial limb decreases sensory processing in one's own limb (Pazzaglia et al., 2016; Pozeg et al., 2017). Therefore it might be promising to integrate methods to induce external ownership, possibly by reactivating previous experiences of control or applying external motor stimulations in therapy and rehabilitation programs to help restoring normal levels of body ownership, body-representation, and body-related sensations in these patients.

Active Ownership and the Sense of Agency

Some studies have shown high correlations in explicit agency and ownership ratings in active object control which has led some researchers to equalize these two concepts (e.g., Ma and Hommel, 2015a,b). This reasoning is however in contrast with studies suggesting a differentiation between the sense of agency and the sense of ownership (e.g., Gallagher, 2000; Jeannerod, 2003; Tsakiris et al., 2007; Kalckert and Ehrsson, 2012). Moreover, ownership of a rubber hand can occur regardless of whether touch is actively generated or passively imposed (Tsakiris et al., 2006; Riemer et al., 2013) while it might be more expressed with active generation (Dummer et al., 2009; Kokkinara and Slater, 2014). These observations with rubber hands are in stark contrast to the findings reviewed above which suggest the necessity of active control for the emergence of ownership experiences with non-corporeal objects (Maravita et al., 2002; Ma and Hommel, 2015a,b; Kirsch et al., 2016; Weser et al., 2017; Liesner et al., 2020a,b). Thus, while for objects with visual similarity to the biological body like rubber hands, active control over these objects might play a smaller role in constructing a sense of ownership, for less corporeal objects, actual (or remembered) control seems key. Conceivably, there is a higher chance to integrate objects into one's body which also resemble the body compared to non-corporeal objects. For non-corporeal objects like cursors or geometrical objects, however, the initial likelihood that these are regarded as part of one's body might be generally very low so that additional control experience from visuomotor matching might have a stronger impact on the sense of ownership for the external object. Similarly, also in the full-body illusion, it has been shown that the more realistic a virtual body looks, the less important becomes additional control over the virtual body for an ownership illusion to emerge (Slater et al., 2010; Maselli and Slater, 2013). All these observations neatly fit with the sense of ownership constructed as a Bayesian information integration approach as suggested by Samad et al. (2015).

Linking Action Control and Active Ownership

Action planning essentially depends on previous experience with the action and the effects which are usually produced by it. Performing an action creates bidirectional links between motor codes of this action and its associated typical sensory effects, both interoceptive and exteroceptive ones (Koch et al., 2004). As explained above, integration of an actively controlled body-external object with one's body is countermanded by the interference of exteroceptive information (from the object) and interoceptive information (from the body) that contradicts the previously learned links between an action and its effects (Ebert and Wegner, 2010; Liesner et al., 2020a,b). In cases of such interference, agents tend to downregulate one of the two components, mostly the interoceptive component, in a seemingly strategical top-down process (Fourneret and Jeannerod, 1998; Knoblich and Kircher, 2004; Müsseler and Sutter, 2009; Sülzenbrück and Heuer, 2009; Heuer and Rapp, 2012; Liesner and Kunde, 2020; Liesner et al., 2020b). This downregulation probably facilitates the generation of actions with interfering interoceptive and exteroceptive information but impairs the integration of actual interoceptive and exteroceptive signals once they occur during movement execution. In a nutshell, to initiate an action, agents seek to overcome the interference of interoceptive and exteroceptive signals. They do so by downregulating, or "attending away" from, the interoceptive effect component. This interference-caused downregulation before action onset subsequently continues during movement execution and hinders the integration of actual interoceptive and exteroceptive signals after action onset because of the low representational strength of the interoceptive signals (see **Figure 1B** for an illustration). In the case where interoceptive and exteroceptive information are compatible and thus do not interfere during an action, there is no need for such downregulation since both anticipated interoceptive and exteroceptive effects can be used for action generation. Without downregulation, actual interoceptive and exteroceptive effects can be integrated into these situations easily (**Figure 1A**). While this model is mainly designed to explain differences in ownership experiences with immediate control experiences, it can also account for the findings discussed previously that past control experience alone can in some cases elicit ownership experiences as well (Liepelt et al., 2017; Cardinali et al., 2021; Pfister et al., 2020). When presenting an object with which a high amount of control experience has been accumulated in the past, the interoceptive and exteroceptive effect codes associated with controlling this object might already be activated to a degree which leads to their integration without a need to perform the action.

Furthermore, additional evidence for the high interrelatedness of action control mechanisms and the

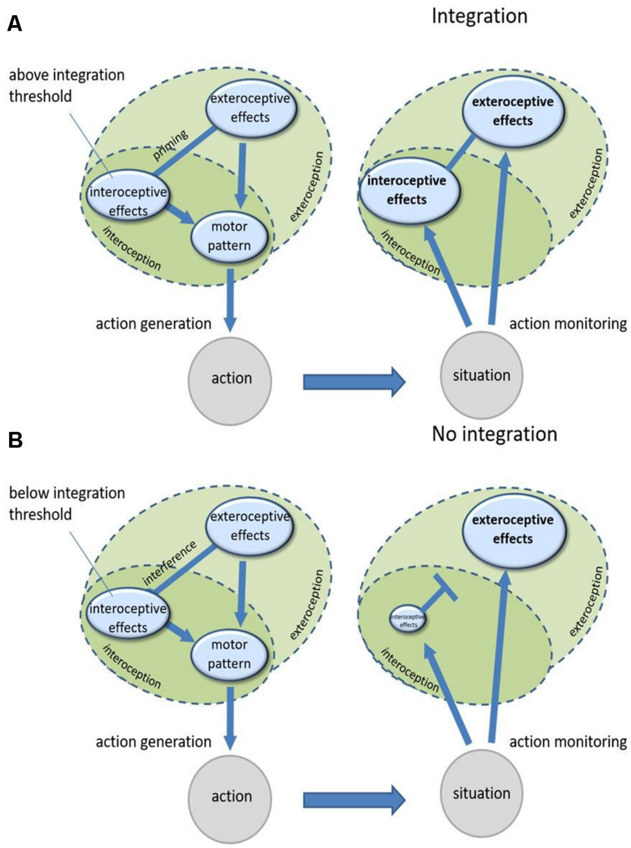

FIGURE 1 | (A) Controlling an object that produces exteroceptive effects which are compatible with the accompanying interoceptive effects. Both effect representations are linked to the same motor patterns and therefore prime each other when generating the action so that both are highly activated. When monitoring the effects of the action, both their representations are highly activated which enables their integration. **(B)** Controlling an object that produces exteroceptive effects which are incompatible with the accompanying interoceptive effects. Both effect representations are linked to interfering motor patterns so that one of them (mostly interoceptive effects) needs to be suppressed for action generation. When monitoring the effects of the action, interoceptive effects are then suppressed to a degree where they cannot be integrated with exteroceptive effects anymore.

experience of ownership stems from studies investigating the neural correlates of both these processes. For example, Evans and Blanke (2013) observed similar mu activity in sensorimotor, premotor, and posterior parietal cortices when participants were experiencing a virtual hand illusion and when they were engaging in a motor imagery task. These results are mirrored by various studies which have demonstrated neural activity in these areas both during ownership illusions (e.g., Ehrsson et al., 2004; Makin et al., 2008) and when engaging in motor planning or motor execution (e.g., Overney and Blanke, 2009; Ionta et al., 2010). Interestingly, Perruchoud et al. (2016) demonstrated that these areas showed specific activation patterns when participants performed a mental rotation task with pictures of hands, but not with pictures of full bodies. While the former task might put a stronger emphasis on sensorimotor simulation the latter might be more related to mental frame of reference rotations.

That downregulating of interfering interoceptive sensations can benefit action control is suggested by the performance of "deafferented" patients, i.e., patients with intact efferent pathways but a more or less complete loss of interoception (e.g., Taub, 1976; Cole and Paillard, 1995). Interestingly, deafferented patients do not show the performance drop in "mirror drawing", where one only sees the mirror image of one's drawing hand while copying an image, compared to standard drawing conditions that neurotypical humans normally show (Lajoie et al., 1992). When neurotypical agents mirror-draw there is a mismatch between visual and proprioceptive information, which obviously cannot occur in patients that lack the proprioceptive component. While such "forced haptic neglect" seemingly helps to perform goal-directed movements in situations which usually pose difficulties for action generation, it also has a strong impact on the way these patients perceive their own body and self (Cole and Paillard, 1995; Gallagher and Cole, 1995; Renault et al., 2018). For example, Cole and Paillard (1995) report that one of the "deafferented" patients experienced a "floating" feeling without any sense of body ownership in the first time after the onset of his condition while another patient often refers to her body as an external "tool" or "machine" rather than something which is part of herself. Interestingly, highly similar subjective experiences of a feeling of "losing" one's body have been reported by users of psychedelic drugs which disrupt proprioceptive sensations (Millière et al., 2018).

The loss of the sense of (body) ownership in cases of deafferentiation fits well with the observation that neurotypical agents experience less, or even no, sense of ownership over controlled objects in situations where agents downregulate interoception in service of action control. Such downregulation might in fact be construed a temporary "deafferentiation". The question however remains on which basis a system "decides" that incoming sensory information from interoception and exteroception interferes to a degree so that downregulation becomes necessary, which then limits the potential to experience ownership.

Development of Active Ownership

Ideomotor theory suggests that agents generate motor activities by the recollection of the perceptual effects of these motor activities which then, in turn, activates these motor activities (e.g., Koch et al., 2004; Shin et al., 2010; Waszak et al., 2012; Hommel, 2013). This however requires that the agent must have accumulated a sufficient amount of experience regarding which motor activities produce which perceptual sensations. It is assumed that this happens based on "motor babbling" in children, i.e., explorative "random" movements through which the child builds associations between specific movements and their sensory effects (e.g., Paulus et al., 2012). Based on this conjecture, also interference between interoceptive and exteroceptive sensations is based on the experience of common action-effect links, or, more specifically, on their violation. Indeed, what is "interfering" in situations in which we commonly observe, for example, difficulties in action generation, is the combination of current and previously learned action-effect combinations which are in contradiction to each other (Kunde, 2001; Koch et al., 2004; Kunde et al., 2004). For example, based on lifelong experience human agents are used to objects that move in the same direction and to the same extent as the body effector controlling these objects. If however, they are confronted with a situation in which these associations are violated, for example by inverting the movements of the controlled object, the anticipated visual effects of the object and proprioceptive effects of the moving body effector are linked to conflicting motor patterns based on one's learning history resulting in inferior performance (Kunde et al., 2007, 2012; Müsseler and Skottke, 2011; Wirth et al., 2015; Liesner et al., 2020a,b) and downregulation of the proprioceptive effects (Heuer and Rapp, 2012; Liesner and Kunde, 2020). The notion that these action-effect relationships are established over time and through experience suggests that the study of children as still developing agents provides insights into the interdependencies of the mechanisms of ideomotor learning, haptic neglect, and active ownership.

Children have accumulated less experience than adults about motor actions and their effects. Therefore, also the "knowledge" which interoceptive and exteroceptive sensations usually coincide when controlling body-external objects might be developed to a much lesser extent. Consequently, violations of the "common mapping" in cases of interference might also be less likely detected by children. At the same time, children as developing agents should be highly sensitive to current contingencies between their own actions and ensuing perceptual events in the environment, given that they still need to learn these action-effect combinations. In line with this, neuroimaging studies comparing activations in sensorimotor regions between children and adults while performing and observing actions have found lower activation patterns in children than in adults when performing the same tasks suggesting that actions might be represented in a less elaborate way in children than in adults (Mall et al., 2005; Morales et al., 2019).

Children of 3 months show less distinction in terms of event-related potentials between self-produced or externally produced stimuli than is typically observed in adults (Bäß et al., 2008; Baess et al., 2011; Meyer and Hunnius, 2021). Additionally, even children between 7 and 12 years have a strong tendency to report "illusory agency" over events objectively not caused by their actions, a bias that gradually decreases over childhood (e.g., Metcalfe et al., 2010; van Elk et al., 2015). Furthermore, children up to 10 years are unable to integrate multisensory information in an optimal fashion (Ernst and Banks, 2002). Instead, children below this age often display "overintegration" or "overbinding" in which one sensory modality is highly attended and the estimation of the other modality is (almost) completely shifted towards the former one (Gori et al., 2008; Cowie et al., 2016; Nava et al., 2020). All these findings suggest that infants and children up to the age of 10 years do not make the clear distinction between action-contingent and action non-contingent perceptual changes that adults make. Instead, they seem to be biased to ascribe perceptual events to their own actions in a less constrained way than adults. Interestingly, while the active rubber hand illusion occurs in children from 4 years on (Nava et al., 2018), it also seems to be less vulnerable to asynchronous visual and tactile stimulation (Cowie et al., 2013) and sometimes already emerges before stimulation (Nava et al., 2017). These findings fit well with the observed "overintegration" of multisensory information in children of this age and extend these findings to the phenomenon of active ownership. This suggests that the previously discussed limitations for active ownership in adults, especially the one of conflicting interoceptive and exteroceptive information, might be less pronounced in children who still develop a model of typical sensorimotor contingencies. Therefore, children, unlike (young) adults, might integrate interoceptive and exteroceptive signals "unselectively" (i.e., independently of their spatiotemporal matching) and this effect might only gradually become more selective throughout childhood.

Moreover, children between 2.5 and 8 years have considerable problems using tools that move incompatibly to their hands (Contreras-Vidal et al., 2005; Beisert and Daum, 2021), i.e., which create situations with interfering interoceptive sensations from the body effector and exteroceptive (visual) sensations from the tool, which exceed the problems that young adults have. At first glance, this might seem contradictory to the previously discussed findings and the claim that children of this age integrate multisensory information regardless of their (mis)match. However, the claim that interfering sensations are integrated in children and that this interference is seemingly not detected as such does not mean that there would be no interference produced by these sensory inputs at all in children. On the contrary, children might simply not have developed the means to overcome such multisensory conflict. Linking observations of "overintegration" of conflicting external events and performance costs in controlling such events would be a valuable contribution of future research. Additionally, the subject of "haptic neglect" has, to our knowledge, not yet been investigated in children and infants at all which would provide a further interesting testbed for the proposed mechanisms.

CONCLUSIONS AND OUTLOOK

In this article, we have reviewed and tried to integrate literature from the fields of the sense of (body) ownership, ideomotor action control, perception and action, and developmental psychology with the aim to provide a description and mechanistic explanations of "active ownership", i.e., how humans construct a sense of ownership over the effects of their actions. While we reviewed the factors supporting and limiting the feeling of active ownership and possible differences to the factors underlying passive ownership, we suggest that the overlap of interoceptive and exteroceptive sensations is the joint factor shaping the sense of ownership in both cases. Specifically, we argue that conflicting interoceptive and exteroceptive sensations stemming from the same action prevent the experience of active ownership due to compensatory downregulation mechanisms of the system to maintain sufficient motor control. This downregulation is probably less developed in children than in adults. Based on the available developmental studies on the reviewed topics, we suggest that this leads to a relatively unselective integration of interoceptive and exteroceptive sensations in children which are less constrained by the factors we have identified for adults.

While there are various studies providing empirical evidence for the phenomena we have reviewed in isolation, we want to stimulate more integrative research in the fields reviewed in this article to test relationships and commonalities of these phenomena. Specifically, the study of these phenomena in developing agents like children allows us to critically test the predictions made by our approach on how active ownership emerges. While we have so far only looked at children as developing agents more generally, it might be very interesting to compare children of different age groups which should obviously differ in brain maturation (Paus et al., 1999; Gogtay et al., 2004), regarding their experience with sensorimotor contingencies and thus also regarding the effects of interest, as has already been shown in various cross-sectional studies (e.g., Contreras-Vidal et al., 2005; Metcalfe et al., 2010; van Elk et al., 2015). Testing our proposed mechanisms and predictions in different age groups could thus provide the most direct evidence for the relationship between the processes underlying active ownership which we have suggested here.

AUTHOR CONTRIBUTIONS

ML: conceptualization, literature search, manuscript—first draft, manuscript—re-writing and editing. N-AH: literature search, manuscript—re-writing and editing. WK: conceptualization, literature search, manuscript—re-writing and editing. All authors contributed to the article and approved the submitted version.

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Exploring the Interaction Between Handedness and Body Parts Ownership by Means of the Implicit Association Test

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The experience of owning a body is built upon the integration of exteroceptive, interoceptive, and proprioceptive signals. Recently, it has been suggested that motor signals could be particularly important in producing the feeling of body part ownership. One thus may hypothesize that the strength of this feeling may not be spatially uniform; rather, it could vary as a function of the degree by which different body parts are involved in motor behavior. Given that our dominant hand plays a leading role in our motor behavior, we hypothesized that it could be more strongly associated with one's self compared to its non-dominant counterpart. To explore whether this possible asymmetry manifests as a stronger implicit association of the right hand (vs left hand) with the self, we administered the Implicit Association Test to a group of 70 healthy individuals. To control whether this asymmetric association is human-body specific, we further tested whether a similar asymmetry characterizes the association between a right (vs left) animal body part with the concept of self, in an independent sample of subjects (N = 70, 140 subjects total). Our results revealed a linear relationship between the magnitude of the implicit association between the right hand with the self and the subject's handedness. In detail, the strength of this association increased as a function of hand preference. Critically, the handedness score did not predict the association of the right-animal body part with the self. These findings suggest that, in healthy individuals, the dominant and non-dominant hands are differently perceived at an implicit level as belonging to the self. We argue that such asymmetry may stem from the different roles that the two hands play in our adaptive motor behavior.

Keywords: body ownership, IAT, handedness, asymmetry, motor behavior

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INTRODUCTION

We all experience the solid and constant feeling of owning a body, i.e., the sense of body ownership (de Vignemont, 2011). Such experience is supposed to build upon the complex integration between interoceptive, exteroceptive, and proprioceptive signals (Tsakiris, 2010; Park and Blanke, 2019; Salvato et al., 2020a). Over the past decades, an increasing number of studies have demonstrated the role of vision, proprioception, and touch in building the sense of body ownership, through various multisensory stimulation paradigms (e.g., Rubber Hand Illusion (RHI); Botvinick and Cohen, 1998; Full Body illusion; Ehrsson, 2007; Mirror Box illusion; Medina et al., 2015; Crivelli et al., 2021). Among these, the most renowned is the RHI, which consists of administering a synchronous tactile stimulation on both the subject's hand occluded from vision and a visible nearby rubber hand (for a review, see Riemer et al., 2019). Due to such visuotactile multisensory conflict, the subject may experience a sense of ownership toward the fake hand. This effect is typically detected via questionnaires (Longo et al., 2008) and by measuring perceptual changes, such as a shift in the perceived position of the unseen hand (proprioceptive drift). The RHI indeed demonstrates the critical role of vision and somatosensation in shaping the sense of body ownership (Botvinick and Cohen, 1998).

Another ingredient seems to play a fundamental role in building a coherent sense of body ownership: movement. For instance, Burin et al. (2015) have showed that hemiplegic patients experienced a stronger illusion when the RHI was administered on their plegic arm, suggesting that the pathological alteration of the normal flow of signals present during movements could influence body part ownership. They have also demonstrated that healthy participants experienced a stronger illusion of ownership over a fake hand after the immobilization of their arm by an orthopedic cast for 1 week (Burin et al., 2017). Crucially, the prolonged immobilization–and not the immobilization itself–produced this effect, since the strength of the illusion was similar before and after the immobilization maneuver, while it was stronger after a week of forced immobilization. These results suggest that when the involvement of a body part in motor behavior is limited for a prolonged period, either as a result of a brain lesion or forced immobilization, the feeling of ownership toward it is weakened, thus more susceptible to alterations of the sense of ownership. It is also interesting to note that in brain-damaged patients, the motor deficit (i.e., complete hemiplegia) seems to be crucial in the generation of the body ownership disorders, such as somatoparaphrenia, i.e., a delusional belief concerning the experienced disownership for the contralesional arm (Bottini et al., 2009; Vallar and Ronchi, 2009; Gandola et al., 2014a,b; Salvato et al., 2016, 2018).

Building upon this evidence, we hypothesize that humans may present a stronger sense of ownership toward body parts that play a leading role in motor behavior. There is already some evidence that different aspects of the representation of a body part may be modulated by the degree of its involvement in our motor behavior. For instance, the representation of the spatial features of the dominant hand is more stable, and thus, less susceptible to experimental manipulations, compared to its non-dominant counterpart and other body parts (Linkenauger et al., 2014). Furthermore, the visual recognition of one's hand is faster when the target hand is the dominant (vs. non-dominant) one, and only when it is presented from an egocentric (vs. allocentric) perspective (Conson et al., 2010). These and similar variations are likely to stem from the different resolution of sensory inflow and motor outflow information associated with each body part (Linkenauger et al., 2015; Peviani et al., 2019; Sadibolova et al., 2019; Peviani and Bottini, 2020), which in turn reflects the role of that body part in our interaction with the environment (Hsiao, 2008).

Here, we put forward the hypothesis that the strength of body part ownership may vary according to the role of the body part in motor behavior, i.e., the degree by which it is involved in motor interactions. A straightforward way to test our hypothesis is measuring whether the strength of body ownership over a body part, such as the dominant hand, is predicted by the degree of its involvement in daily-life actions, which is well-captured by handedness questionnaires (Oldfield, 1971; Dragovic and Hammond, 2007; Nicholls et al., 2013).

Research addressing the role of handedness on the RHI, in which the strength of body ownership over the hand has been often inferred as inversely proportional to the susceptibility to the RHI (i.e., illusion strength) induced over the homologous fake hand, led to inconsistent findings. For instance, some works have reported that it is harder to induce alterations of the sense of ownership over the dominant hand using the RHI (Reinersmann et al., 2013; Dempsey-Jones and Kritikos, 2019). However, by using the same approach, other investigations did not replicate such pattern of findings (Mussap and Salton, 2006; Ocklenburg et al., 2011; Smit et al., 2017). It is important to remark that these works rely on the assumption that the stronger is the illusion of owning a fake body part, the weaker is the sense of ownership toward the homologous real body part (van Stralen et al., 2013).

Here, we collect a measure of ownership strength toward a body part, i.e., the degree to which the body part is implicitly represented as associated with the self, by taking a different perspective. In detail, we explored this association by means of an established and widely-used experimental paradigm, the Implicit Association Task (IAT; Greenwald et al., 1998), which has been already applied to measure the association of concepts and representations with one's self (Bar-Anan et al., 2006; Trope and Liberman, 2010). For the first time, we use it to explore the association of a body part with the self. This approach aims to provide a more direct measure of the strength and solidity of the association between a body part and one's self, which so far has been inferred indirectly from the temporary feeling of owning a fake body part.

We hypothesized that the strength of ownership toward a body part is modulated by the role of this body part in our motor interaction with the environment. Specifically, we expect that the strength of the association between one's own right hand and the self (measured through the IAT) would vary as a function of the degree to which the right hand participates in daily-life actions (measured through the Handedness Questionnaire; Oldfield, 1971). Moreover, to test whether this possible association is human-body specific, and it is not explained by a broader association between the concepts "Right" and "Self," we administered the same IAT, but addressing the association between "Right Animal Body Part" and "Self" to another group of participants.

MATERIALS AND METHODS

Sample Size Estimation

To our knowledge, this is the first study that employed the IAT to investigate body ownership and/or handedness differences. Thus, considering the novelty of our experimental approach, we based our sample size calculation on recent work (Dempsey-Jones and Kritikos, 2019), which measured the effect of handedness on a measure of body ownership, i.e., proprioceptive drift in the RHI (Botvinick and Cohen, 1998). In this work, the authors recruited thirty-five right-handed and thirty-four left-handed, four of which were excluded from the analysis, participants (N = 65). We thus decided to approximate our sample size to seventy participants for each IAT's conditions, for a total of one hundred forty participants.

Participants

One-hundred-forty healthy volunteers (108 females; age range: 18–61 years old; M = 27.5, SD = ± 7.21; education: range 8–21 years; M = 16.1, SD = ± 2.80) participated in this online study. All participants were native Italian speakers, had a normal or corrected-to-normal vision, and had no previous mental or neurological illness history. The two groups of participants (**Figure 1**; Condition 1–Human Body Part: N = 70; Condition 2–Animal Body Part: N = 70) did not differ in age [$t(138) = 0.866$, $p = 0.388$] and education [$t(138) = -0.361$, $p = 0.719$].

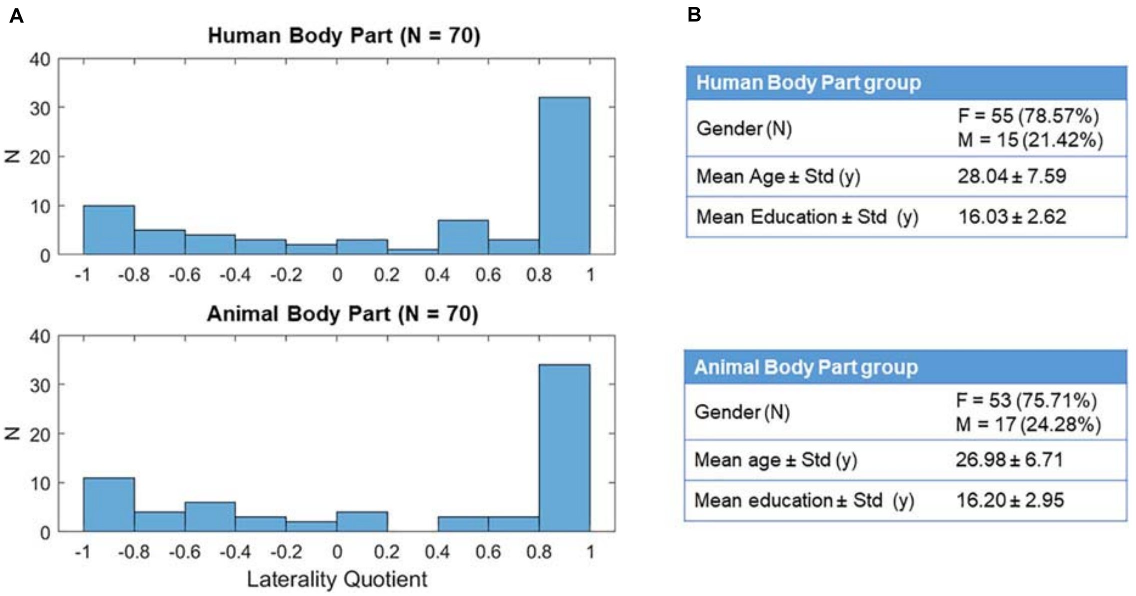
Volunteers were recruited from the University of Pavia (Italy) participant database and received course credits for their participation. Right-handed and left-/mixed- handed subjects were recruited separately by explicitly targeting one population or the other in advertising the experiment. Before starting the experiment, all participants gave their informed consent by filling an online form. The experimental procedures were approved by the Ethical Committee of the Department of Brain and Behavioral Sciences of Pavia University, and they were in accordance with the Declaration of Helsinki.

Handedness

Participant's handedness was evaluated via online administration (using Google Modules) of the Edinburgh Handedness Inventory (EHI; Oldfield, 1971). The EHI is a self-report questionnaire composed of 10 items that assess the subject's hand preference in performing different actions (e.g., writing, using scissors, using the fork). For each item, a strong preference for the right (R) or left (L) hand is reported by assigning 2 points to the relative hand, while the absence of a clear preference is reported by assigning 1 point to each hand. The laterality quotient (LQ) is then calculated by the formula (R - L)/(R + L). The EHI considers a subject dextral if his/her LQ is higher than 0.5; left-handed if it is lower than −0.5; mixed-handed if it is comprised between 0.5 and −0.5 included (EHI; Oldfield, 1971). In this experiment, we used the LQ as a continuous index because we were not interested in categorizing our subjects (identifying the "direction" of hand dominance), but rather, we aimed to use it as a way to measure how much more the dominant hand is used over the non-dominant one ("consistency" of handedness; Edlin et al., 2015). The participant's laterality quotient was balanced between the two different experimental conditions [**Figure 1**; $t(138) = 0.175$, $p = 0.862$].

IATs

The IAT (Greenwald et al., 1998) aims to measure the association between a target category and an attribute category. Both the



Human Body Part group	
Gender (N)	F = 55 (78.57%) M = 15 (21.42%)
Mean Age ± Std (y)	28.04 ± 7.59
Mean Education ± Std (y)	16.03 ± 2.62

Animal Body Part group	
Gender (N)	F = 53 (75.71%) M = 17 (24.28%)
Mean age ± Std (y)	26.98 ± 6.71
Mean education ± Std (y)	16.20 ± 2.95

FIGURE 1 | Description of the experimental sample. Panels **(A,B)** shows, respectively, the distribution of the laterality quotient and the demographic characteristics of the two experimental groups.

IAT versions we used were adapted from Salvato et al. (2020b) and differed in terms of target and attribute categories and their respective stimuli (**Table 1**), which were selected to test our hypothesis. The two IAT versions were administered in a between-subjects fashion.

One IAT version (Condition 1, Human Body Part) was designed to measure the association between the target category "Self" and the attribute category "Right Human Body Part" (Hand). In this IAT, the target categories were "Self" and "Other," whereas its attribute categories were "Right Human Body Part" and "Left Human Body Part." As stimuli, we selected five Italian words that are representative of each category (see **Table 1** for the Italian stimuli). Regarding the target category "Self," the stimuli were *I*, *me*, and *my*; this latter in three Italian declinations referred to a male, female or plural noun). For the target category "Other", we selected the following stimuli: *other*, *others*, and *they*; this latter in three Italian forms (referred to a male or female noun, or synonym). Regarding the attribute category "Right Human Body Part", the stimuli were: *right finger*, *right wrist*, *right knuckle*, *right-hand dorsum*, *and right-hand palm*. Finally, for the attribute category "Left Human Body Part," we included: *left finger*, *left wrist*, *left knuckle*, *left-hand dorsum*, *and left-hand palm*.

The other IAT version (Condition 2, Animal Body Part) was devised to measure the association between the target category "Self" and the attribute category "Right Animal Body Part". Its target categories (and respective stimuli) were the same as the previously described IAT ("Self" and "Other"). In contrast, the attribute categories were "Right Animal Body Part" and "Left Animal Body Part." For each attribute category, we selected five representative stimuli. Regarding the attribute category "Right Animal Body Part," we chose the following stimuli: *right claw*, *right chela*, *right plinth*, *right pad*, *and right spur*. As for the attribute category "Left Animal Body Part", we included: *left claw*, *left chela*, *left plinth*, *left pad*, *and left spur*.

Each IAT (**Figure 1**) was composed of five blocks, each including a certain number of trials, as detailed below. In each trial, participants were required to categorize a stimulus (appearing at the center of the screen) into one out of two categories (appearing at the top-left and top-right portions of the screen). Before starting each block, participants were presented with the target and attribute categories and stimuli, informed about the locations on the screen in which the attribute and target stimuli would have been presented, and instructed to categorize them as fast as possible according to the rules of a given block (**Figure 1**). To categorize stimuli, participants were asked to press either the "A" or "L" key using their left or right index fingers, respectively.

In the first block (20 trials), which was the same across the two IAT conditions, participants were asked to categorize each trial stimulus as belonging to the target category "Self" (appearing on the top-left portion of the screen) or "Other" (appearing on the top-right portion of the screen). In block 2 (20 trials), participants were instructed to categorize each trial stimulus as belonging to the attribute category "Right Human Body Part" (Condition 1)/"Right Animal Body Part" (Condition 2) or "Left Human Body Part" (Condition 1)/"Left Animal Body Part" (Condition 2), appearing on the top-left and top-right portions of the screen, respectively. In block 3 (80 trials), each trial stimulus belonged to either an attribute or target category, the attribute and target categories "Self" and "Right Human Body Part"/"Right Animal Body Part" were both showed on the top-left portion of the screen, whereas the attribute and target categories "Other" and "Left Human Body Part"/"Left Animal Body Part" were both showed on the top-right portion of the screen. Block 4 (20 trials) was identical to Block 1, but the position of the target categories on the screen was reversed (i.e., "Self" was presented on the top-right portion of the screen and "Other" on the top-left portion of the screen). In block 5 (80 trials), similar to block 3, attribute and target categories were again showed together but in the opposite combination. In detail, "Right Human Body Part"/"Right Animal Body Part" were both presented associated with "Other" on the top-left portion of the screen, while "Left Human Body Part"/"Left Animal Body Part" and "Self" were both presented on the top-right portion of the screen. While Blocks 1, 2, and 4 only function as practice trials, blocks 3 and 5 are critical for the IAT, because the logic behind this paradigm is that stronger associated categories will produce faster and more accurate responses than weaker combinations. In other words, if

TABLE 1 | The original stimuli (in Italian) and their English translations are reported for each IAT Condition and category.

	IAT condition human body part			IAT condition animal body part		
	Categories	**Stimuli**	**English translation**	**Categories**	**Stimuli**	**English translation**
Target	**Self**	*io*, *me*, and *mio*, *mia* and *miei*	*I*, *me*, and *my* (male–female–plural)	**Self**	*io*, *me*, and *mio*, *mia* and *miei*	*I*, *me*, and *my* (male–female–plural)
	Other	*altre* and *altri*, *loro*, *essi*, and *esse*	*other*, *others*, and *they* (male–female–synonym)	**Other**	*altre* and *altri*, *loro*, *essi*, and *esse*	*other*, *others*, and *they* (male–female–synonym)
Attribute	**Right human body part**	*dito destro*, *polso destro*, *nocca destra*, *dorso destro*, and *palmo destro*	*right finger*, *right*, *wrist*, *right knuckle*, *right hand dorsum*, and *right hand palm*	**Right animal body part**	*artiglio destro*, *chela destra*, *zoccolo destro*, *cuscinetto destro*, and *sperone destro*	*left claw*, *left chela*, *left plinth*, *left pad*, and *left spur*
	Left human body part	*dito sinistro*, *polso sinistro*, *nocca sinistra*, *dorso sinistro*, and *palmo sinistro*	*left finger*, *left*, *wrist*, *left knuckle*, *left hand dorsum*, and *left hand palm*	**Left animal body part**	*artiglio sinistro*, *chela sinistra*, *zoccolo sinistro*, *cuscinetto sinistro*, and *sperone sinistro*	*left claw*, *left chela*, *left plinth*, *left pad*, and *left spur*

someone presents a stronger association between "Right Human Body Part" and "Self" compared to "Right Human Body Part" and "Other" will categorize the stimuli faster and more accurately in Block 3 vs. Block 5. The order of the Blocks was fixed for all participants.

As detailed in the analysis section, from the IAT data, we computed the Greenwald et al.'s (2003), which is a measure of the strength of the association between the concept of "Self" and "Right Human Body Part" or "Right Animal Body Part" The task was programmed in OpenSesame (Mathôt et al., 2012).

Procedure

Data collection was carried out during the Covid-19 pandemic; therefore, we recruited participants via e-mail and administered the task from remote. Each eligible participant received an e-mail containing the instructions to participate in the experiment. Before the detailed instructions, participants were required to read and fill in the informed consent. Participants were instructed to sit in front of a pc in a quiet room and minimize environmental distractors for at least 30 min, (the whole experiment generally lasted from 10 to 20 min). Afterwards, they were required to start the IAT by clicking on the link generated through JATOS (Lange et al., 2015), an open-source web platform for online studies. IAT instructions were presented at the beginning of each IAT block (see IAT section above). Finally, participants were asked to provide their demographic information (i.e., gender, age, and educational level) and fill in the EHI via Google Modules. We opted for a between-subject design to avoid a possible carry-over effect since the two IATs were, apart from the attribute's category words, identical. Moreover, we aimed to simplify as much as possible the experimental task, considering that the experiment was administered online.

Statistical Analysis Plan

For each participant, we computed the Greenwald's d as follows [Greenwald et al., 2003; Salvato et al., 2020b: (Block 5 mean response times - Block 3 mean response times)/Blocks 3 and 5 pooled standard deviation]. Notably, the response times (RTs) were corrected accounting for the accuracy. RTs associated with incorrect responses were substituted with the average RT of the same block and adding a fixed penalty of 600 ms to those trials (Greenwald et al., 2003; Salvato et al., 2020b). The more positive the Greenwald's d value is, the stronger the association between the concepts "Right human body part"/"Right animal body part" and "Self" (but also "Left human body part"/"Left animal body part" and "Other"). On the contrary, the more negative the Greenwald's d value is, the stronger the association between the concepts "Right human body"/"Right animal body part" and "Other" (but also between "Left human body part"/"Left animal body part" and "Self"). A zero score indicates no bias at all.

To explore if handedness predicted the subject's performance at the two IAT, we performed a linear regression for each IAT condition, with the Greenwald's d as the dependent variable and the LQ as a continuous predictor. To directly compare whether the linear association varied between conditions, we used a general linear model to explore whether handedness modulated the IAT's score differently across tasks. In detail, Condition (Human Body Part and Animal Body Part), LQ and their interaction were modeled as fixed effects, while the Greenwald's d was modeled as dependent variable.

To assess that the assumptions of the linear model were not violated, we checked that the residuals of the three models were normally distributed by visually examining Q–Q plots (see **Supplementary Material**) and by means of the Kolmogorov-Smirnov test for normality. In all models, the residuals were normally distributed (Model Human Body Part: $D = 0.0706$, $p = 0.852$; Model Animal Body Part: $D = 0.0490$, $p = 0.993$; Combined model: $D = 0.0401$, $p = 0.978$). Concerning the last model, we checked for the assumption of variance homogeneity through Levene's test, which was not significant [$F(1,138) = 0.933$, $p = 0.336$].

Finally, for each linear model, we reported Bayes factors (BF_{10}), which represent the likelihood of the presence of the effect (H_1) to the likelihood of the absence of such effect (H_0), given the data. BF_{10} values larger than 1 represent evidence for the alternative hypothesis (H_1) (Rouder et al., 2009).

Frequentist analyses were carried out using Jamovi (Sahin and Aybek, 2019; Version 1.2; The Jamovi project, 2020), while Bayesian analysis was carried out using JASP (Version 0.8.6; JASP Team, 2018).

RESULTS

Results showed that in the first IAT condition (Human Body Part) handedness significantly predicted the Greenwald's d score. In detail, a significant regression equation was found [$F(1,68) = 34.8$, $\beta = 0.582$, $p < 0.001$, $BF_{10} = 90611.110$], with an R^2 of 0.339 (see **Figure 3**, panel *A*).

In contrast, in the second IAT condition (Animal Body Part) handedness did not predict the Greenwald's d score. The linear regression model was found to be not significant [$F(1,68) = 3.37$, $\beta = 0.217$, $p = 0.071$, $BF_{10} = 1.024$], with an R^2 of 0.0472 (see **Figure 3**, panel *B*).

The general linear model performed on the whole dataset [$F(3,136) = 11.4135$, $p < 0.001$, with an R^2 of 0.201] revealed a significant main effect of LQ, which linearly predicted the Greenwald's d score [$F(3,136) = 11.4135$, $\beta = 0.\ 4081$, $p < 0.001$, $BF_{10} = 14933.293$]. In contrast, the main effect of Condition was not significant [$F(3,136) = 0.0374$, $\beta = -0.0296$, $p = 0.847$, $BF_{10} = 0.177$]. Critically, the interaction between LQ and Condition was significant [$F(3,136) = 6.8278$, $\beta = -0.4008$, $p < 0.01$, $BF_{10} = 4.121$], showing that the strength of handedness modulation on the IAT's score was different when the subjects had to associate "Self" with "Right Human Body Part" or "Right Animal Body Part" (see **Figure 3**, panel *C*).

DISCUSSION

The sense of body ownership is built upon the integration between several multisensory signals and pre-acquired information about one's own body (Tsakiris, 2010). The brain disposes of quantitatively and qualitatively varied information on different body parts, according to their role in our motor interaction with the environment. Previous research has

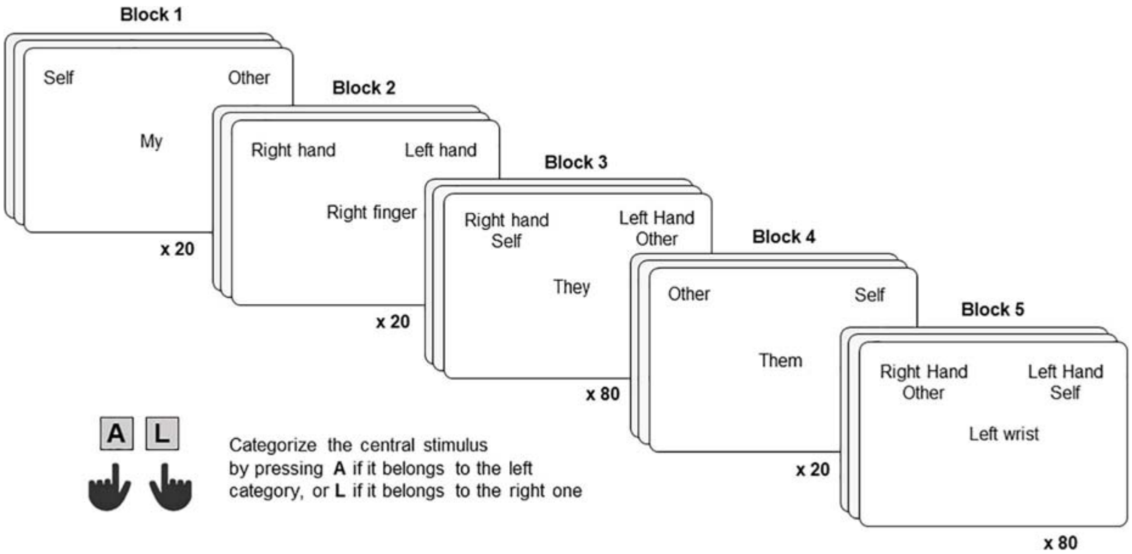


FIGURE 2 | For each block of the Human Body Part condition, one exemplificative trial is represented. In each trial, participants were required to categorize the word displayed at the center as belonging to the leftward or rightward category, by pressing the "A" or "L" key, using their left or right index finger, respectively.

shown that information generated by everyday movement may play a relevant role in constructing body ownership (Burin et al., 2015, 2017).

Here, we hypothesized that the degree by which a body part is represented as belonging to the self (i.e., body-part ownership) varies in the degree of its involvement in motor behavior. We expected that handedness, measured as the subjective hand preference in a series of daily-life adaptive actions (EHI; Oldfield, 1971), would predict the strength of the implicit association between the right hand and the self (measured through the IAT). In line with our hypothesis, we found that in the Human Body Part condition the laterality quotient (LQ), whose value indicates hand dominance, predicted the implicit association between "Self" and "Right Human Body Part," measured through the IAT. More in detail, we found that the strength of this association increased as a function of the degree by which healthy subjects reported a preference for the right (over the left) hand in performing daily-life actions.

Hand dominance is associated with different aspects of human behavior, which may explain our results. For instance, it could be argued that the dominant hand is preferred over the non-dominant one simply because, semantically, the concept of "Right" is more familiar and closer to the self for dextral individuals, and vice versa for left-handers. In fact, it was shown that right-handers tend to associate "Right" with positive concepts while left-handers, in contrast, presented the opposite patterns (Casasanto, 2009). However, a purely conceptual association between "Right" and "Self" is not sufficient to explain the entirety of our data. Indeed, we found that handedness significantly predicted the association between "Right Human Body Part" and "Self," but not between "Right Animal Body Part" and "Self" (Condition 2).

Another possible explanation for our results could be that hand dominance often reflects differences in functional brain organization. Indeed, dextral individuals present robust hemispheric lateralization for specific cognitive functions, such as language (Steinmetz et al., 1991; Badzakova-Trajkov et al., 2010) and spatial processing (Vogel et al., 2003). It could then be argued that the different IAT outcomes in right- and left-handed participants could mirror such neuro-functional asymmetries, similarly to what has been found in other body representation tasks. For instance, Linkenauger et al. (2009) showed that the dominant arm is perceived as longer than the non-dominant counterpart, only in right-handed individuals. Furthermore, right-handed individuals tend to perceive right body landmarks (e.g., the right hip) as more distant from their midsagittal plane than their left counterparts, showing poorer body exploration skills over their left (vs. right), hemibody. Crucially, such difference was not present in left-handed subjects (Hach and Schütz-Bosbach, 2010). While these works have demonstrated a lateralized pattern of performance in right-handed individuals only (Linkenauger et al., 2009; Hach and Schütz-Bosbach, 2010), we found that right- and left-handed individuals showed similar, albeit mirrored, response patterns when it comes to the sense of ownership over the dominant vs non-dominant hand. In other words, our data indicated that the association between the dominant hand with the self is similarly present in the right- and left-handed individuals (see **Figure 3**, panel A). Therefore, our results cannot be explained by the greater lateralization of certain neurocognitive functions in right-handed compared to left-handed individuals.

We argue that stronger ownership toward the dominant hand could be associated with its leading role in motor behavior, and that this may be adaptive to our interaction with the environment. Compared to other mammals, humans show a stronger manual preference in unimanual actions (Bryden et al., 2000; Annett, 2004). When engaged in daily-life bimanual actions, the two hands play different roles: the

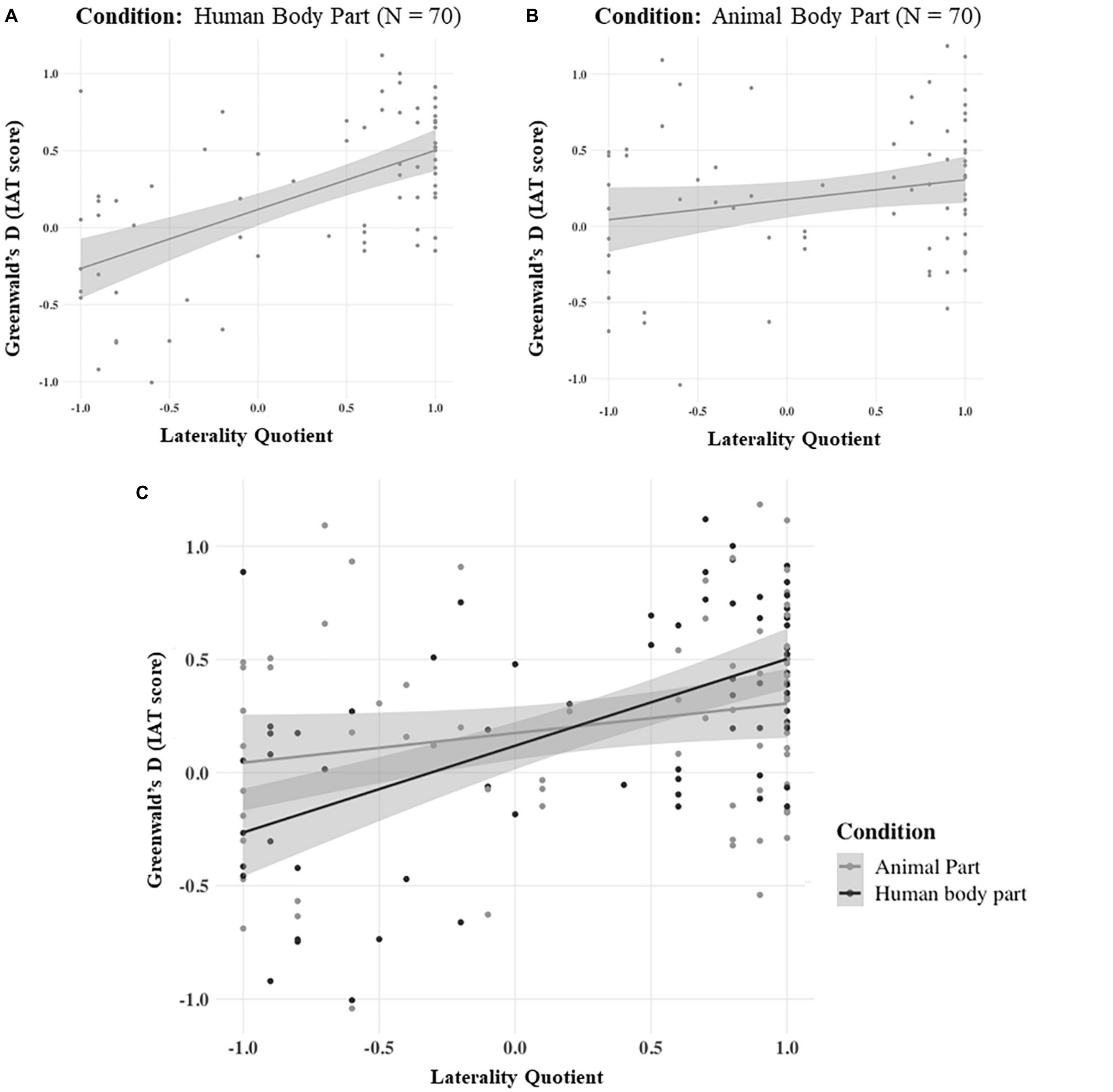


FIGURE 3 | The linear relationship between the Greenwald's d, on the Y axis, and the Laterality Quotient, on the X axis, in the Human Body Part **(A)**, Animal Body Part **(B)**, and Combined **(C)** conditions. The gray shade near each line represents the standard error of the respective model.

dominant hand has a leading role, while the non-dominant has a supporting role (Guiard, 1987; Stone et al., 2013). Many items included in handedness questionnaires (Oldfield, 1971; Dragovic and Hammond, 2007; Nicholls et al., 2013) bring examples of daily-life actions in which the two hands play very different roles (e.g., holding the scissors with the dominant hand and the paper sheet with the non-dominant one). Moreover, representational asymmetries between the two hands have been already documented. For instance, the representation of the spatial features of the dominant hand is more stable (Linkenauger et al., 2014); and such stability is possibly functional and adaptive for the dominant hand to be used as a "natural perceptual metric" (Linkenauger et al., 2013, 2014). Notably, these asymmetries pertaining to the internal representation of the hands are mirrored by asymmetries of their homologous cortical representations, involving not only the structural and functional properties of the "hand-knob" in homologous primary motor cortices, but also those of subcortical and white-matter regions (Volkmann et al., 1998; Grabowska et al., 2012; Germann et al., 2019). Indeed, the dominant hand has a crucial role in our functional interaction with the environment. A stable representation of its spatial properties and relation to the self may serve adaptive behavior.

Although quantitative observations are hampered by the low occurrence of disorders of body ownership following brain vascular accidents, our results are also coherent with the fact that these disorders seem to follow a lateralized pattern in right-handed patients. In a review considering the epidemiology of somatoparaphrenia (Vallar and Ronchi, 2009), it has been reported that the great majority of dextral patients (51/55) did not recognize their left side of the body as their own. Interestingly, the only left-handed patient showed pathological disownership toward his non-dominant hand.

Previous RHI studies exploring the role of handedness in modulating the strength of body-part ownership have produced inconsistent findings. For instance, some studies have shown that the illusion strength, measured by subjective reports and/or perceptual changes, did not vary between the dominant and non-dominant hands (Mussap and Salton, 2006; Smit et al., 2017). Other studies have reported a stronger illusion over the left hand in both right-handed and left-handed subjects (Ocklenburg et al., 2011). On the contrary, RHI susceptibility was also shown to be greater for the left hand in dextral subjects (Reinersmann et al., 2013) and to increase as a function of hand-dominance strength (Niebauer et al., 2002). Coherently, further investigations have reported a stronger RHI over the non-dominant hand in both right-handed and left-handed subjects (Dempsey-Jones and Kritikos, 2019). A possible reason for this inconsistency may be related to the intrinsic features of the RHI paradigm, which might not be well-suited to fully capture the existent asymmetry concerning the strength of ownership over the dominant and non-dominant hands. The RHI is an indirect measure of the ownership strength toward a body part, hypothesized to be inversely proportional to the susceptibility to the RHI (van Stralen et al., 2013). In other words, many RHI investigations rely on the assumption that the stronger is the illusion of owning a fake body part, the weaker is the estimated sense of ownership toward the homologous real body part. This inference can lead to informative estimates but may do not fully account for the role of the several sources of bodily information that contribute to the sense of body ownership. Some of these sources may not be necessarily affected by the RHI, such as the conscious awareness that the fake hand does not belong to the self, or the deep-rooted association of individuals' body parts with themselves. Therefore, it is likely that the susceptibility to the RHI does not neatly reflect the strength by which a body part is associated with the self. Our work represents the first attempt to directly measure the strength of body-part ownership without inferring it from the illusory feeling of embodiment toward a fake body part. We showed that relevant aspects related to the bodily self could be unveiled not only when body ownership is artificially or pathologically altered, but also when it is healthily and fully present.

CONCLUSION

By adopting an original approach to measure body ownership in healthy subjects, this study provided evidence of stronger ownership toward the dominant vs non-dominant hand. Contrarily to more traditional experimental approaches, which elicit alterations of the sense of body ownership to explore how a body part is represented as one's own, we directly measured the degree by which a body part is implicitly associated with the self. We argue that such asymmetry may stem from the different roles that the two hands play in our adaptive motor behavior and possibly be reflected by their different cortical representations. One possible limitation of our study is that we measured participants' handedness through a self-report questionnaire, which principal aim is to provide a trichotomous categorization of hand preference rather than obtaining fine-grained information about how much a hand is used compared to the other. Nevertheless, it is important to note that the EHI has already been used as a measure of hand dominance "consistency" in psychology and cognitive neuroscience (for a review, see Edlin et al., 2015). Future investigations could explore these aspects by using a more objective index of handedness, such as a motor performance measure (Peters and Durding, 1979; Bryden et al., 2000), while also investigating how they unfold not only in healthy but also in pathological individuals.

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 Ethical Committee of the University of Pavia, Department of Brain and Behavioral Sciences. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

DC and VP conceptualization, investigation, visualization, data curation, formal analysis, and writing–original draft. DC methodology. GS and GB conceptualization, project administration, methodology, supervision, and writing–review and editing. 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/fnhum.2021.681904/full#supplementary-material

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The Perceived Match Between Observed and Own Bodies, but Not Its Accuracy, Is Influenced by Movement Dynamics and Clothing Cues

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Own-perceived body matching – the ability to match one's own body with an observed body – is a difficult task for both general and clinical populations. Thus far, however, own-perceived body matching has been investigated in situations that are incongruent with how we are used to experience and perceive our body in daily life. In the current study, we aimed to examine own-perceived body matching in a context that more closely resembles real life. More specifically, we investigated the effects of body movement dynamics and clothing cues on own-perceived body matching. We asked participants to match their own body with an externally perceived body that was a 3D-generated avatar based on participants' real bodies, fitted with a computer-generated dress. This perceived body was (1) either static (non-walking avatar) or dynamic (walking avatar), (2) either bigger, smaller, or the same size as participants' own body size, and (3) fitted with a dress with a size either bigger, smaller, or the same as participants' own dress size. Our results suggest that movement dynamics cues did not improve the accuracy of own-perceived body matching, but that confidence about dress fit was higher for dynamic avatars, and that the difference between dynamic and static avatars was dependent on participants' self-esteem. Furthermore, when participants were asked to rate the observed body in reference to how they wanted to represent themselves to others, dynamic avatars were rated lower than static avatars for the biggest-sized bodies only, possibly reflecting the influence of movement cues on amplifying socio-cultural stereotypes. Finally, while smaller body/dress sizes were systematically rated higher than bigger body/dress sizes for several self-report items, the interplay between body and dress size played an important role in participants' self-report as well. Thus, while our research suggests that movement and garment dynamics, allowing for realistic, concrete situations that are reminiscent of daily life, influence own-body perception, these cues did not lead to an improvement in accuracy. These findings provide important insights for research exploring (own-) body perception and bodily self-awareness, with practical (e.g., development of online avatars) and clinical (e.g., anorexia nervosa and body dysmorphic disorder) implications.

Keywords: body representation, body perception, bodily self-awareness, movement, self-esteem, avatar

INTRODUCTION

We experience and interact with the world through our body. In order to do so efficaciously and efficiently, humans need to be able to accurately and dynamically perceive their own body. Own-body perception has been extensively investigated using body illusions where the perception of one's body deviates from the physical one (for a review see Kilteni et al., 2015). These include body distortion illusions, in which the size or posture of the body or its body parts are perceived as distorted (e.g., Goodwin et al., 1972; Ramachandran and Hirstein, 1998); out-of-body illusions, in which people perceive their self to be dislocated from their own body and/or people look at their body from a distance (e.g., Ehrsson, 2007; Lenggenhager et al., 2007); and body ownership illusions, in which non-bodily objects are perceived as a part of one's own body (e.g., Botvinick and Cohen, 1998; Petkova and Ehrsson, 2008; Dummer et al., 2009; Peck et al., 2013; Maselli and Slater, 2014). These illusions demonstrate that the sense of body ownership, defined as the experience of one's body and its body parts as one's own, and necessary to move through the world and interact with others (Martin, 1995; Gallagher, 2000; Ehrsson, 2012; Gallagher and Daly, 2018), is a dynamic and malleable process that is determined by multisensory integration mechanisms (Ehrsson, 2012; Kilteni et al., 2015; Ehrsson and Chancel, 2019; Chancel and Ehrsson, 2020).

In addition to perceiving our own body from within through the integration of multisensory and sensorimotor inputs (Kilteni et al., 2015), own-body perception also takes places when confronted with the task of matching an externally perceived body with our own. This matching of our own body with an externally perceived body (own-perceived body matching) has been shown to be largely inaccurate, with people systematically over-estimating (Hashimoto and Iriki, 2013; Linkenauger et al., 2017; Sadibolova et al., 2019) or under-estimating (Valentina Tovée et al., 2003; Cazzato et al., 2016b; Ralph-Nearman et al., 2019) their body shape and size. These distortions in our body image have been measured both explicitly (Hashimoto and Iriki, 2013; Linkenauger et al., 2017; Pitron and de Vignemont, 2017; Sadibolova et al., 2019) and implicitly (Longo and Haggard, 2010, 2011; Maister et al., 2021). Importantly, they impact general well-being and have been linked to various clinical disorders (Stice and Shaw, 2002; Kaplan et al., 2013; Dakanalis et al., 2016). Furthermore, this inability to match own and perceived body has several practical implications, such as for the design of self-avatars for online gaming (Ducheneaut et al., 2009) and retail (Merle et al., 2012) experiences. The latter, for example, suffers from general dissatisfaction with purchased items and high return rates (Gallup, 1970; Petersen and Kumar, 2009; Saarijärvi et al., 2017), which have been partly attributed to a lack of resemblance between consumers and their online model/avatar (Kim and Forsythe, 2008). Nevertheless, despite its clinical and practical importance, this form of own-body perception, which involves matching an externally perceived body with one's own, has remained difficult to improve.

In a study comparing healthy controls with individuals diagnosed with anorexia nervosa, researchers achieved this seemingly difficult task by generating personalized realistic avatars using a combination of 3D scanning and computer-generated imagery (CGI) techniques (Cornelissen et al., 2017). While an over-estimation of own body measurements was still observed in the group of individuals diagnosed with anorexia nervosa, the healthy control group showed accurate body size estimation. The authors suggested that their combined 3D-CGI method might be less prone to visual artifacts and may provide a clearer insight into the size and shape that someone considers him/herself to be. Additionally, they argue that contextualizing own-body evaluation in ecologically valid situations (e.g., looking in the mirror) is vital for future research in the field. While they suggest that the only way to truly achieve this is by allowing participants to inhabit a personalized 3D avatar in whom participants can manipulate body changes in real time, this method has rendered conflicting results (Piryankova et al., 2014; Preston and Ehrsson, 2014; Dakanalis et al., 2017) and poses practical challenges that are difficult to implement in daily life (e.g., the widespread availability of at-home technology to inhabit 3D avatars). Furthermore, during body perception/estimation experiments, own-perceived body matching is often performed in a way that is incongruent with how we are used to experiencing and observing our own body in daily life. First, while we are used to experience our own body in movement, movement dynamics have thus far not been included when investigating own-perceived body matching, although action and motor experience have been shown to be important in the development and maintenance of body ownership (e.g., Dummer et al., 2009; Nava et al., 2018). Second, the avatar/model bodies during own-perceived body matching are usually presented either without clothing (e.g., De Coster et al., 2020) or with static clothing that does not provide additional cues (e.g., wrapping of different sizes of clothing around the body, movement of clothing when body moves) for body size estimation (e.g., Cornelissen et al., 2017; Mölbert et al., 2018; Thaler et al., 2018; Sadibolova et al., 2019). While it has been shown that dynamics play an important role in the perception of clothing (Aliaga et al., 2015) and that observers are able to infer certain body properties (e.g., body stiffness) from clothing dynamics (Romero et al., 2020), as well as the clothing's mechanical properties (Bi and Xiao, 2016), the question whether body size can be predicted by these dynamics and whether own-perceived body matching would be improved by these additional cues remain open questions. In sum, while movement and clothing dynamics likely play an important role in own-body perception in daily life, they have thus far not been investigated.

In the current study, we built upon the idea of emulating real-life practical situations when investigating own-body perception in the context of matching own with a perceived body. More specifically, the aim of this research was to systematically examine the influence of movement dynamics and clothing, two factors that are usually present when we perceive our own body in daily life, on own-perceived body matching. While it has been claimed that we do not have access to observing our body in motion (Kadambi and Lu, 2018), we argue that we rarely observe our own bodies and the accessories that come along with it in purely static positions (e.g., twisting and turning in front of a mirror). Furthermore, while the recognition of our body in motion depends on the integration of the combination of visual, somatosensory, proprioceptive, and motor information (Myers and Sowden, 2008), as well as auditory information (Tajadura-Jiménez et al., 2015), we believe that the contribution of visual motion cues alone may still be of relevance to this recognition process. In order to achieve this aim, we created several realistic 3D avatars of different sizes based on participants' bodies using Skinned Multi-Person Linear modeling (SMPL; Loper et al., 2015). This parametric modeling method is thought to be more accurate and easier to use than other methods, partly because it avoids the intense manual effort inherent to commercial approaches (e.g., CGI). In accordance with a previous study using a similar method (De Coster et al., 2020) and previous research using other techniques (Valentina Monteath and McCabe, 1997; Tovée et al., 2003; Johnson et al., 2008; Fikkan and Rothblum, 2012; Cazzato et al., 2015; Spahlholz et al., 2016; Robinson and Kersbergen, 2017; Steinsbekk et al., 2017; Ralph-Nearman et al., 2019), we expected participants to not be able to accurately match their own with a perceived body. More specifically, we expected them to show a preference for smaller- compared to bigger-sized avatars, irrespective of their own body size. Importantly, we contextualized the task of matching own and perceived body in a real-life situation by (1) comparing the accuracy of matching participants' own with a perceived avatar's body that was either static or dynamic (walking avatar), (2) fitting the observed model/avatar with a computer-simulated dress in different sizes, and (3) specifically asking participants about their wish to use the perceived model/avatar for online shopping (De Coster et al., 2020). Concerning the effect of movement dynamics, we hypothesized that the addition of dynamic movement cues would increase participants' ability to accurately determine their own body size/shape given the additional information that these movement cues provide and the resemblance to our everyday real-life environment. This comparison of static vs. dynamic avatars was our main effect of interest, since we expected these findings to render important insights into the role of action cues in own-body perception and bodily self-awareness, with both clinical and practical implications. To further examine these implications, we investigated whether this effect of movement dynamics was modulated by bodily self-esteem and personality differences given that previous research has shown that both self-esteem (e.g., Maister et al., 2021) and personality variables (e.g., De Coster et al., 2020) influence body size estimation. Both healthy (Cornelissen et al., 2013) and clinical (Gardner and Brown, 2014) populations with negative attitudes toward their own body weight, as well as healthy populations scoring higher on neuroticism (Hartmann and Siegrist, 2015), have been shown to overestimate their own body size. We consequently expected that the addition of dynamic cues – which we hypothesized would lead to more accurate body size estimation – might have a different effect (e.g., due to differences in the processing of bodily information; Irvine et al., 2019) for participants with certain personality traits (e.g., neuroticism) and participants scoring low on bodily self-esteem measures, compared to other participants. Finally, we added a dress simulation in different sizes to ensure that the perception of the avatar's body was congruent with how we generally observe our bodies in everyday situations where we mostly perceive ourselves with, rather than without, clothes (note that this dress simulation was also influenced by the body's movement dynamics). Thus, we expected that a correct dress size would improve the detection of participants' own body size.

MATERIALS AND METHODS

Participants

Sample size was dictated by a Bayesian approach using JASP (JASP Team, 2020). Participants were recruited from a subject pool of participants who participated in previous experiments, with the following inclusion criteria: (1) given that the experimental stimuli had to be based on videos of participants' actual bodies (see below), participants were only eligible if such videos were available since the COVID-19 pandemic and the videos' specific requirements (e.g., correct distance between the participant and the camera, no background items present, specific clothing for the participant to wear) made it impossible for us or for the participants themselves to record new videos, (2) in order to be able to model both a dress size below and above participants' real dress size, only participants with a self-reported dress size of 38 or 40 (EU sizes) were eligible (only EU dress sizes 36, 38, 40, and 42 were available to be modeled), (3) to exclude gender effects (He et al., 2020), all participants had to be female. Considering these criteria, the size of our initial available subject pool was 20. We scheduled to test 15 participants, and planned to check the Bayes Factor (BF; prior based on a Cauchy distribution, default scale of 0.707, zero-centered) after data collection for this group was completed. If a stopping criterion had not been reached, we planned to repeat this procedure for the additional five participants, and expand the subject pool if necessary. The stopping criteria included: (1) the BF reached the threshold for moderate evidence to either support ($BF_{10} < 1/3$) or reject ($BF_{10} > 3$) the null hypothesis for the effect of dynamic vs. static avatars (our main effect of interest) for all self-report items, (2) the pre-specified end date (30/06/2020) had been reached. The experiment was terminated due to reaching the first criterion, and data collection was halted at 15 participants.

Fifteen adults (age in years: range = 18–28, M = 21.60, SD = 2.65; 11 participants with dress size 38, four participants with dress size 40), all female and residing in Spain, participated in the study in exchange for a gift card of 10 euros. Body mass index (BMI) in our sample ranged between 19.3 and 24.1 (M = 21.49, SD = 1.55), which lies within the healthy range (18.5–24.9) as defined by the World Health Organization. One participant scored more than two standard deviations below the sample average on all subscales of the bodily self-esteem questionnaire (see below; see **Table 1** for questionnaire data). Removing this participant from the analyses did not change the results. The study was conducted in accordance with the 1964 Declaration of Helsinki and was granted ethical approval by the local ethics committee at Universidad Carlos III de Madrid. All participants provided informed written consent beforehand.

Stimuli and Apparatus

Figure 1 shows an example frame of the experimental stimuli within the experimental procedure. Example videos (all Body/Dress size combinations are represented in one video for the dynamic and static condition separately) can be found in the **Supplementary Material**.

After obtaining a 360° full-body capture of participants, existing software COLMAP (Schönberger and Frahm, 2016; Schönberger et al., 2016) and custom-made scripts were used to create an avatar representing participants' real bodies. This avatar was represented using SMPL (Loper et al., 2015) which includes several parameters to modify the avatar mesh. For each participant, different avatars were created by increasing or decreasing the second shape parameter, which primarily reflects changes in waist circumvention (although the avatar's full body changed proportionally with respect to participants' original body size, i.e., Body size 0). This resulted in three different avatars per participant: an avatar with a body size smaller than participants' original body size (Body size −1; approximately 4 cm waist reduction), an avatar representing participants' original body size (Body size 0), and an avatar with a body size bigger than participants' original body size (Body size +1; approximately 4 cm waist increase; for full details on the avatar creation process see De Coster et al., 2020).

TABLE 1 | Mean (M) and standard deviations (SD) for the subscales of the Body Esteem Scale for Adolescents and Adults (BESAA; rated on a scale from 0 to 4) and the Big 5 Inventory-10 (BFI-10; rated on a scale from 1 to 5).

Questionnaire subscale	M	SD
BESAA Appearance	2.54	0.76
BESAA Attribution	2.47	0.50
BESAA Weight	2.72	0.95
BFI-10 Extraversion	3.00	0.80
BFI-10 Agreeableness	2.90	0.64
BFI-10 Conscientiousness	3.77	0.77
BFI-10 Neuroticism	2.93	0.79
BFI-10 Openness	3.73	0.95

Additionally, a digital dress was created after extracting the patterns and creating 3D meshes from a real dress that was bought in different sizes (36, 38, 40, and 42). The patterns and initial resting position of the virtual dress were created with CLO3D[1]. Before extracting the dress' 3D mesh, the dress was partially inflated to separate it from the skin of the avatar mesh, to ensure that there were no initial collisions in the simulation. Similar to the body size manipulation, different dress sizes were created: a dress size that was a size smaller than participants' original dress size (Dress size −1), a dress size that reflected participants' original dress size (Dress size 0), and a dress size that was a size bigger than participants' original dress size (Dress size +1). This resulted in nine body/dress size combinations that were randomized per participant.

In order to allow for dynamic stimuli that represented real-life body/dress behavior during action movement, a walking animation was simulated for all avatars (Varol et al., 2017). The dress simulation was added using the simulation engine ARCSim, which allows for fine details and the preservation of fine-scale dynamic behavior (Narain et al., 2012, 2013; Pfaff et al., 2014). The application of one of the default materials (Wang et al., 2011) resulted in a sequence of meshes that represented the dress in different states of the avatar animation. Subsequently, videos of front and back views of the walking avatars with the dress simulation were rendered using Maya (Autodesk, 2019), and combined into one 4-s video in MATLAB (front view of the avatar on the left side, back view of the avatar on the right side).

Finally, two different video types (1,280 × 720 pixels) were created that were used as experimental stimuli. For the dynamic stimuli, videos of the walking avatars were looped four times to allow for sufficient time to inspect both the front and back view of the avatars (16 s; this duration was selected based on a pilot where several durations were tested). For the static stimuli, two frames (one frame where the avatar has the left foot in front, and another frame where the avatar has the right foot in front) were selected out of the original 4-s videos using Matlab. These frames were combined into a 4-s video in which each frame was shown for 2 s, and looped four times such that the total duration of these static stimuli was equal to that of the dynamic stimuli (16 s).

Self-Report Measures

As described above, an experimental trial consisted of participants observing one of the stimuli for 16 s. At the end of each trial, participants were presented with nine self-report items that had to be rated on a continuous scale from −100 to +100. These items were adapted from previous research (Jin, 2010; Latoschik et al., 2017; De Coster et al., 2020), and measured participants' own body perception in terms of perceived match between the observed avatar's body and their own, as well as participants' preferences toward the observed avatar across different dimensions (see **Table 2** for a description of the items). The items were always presented in the same order: "Dress," "Dress confidence," "Measurements," "Measurements confidence," "Body," "Myself," "Others," "Attractiveness," and "Rebrowse." Explicit certainty judgments (i.e., items related

[1] https://www.clo3d.com/

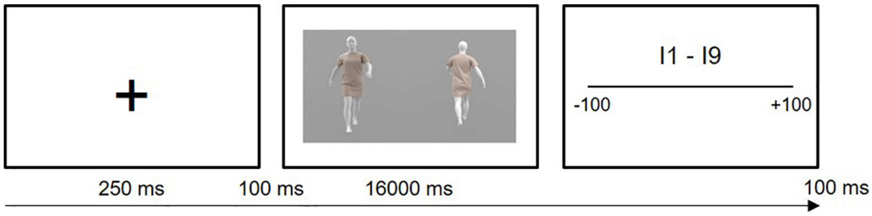

FIGURE 1 | Schematic overview of the experimental procedure. During dynamic trials, a 4 s video of a walking avatar was shown in a loop four times for 16 s. During static trials, two frames were selected out of these 4 s videos, and were then also looped for 16 s. Participants were shown both the front and back view of the avatars in both types of trials.

TABLE 2 | Description of the self-report items, in the order that they were administered at the end of each trial.

Item	Question/statement
Dress	How likely do you think it is that this dress fits you?
Dress confidence	How certain are you?
Measurements	How likely do you think it is that this avatar's measurements correspond to your own?
Measurements confidence	How certain are you?
Body	I feel as if the body of the avatar is my own body
Myself	The avatar reflects how I consider myself to be
Others	I consider the avatar to reflect how I want to present myself to others
Attractiveness	How attractive do you find the woman represented by this avatar?
Rebrowse	How likely do you think it is that you would choose this avatar as your avatar for online shopping?

to confidence) for the "Dress" and "Measurements" items were added given that research has shown that the reliability of perception across different decisions might be related to subjective rather than objective accuracy (Fairhurst et al., 2018).

Body Esteem and Personality Questionnaires

Body Esteem Scale for Adolescents and Adults

The Body Esteem Scale for Adolescents and Adults (BESAA) is a 23-item questionnaire that measures people's affective attitudes toward their own bodies (Mendelson et al., 2010). The questionnaire is comprised of three subscales that address general feelings about one's appearance (Appearance), evaluations attributed to others about one's body appearance (Attribution), and satisfaction with one's body weight (Weight). The questionnaire items are rated on a Likert scale from 0 to 4, with higher scores reflecting more positive attitudes. Cronbach's α in the current study was 0.89 (Appearance), 0.74 (Attribution), and 0.95 (Weight).

Big 5 Inventory-10

The Big 5 Inventory-10 (BFI-10) is a 10-item version of the Big 5 Personality Test (Benet-Martínez and John, 1998) that measures personality traits. Items are rated on a Likert scale from 1 to 5, and they correspond to five subscales: Extraversion (Cronbach's α 0.65), Agreeableness (Cronbach's α 0.71), Conscientiousness (Cronbach's α 0.67), Neuroticism (Cronbach's α 0.54), and Openness (Cronbach's α 0.88; Benet-Martínez and John, 1998; Rammstedt and John, 2007).

Procedure

Gorilla Experiment Builder (Anwyl-Irvine et al., 2020) was used to create and host the experiment online. Participants were instructed to complete the experiment individually and in one setting (verified afterward by the experimenter by checking completion dates/times). Participants were then told that they would observe avatars of different sizes (based on their own body) wearing a dress, and that they would have to answer several questions about the avatars they observed. The experiment consisted of 72 randomized trials (four times nine static and nine dynamic videos of a combination of three different body and dress sizes). On each trial, a fixation cross was presented for 250 ms, and after a 100 ms blank screen, the avatar video was shown for 16,000 ms. Immediately after the end of this video, participants responded to the nine self-report items at their own pace (see **Figure 1**). After completion of the self-report items and an inter-trial interval of 100 ms, the next trial started. At the end of the experiment, participants filled in the body esteem and personality questionnaires and were instructed to contact the experimenter to receive their monetary compensation. The experiment had a maximum total duration of 30 min.

Design and Data Analysis

Normality checks were performed with Shapiro-Wilks tests (all $ps > 0.237$). A 2 × 3 × 3 repeated-measures design was used for each self-report item separately, with three within-subject factors: Animation (Static vs. Dynamic), Body size (Body −1 vs. Body 0 vs. Body +1), and Dress size (Dress −1 vs. Dress 0 vs. Dress +1). Follow-up paired samples t-tests and correlations between effects of interest and questionnaire data were corrected for multiple comparisons using false discovery rate (fdr) correction. Data were analyzed using a frequentist approach in R (R Core Team, 2020) as well as a Bayesian approach in JASP (JASP Team, 2020). The latter approach was used to test (1) whether there was moderate to strong evidence to reject the null hypotheses under a Bayesian framework in case of a significant effect and (2) whether potential null results could be considered support for the absence of any effects. For the Bayesian analysis, we obtained BF_{10} – representing the observation of the data under the alternative hypothesis compared to the null hypothesis (Wagenmakers et al., 2018) – for each main and interaction effect. We employed a threshold of moderate evidence to support (BF_{10} < 1/3) or reject (BF_{10} > 3) the null hypothesis.

RESULTS

Main Effects

The main effects of Animation, Body size, and Dress size are summarized in **Figure 2**. For Animation, a significant effect was observed for the "Dress confidence" item only [$F(1,13) = 6.33$, $p = 0.026$, $\eta_p^2 = 0.33$, $BF_{10} = 3.137$], indicating more confidence about dress fit for dynamic ($M = 56.90$, SD = 5.96) compared to static ($M = 50.90$, SD = 5.98) avatars (see **Figure 2A**). None of the other self-report items showed an effect of Animation (all $ps > 0.253$, all $BF_{10} < 0.223$).

For Body size, a significant effect was observed for the items "Dress" [$F(2,12) = 5.86$, $p = 0.017$, $\eta_p^2 = 0.49$, $BF_{10} = 2.429e^{+7}$], "Others" [$F(2,12) = 23.51$, $p < 0.001$, $\eta_p^2 = 0.80$, $BF_{10} = 3.090e^{+28}$], "Attractiveness" [$F(2,12) = 17.87$, $p < 0.001$, $\eta_p^2 = 0.75$, $BF_{10} = 8.481e^{+8}$], and "Rebrowse" [$F(2,12) = 4.09$, $p = 0.044$, $\eta_p^2 = 0.41$, $BF_{10} = 1.378e^{+9}$]. **Figure 2B** shows that a negative linear relationship was consistently observed for these items across the three body sizes.

Finally, for Dress size, a significant effect was found for the items "Body" [$F(2,12) = 5.84$, $p = 0.017$, $\eta_p^2 = 0.49$, $BF_{10} = 0.530$] and "Myself" [$F(2,12) = 6.12$, $p = 0.015$, $\eta_p^2 = 0.50$, $BF_{10} = 0.511$]. Similar to the effects of Body size, bigger dress sizes were rated lower than smaller dress sizes (see **Figure 2C**).

For significant pairwise comparisons that survived fdr-correction of the effects of Body and Dress size, see **Table 3**. Note that while the significant effects for Animation and especially Body size all reached the threshold of moderate evidence to reject the null hypothesis (set in the Bayesian analysis), this was not the case for the significant effects concerning Dress size.

Interaction Effects

An interaction between Animation and Body size was found for the "Others" item [$F(2,12) = 4.26$, $p = 0.040$, $\eta_p^2 = 0.42$, $BF_{10} = 7.829e^{+26}$]. The difference between static and dynamic avatars was only significant for Body +1 ($t(14) = 2.91$, $p = 0.033$, $d = 0.22$; see **Figure 3A**), with dynamic avatars ($M = -68.36$, SD = 31.38) rated lower than static avatars ($M = -61.20$, SD = 32.52).

Furthermore, a two-way interaction between Body and Dress size was observed for the items "Dress" [$F(4,10) = 3.87$, $p = 0.038$, $\eta_p^2 = 0.61$, $BF_{10} = 35373.918$], "Dress confidence" [$F(4,10) = 3.68$, $p = 0.043$, $\eta_p^2 = 0.60$, $BF_{10} = 0.074$], "Measurements confidence" [$F(4,10) = 4.87$, $p = 0.019$, $\eta_p^2 = 0.66$, $BF_{10} = 0.005$], "Body" [$F(4,10) = 4.25$, $p = 0.029$, $\eta_p^2 = 0.63$, $BF_{10} = 1128.508$], and "Myself" [$F(4,10) = 4.90$, $p = 0.019$, $\eta_p^2 = 0.66$, $BF_{10} = 506.754$]. **Figure 3B** and **Table 3** suggest that for the "Dress confidence" and "Measurements confidence" items, Dress −1 was rated significantly higher than Dress +1 for Body +1 only, suggesting that participants were more confident about their answers when

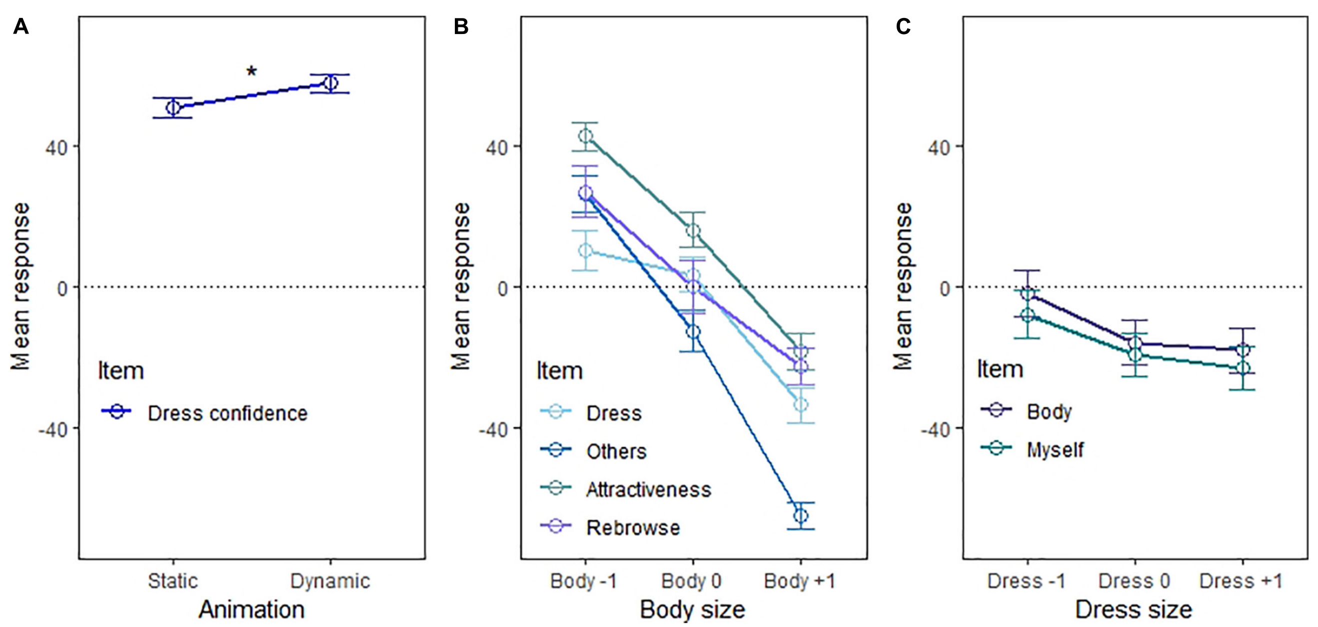

FIGURE 2 | Main effects of **(A)** Animation, **(B)** Body size, and **(C)** Dress size. Dress = *How likely do you think it is that this dress fits you?*, Dress confidence = *How certain are you?*, Body = *I feel as if the body of the avatar is my own body*, Myself = *The avatar reflects how I consider myself to be*, Others = *I consider the avatar to reflect how I want to present myself to others*, Attractiveness = *How attractive do you find the woman represented by this avatar?*, Rebrowse = *How likely do you think it is that you would choose this avatar as your avatar for online shopping?* Body/Dress –1 = One body/dress size smaller than participants' real body/dress size, Body/Dress 0 = Participants' real body/dress size, Body/Dress +1 = One body/dress size bigger than participants' real body/dress size.

TABLE 3 | Pairwise comparisons of the main and interaction effects of Animation, Body size, and Dress size.

Effect	Item	Comparison	fdr-corrected *p*-value	Cohen's *d*
Animation	Dress confidence	Static vs. Dynamic	0.026	1.01
Body size	Dress	Body −1 vs. Body +1	0.027	3.61
		Body 0 vs. Body +1	0.015	3.67
	Others	Body −1 vs. Body 0	0.001	3.97
		Body −1 vs. Body +1	<0.001	10.41
		Body 0 vs. Body +1	<0.001	5.85
	Attractiveness	Body −1 vs. Body 0	0.003	2.97
		Body −1 vs. Body +1	<0.001	6.96
		Body 0 vs. Body +1	<0.001	3.77
	Rebrowse	Body −1 vs. Body +1	0.021	5.02
		Body 0 vs. Body +1	0.021	3.84
Dress size	Body	Dress −1 vs. Dress +1	0.015	2.66
	Myself	Dress −1 vs. Dress +1	0.009	2.70
Animation x Body size	Others	Body +1: Static vs. Dynamic	0.033	0.22
Body size x Dress size	Dress	Dress −1: Body −1 vs. Body +1	0.014	1.49
		Dress −1: Body 0 vs. Body +1	0.014	1.08
		Dress 0: Body 0 vs. Body +1	0.015	0.74
	Dress confidence	Body +1: Dress −1 vs. Dress +1	0.030	0.58
	Measurements confidence	Body +1: Dress −1 vs. Dress +1	0.024	0.49
	Myself	Dress −1: Body −1 vs. Body +1	0.045	1.31
		Dress −1: Body 0 vs. Body +1	0.045	0.83

Dress = How likely do you think it is that this dress fits you?, Dress confidence = How certain are you?, Measurements confidence = How certain are you? (In response to How likely do you think it is that this avatar's measurements correspond to your own?), Body = I feel as if the body of the avatar is my own body, Myself = The avatar reflects how I consider myself to be, Others = I consider the avatar to reflect how I want to present myself to others, Attractiveness = How attractive do you find the woman represented by this avatar?, Rebrowse = How likely do you think it is that you would choose this avatar as your avatar for online shopping? Body/Dress −1 = One body/dress size smaller than participants' real body/dress size, Body/Dress 0 = Participants' real body/dress size, Body/Dress +1 = One body/dress size bigger than participants' real body/dress size.

presented with the biggest body size. Additionally, for the "Dress," "Body," and "Myself" items, the difference between Body +1 and the other body sizes was stronger for Dress −1 and Dress 0 compared to Dress +1 (see **Figure 3C** and **Table 3**; note that for the "Body" item, however, none of the comparisons survived correction).

Note that all significant interactions reached the threshold of moderate evidence to reject the null hypothesis, except for the items related to confidence of dress and measurements fit when looking at the interaction between Body and Dress size. No interactions between Animation and Dress size or three-way interactions were observed.

Correlation Analyses With Body Esteem and Personality Questionnaires

In order to reduce the number of tests, we restricted our correlation analyses with the body esteem and personality questionnaires to the main effect of Animation (Dynamic–Static) for all items, given that this was our main effect of interest. For the "Dress confidence" item, a significant negative relationship was observed for the Appearance ($r = -0.58$, $p = 0.045$) and Attribution ($r = -0.66$, $p = 0.033$) subscales of the BESAA, suggesting that the ratings difference between dynamic and static avatars for confidence about dress fit was bigger for participants with more negative feelings (see **Figure 4A**) and evaluations attributed to others concerning their own body appearance (and vice versa; see **Figure 4B**). A negative correlation was also found between the Attribution subscale of the BESAA and the "Measurements confidence" item ($r = -0.64$, $p = 0.042$), indicating that the same negative relationship existed when participants were asked to rate confidence about measurements correspondence (see **Figure 4B**). There were no other significant correlations for the effect of Animation (all $ps > 0.06$).

DISCUSSION

In the current study, we investigated own-body perception in a real-life practical setting by asking participants to match their own body with an externally perceived body that was a 3D-generated avatar based on participants' real bodies, fitted with a computer-generated dress. This perceived body was (1) either static or dynamic, (2) either bigger, smaller, or the same size as participants' own body size, and (3) fitted with a dress with a size either bigger, smaller, or the same as participants' own dress size. Although we expected the addition of action cues (i.e., a walking avatar) to improve the ability to match own and an avatar's body size (i.e., own body perception ratings), we only observed an effect of moving vs. non-moving avatars when participants had to indicate their confidence in their answer about whether the dress they had just seen would fit them (irrespective of the accuracy of their answer to the item on

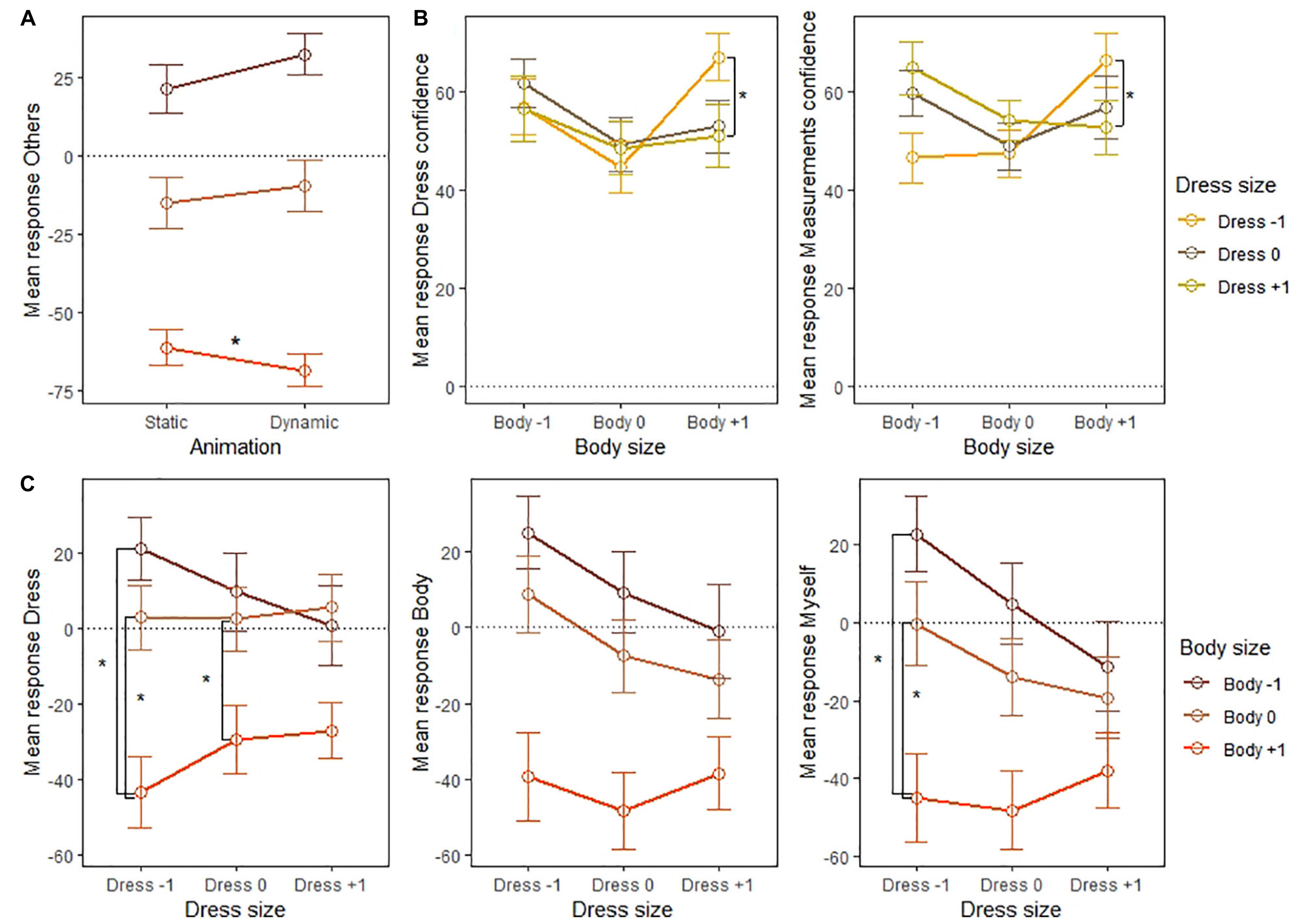

FIGURE 3 | Interaction effects of **(A)** Animation and Body size for the Others item, **(B)** Body size and Dress size for the Dress confidence and Measurements confidence items, and **(C)** Body size and Dress size for the Dress, Body, and Myself items. Dress = *How likely do you think it is that this dress fits you?*, Dress confidence = *How certain are you?*, Measurements confidence = *How certain are you?* (In response to *How likely do you think it is that this avatar's measurements correspond to your own?*), Body = *I feel as if the body of the avatar is my own body*, Myself = *The avatar reflects how I consider myself to be*, Others = *I consider the avatar to reflect how I want to present myself to others*. Body/Dress −1 = One body/dress size smaller than participants' real body/dress size, Body/Dress 0 = Participants' real body/dress size, Body/Dress +1 = One body/dress size bigger than participants' real body/dress size.

dress fit). Importantly, however, this observed difference between static and dynamic avatars was dependent on participants' bodily self-esteem: participants with more negative feelings toward their own body felt more confident when confronted with dynamic avatars than participants with less negative feelings. Furthermore, when asked to rate how well the avatar reflected how participants wanted to represent themselves to others, we observed that dynamic avatars were rated lower than static avatars for the biggest-sized bodies only. For several self-report items, participants systematically rated smaller body/dress sizes higher than bigger body/dress sizes. When asked about confidence about dress and measurements fit, however, the higher ratings for smaller dress sizes were only present for the biggest body size. Finally, when participants had to rate dress fit, how strongly they felt that the avatar's body was their own, and how the avatar represented how they considered themselves to be, the difference between the biggest body size and the other body sizes was strongest for the smallest dress sizes. We discuss these observed effects and potential limitations in more detail in the following sections.

Effects of Animation

The role of the motor system in shaping and maintaining the bodily self and body ownership in particular has been well-documented by neuroimaging studies showing the emergence of premotor cortex activity lying at the root of our body schema (Graziano et al., 1994; Fogassi et al., 1996; Ehrsson et al., 2004, 2005; Convento et al., 2018), as well as body distortion illusions in healthy (Dummer et al., 2009; Vallar and Ronchi, 2009; Garbarini et al., 2013; Bolognini et al., 2014; Hara et al., 2015; della Gatta et al., 2016) and patient (Burin et al., 2015; Nava et al., 2017) populations. Thus, it seems that the sensory and motor system dynamically interact to develop our bodily self-awareness and self-consciousness (Nava et al., 2018). Interestingly, however, the influence of dynamic action cues on own-body perception when

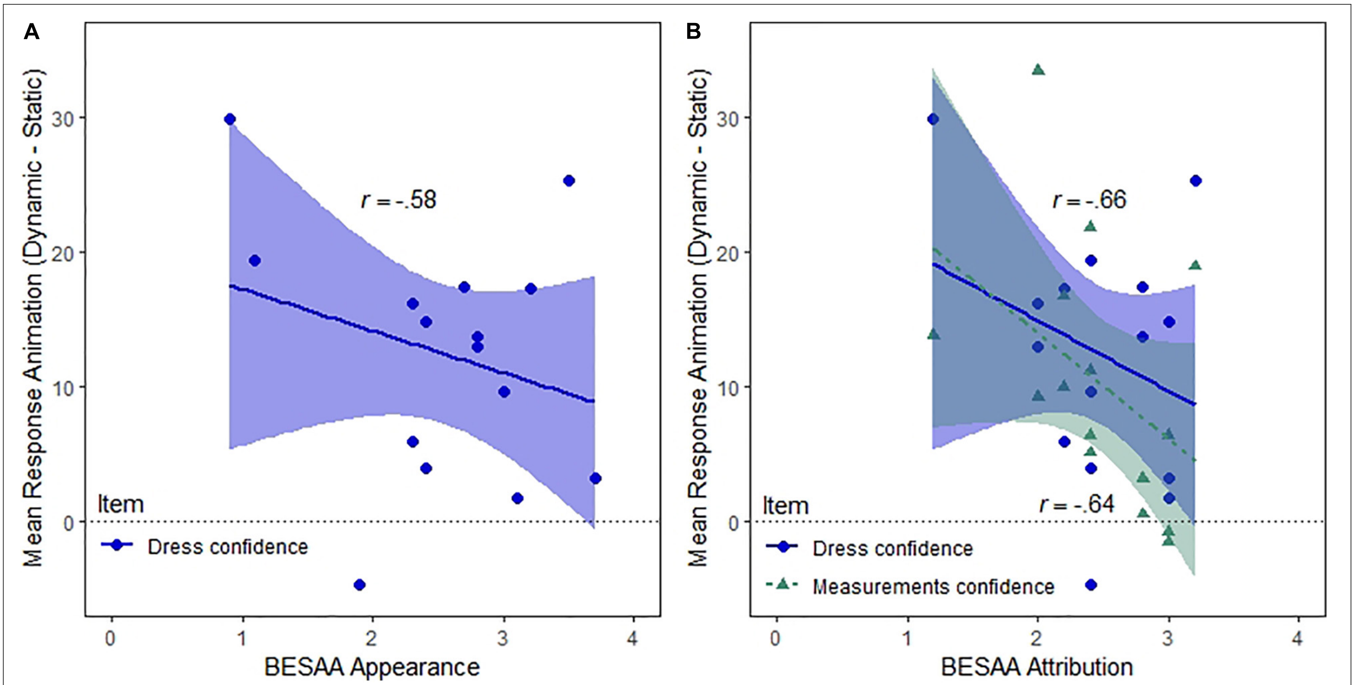

FIGURE 4 | Correlations between the main effect of Animation and the **(A)** Appearance (general feelings about one's appearance) and **(B)** Attribution (evaluations attributed to others about one's body appearance) subscales of the Body Esteem Scale for Adolescents and Adults (BESAA). Higher scores on the BESAA reflect more positive attitudes. Dress = *How likely do you think it is that this dress fits you?*, Dress confidence = *How certain are you?*, Measurements confidence = *How certain are you?* (In response to *How likely do you think it is that this avatar's measurements correspond to your own?*).

confronted with the task of matching own with an externally perceived body has thus far received little attention.

Our study, which compared dynamic and static avatars by adding walking animations (Varol et al., 2017), indicated that dynamic avatars were only rated higher than static avatars when participants had to rate the confidence in their answer concerning dress fit, suggesting that dynamic avatars increased participants' certainty about dress fit irrespective of the accuracy of their answer to this item. Furthermore, this difference in ratings between walking and non-walking avatars was bigger for participants with low bodily self-esteem (in terms of confidence about both dress and measurement fit). The question that arises is what prompted participants with negative feelings toward their own body to feel more confident when confronted with dynamic avatars. It has been shown that people who tend to overestimate their own body measurements show disturbed fixation patterns when observing different bodies (Irvine et al., 2019), largely focusing on uninformative areas (Cornelissen et al., 2016). Our results indicate that people with low bodily self-esteem (commonly associated with over-estimation of own body size, see e.g., Ahadzadeh et al., 2018) might also focus their attention differently when dynamic action cues are added to observed avatars, possibly needing or caring more about the added value of these cues. Future research is warranted, however, to explore fixation patterns in own-body perception of dynamic bodies, and the influence of individual personality differences. Finally, when participants were asked to rate whether the avatar they were presented with reflected how they wanted to present themselves to others, dynamic avatars were rated lower than static avatars when they observed avatars with bigger-sized bodies. Thus, it seems that action cues lead to a lower preference of bigger-sized moving avatars when participants had to consider their bodies in a social context, possibly suggesting that movement dynamics cues are especially informative for bigger-sized bodies and consequently exacerbate the socio-cultural weight stigma (Fikkan and Rothblum, 2012; Spahlholz et al., 2016). While it has been shown that body image is partly a social construct (Davison, 2012), further research is needed to investigate the role of action cues in own-body perception, particularly when considering its social implications.

There are several reasons why our Animation manipulation might not have improved own-perceived body matching to the degree that we expected it to. First, it is possible that our static condition introduced implied motion. Previous research has shown that the observation of bodily actions employs visual (Grossman and Blake, 2002; Kable and Chatterjee, 2006) and motor areas (Rizzolatti and Craighero, 2004), even when motion is merely implied by static human postures (Urgesi et al., 2006, 2007; Candidi et al., 2008). Furthermore, it has been observed that body size and implied motion interact in influencing aesthetic appreciation of human bodies (Cazzato et al., 2012, Cazzato et al., 2016a), such that implied motion increases the aesthetic preference for thinner bodies (Cazzato et al., 2012). Thus, while the static condition in the current experiment did not offer the same action cues as the dynamic condition, the use of static human postures (representing dynamic movements) likely introduced implied motion of the observed bodies and dresses. Future research should address this important confound, and explore the contribution of dynamic cues when they are contrasted to a purely static condition. Second, an implicit measure of own-body recognition might have been more appropriate than our explicit self-report measure to access bodily representations that use motor/dynamic information. It has been shown that explicit and implicit recognition of our own body depend on different cortical mechanisms (Candini et al., 2016), and that only the former is based on motor information (Ferri et al., 2011). Thus, the explicit task in the current experiment might have only minimally relied on the dynamic cues provided by the Animation manipulation. Follow-up research using more implicit measures of own-body recognition is necessary to shed more light on this issue. Finally, we opted to manipulate movement dynamics by adding walking movements, rather than movements that people typically perform in front of a mirror (e.g., twisting and turning), because we believed they would be more informative and because they offer a viewpoint that we normally don't (but probably would like to) have access to. However, the choice for these walking movements made the movement dynamics cues less compatible with real-life experiences, which may have affected our findings.

Effects of Body Size

In line with previous research (Longo and Haggard, 2012; Hashimoto and Iriki, 2013; Kaplan et al., 2013; Linkenauger et al., 2017; Sadibolova et al., 2019; Maister et al., 2021), we observed that participants were unable to accurately identify their own body measurements. Furthermore, we replicated results from a previous study (De Coster et al., 2020), showing that participants – irrespective of their own body size – rate smaller-sized bodies higher (i.e., more attractive, more as a body that represents how you want to present yourself to others and that you would use for online shopping) than bigger-sized bodies, even when this own-perceived body matching takes place in a concrete context with practical implications. These findings, obtained using technology that was able to generate highly realistic avatar bodies (Loper et al., 2015), are in line with the body weight stigma that is especially pervasive in women (Fikkan and Rothblum, 2012; Spahlholz et al., 2016), and with research indicating that people tend to underestimate their body size (e.g., Monteath and McCabe, 1997; Tovée et al., 2003; Cazzato et al., 2015; Robinson and Kersbergen, 2017; Steinsbekk et al., 2017; Ralph-Nearman et al., 2019).

Effects of Dress Size

Importantly, we fitted the different avatar bodies with different sizes of a highly realistic computer-generated dress (Narain et al., 2013; Pfaff et al., 2014) to further increase the experiment's ecological validity and realism. Similar to the effect of body size, our results indicated that participants rated the smallest dress sizes higher than the bigger ones. This difference was only present for the biggest-sized bodies when participants had to rate confidence in their answers concerning dress and measurement fit, however, seemingly suggesting that the biggest body size made it easier for participants to discern the difference between the smallest and the biggest dress sizes. The same was true for the difference between the biggest and smallest body sizes, which was strongest for the smallest dress size for the "Dress" (*How likely do you think it is that this dress fits you?*), "Body" (*I feel as if the body of the avatar is my own*), and "Myself" (*The avatar reflects how I consider myself to be*) items. Together, these results indicate that own-body perception relies on a combination of an avatar's body and clothing information when participants are presented with realistic avatars and garments. Thus, this suggests that garment fit and movement might provide important relevant cues for body size estimation. Importantly, however, the addition of these realistic, ecologically valid cues did not improve own-body perception in terms of the ability to match an externally perceived body with one's own (contrary to Cornelissen et al., 2017), since participants remained unable to identify their own body and dress size accurately. It has to be noted, though, that both the main effect of dress size and its interaction with body size for the confidence items did not meet the threshold to reject the null hypothesis based on moderate evidence set during our Bayesian analysis, which suggests that these effects should be interpreted with caution and warrant further exploration.

Limitations and Implications

The study has several important limitations. First, although BMI measures in the current sample were inside the "normal" or "healthy" range, we did not include any measures of pathological and/or negative body image, nor were participants excluded based on current or previous history of eating or body dysmorphic disorders. The influence of these disorders should be addressed in further research, since it has been shown that they greatly impact body size estimation (Tovée et al., 2003; Cornelissen et al., 2017). Second, the sample size in our study (15 participants) was relatively low. Due to several restrictions imposed by the COVID-19 pandemic at the time of the study, the available subject pool was limited (e.g., 360° videos of participants' bodies had to be at our disposal). However, a Bayesian power analysis indicated that our sample was sufficiently large to answer our main research questions. Finally, it is important to note that we were unable to assess order effects related to the self-report items in the current study, given that the items were always presented in the same order (note that this does not apply to the order of the experimental conditions, which was randomized). Although this was done deliberately to make the task easier for participants, follow-up research should explore the possibility of order effects for the self-report items. Furthermore, the "Attractiveness" item ("*How attractive do you find the woman represented by this avatar?*") could have been confusing to participants, given that they were informed that they would observe avatars based on their own body (but of different sizes). While this might have induced participants to self-evaluate their own perceived attractiveness, the observation that smaller-sized bodies were rated as more attractive than bigger-sized bodies seems to suggest that our manipulation was (at least partly) successful.

The influence of eating and/or body dysmorphic disorders on body size estimation is a topic of extensive research. Research suggests, for example, that body size overestimation is a defining feature of anorexia nervosa (Hennighausen et al., 1999; Gardner and Brown, 2014; Dakanalis et al., 2016; Gadsby, 2017; Malighetti et al., 2020; but see Cornelissen et al., 2013 who showed that body size overestimation in women with anorexia nervosa is not qualitatively different from the overestimation observed in women without anorexia nervosa), and that this overestimation is robust to manipulations that improve the accuracy of body size perception in healthy controls. While we expect that the addition of action cues might lead to stronger effects in clinical populations, in part suggested by the observation in the current study that participants with low bodily self-esteem showed an increased advantage of dynamic avatars, and based on previous studies that suggest that people with anorexia nervosa have a heightened sensitivity to visual bodily cues (Eshkevari et al., 2012; Keizer et al., 2014; Crucianelli et al., 2019; see Martinaud et al., 2017 for similar results in neurological patients), it is unclear which direction this influence would take (increased vs. decreased accuracy), especially given the fact that our Animation manipulation did not alter the accuracy of own-perceived body matching. However, as described above, future research should include screening for clinical disorders as well as more implicit measures in order to address the clinical implications of our findings better. Furthermore, the use of implicit tasks might also provide more information concerning the practical implications of the current research. Avatar design and development for online retail experiences, for example, depend on maximizing the congruency between the observed avatar and the self for better outcomes (e.g., greater purchase intentions, lower return rates; Kim and Forsythe, 2008). While dynamic cues did not increase accuracy of matching own with a perceived avatar's body, research suggests that only implicit measures might be susceptible to such cues (Ferri et al., 2011).

CONCLUSION

In sum, the current study aimed at contextualizing own-body perception in a real-life, practical situation by uniquely combining different technologies to create realistic, walking, dress-fitted avatars. None of these factors, however, seemed to improve own-perceived body matching, indicating that participants' own body representations largely remain inaccurate (Hashimoto and Iriki, 2013; Linkenauger et al., 2017; Pitron and de Vignemont, 2017; Sadibolova et al., 2019; Maister et al., 2021) even in a realistic, concrete situation that has practical implications. These findings provide important insights for research exploring the development of online avatars (Kim and Forsythe, 2008) and research investigating own-body perception in clinical disorders such as anorexia nervosa and body dysmorphic disorders (e.g., Tovée et al., 2003; Cornelissen et al., 2017).

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding authors.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the local ethics committee at the Universidad Carlos III de Madrid. The patients/participants provided their written informed consent to participate in this study. Written informed consent was obtained from the individual(s) for the publication of any potentially identifiable images or data included in this article.

AUTHOR CONTRIBUTIONS

All authors designed the research and reviewed the manuscript. LDC and PS-H developed the experimental stimuli. LDC implemented the experimental procedure, carried out the experiments, performed the analyses, and wrote the first draft of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fnhum.2021.701872/full#supplementary-material

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Action Sounds Informing Own Body Perception Influence Gender Identity and Social Cognition

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Sensory information can temporarily affect mental body representations. For example, in Virtual Reality (VR), visually swapping into a body with another sex can temporarily alter perceived gender identity. Outside of VR, real-time auditory changes to walkers' footstep sounds can affect perceived body weight and masculinity/femininity. Here, we investigate whether altered footstep sounds also impact gender identity and relation to gender groups. In two experiments, cisgender participants (26 females, 26 males) walked with headphones which played altered versions of their own footstep sounds that sounded more typically male or female. Baseline and post-intervention measures quantified gender identity [Implicit Association Test (IAT)], relation to gender groups [Inclusion of the Other-in-the-Self (IOS)], and perceived masculinity/femininity. Results show that females felt more feminine and closer to the group of women (IOS) directly after walking with feminine sounding footsteps. Similarly, males felt more feminine after walking with feminine sounding footsteps and associated themselves relatively stronger with "female" (IAT). The findings suggest that gender identity is temporarily malleable through auditory-induced own body illusions. Furthermore, they provide evidence for a connection between body perception and an abstract representation of the Self, supporting the theory that bodily illusions affect social cognition through changes in the self-concept.

Keywords: body representation, body perception, multisensory perception, sound, own body illusion, self-concept, gender identity, implicit association test (IAT)

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INTRODUCTION

The brain has a mental representation of the body (e.g., its size, shape, configuration) which is continuously updated through multimodal sensory information from body-environment interactions (Tsakiris, 2010; Ehrsson, 2012). By experimentally altering such sensory information, the mental body representation can be temporarily changed (Botvinick and Cohen, 1998). A suitable method for inducing *own body illusions*, during which the body is perceived differently from its physical state, is altering auditory information from body-environment interactions

(Stanton and Spence, 2020). In several studies, auditory feedback has been used to alter body weight perception (Tajadura-Jiménez et al., 2015), body height perception (Tajadura-Jiménez et al., 2018), and perception of the properties of limbs (Senna et al., 2014; Tajadura-Jiménez et al., 2017b). In this paper, we investigate if alterations of auditory feedback can lead to changes in the self-concept and feelings of belonging to a group.

While audition is a newcomer to research in multisensory changes in body perception, other studies have manipulated visual feedback to induce *body swap illusions*, in which participants are perceptually "swapped" into another body, for example an avatar in Virtual Reality (VR). Crucially, the embodiment of an avatar with physical features of an outgroup relative to the participant (i.e., different ethnicity, gender, age) has been shown to affect implicit attitudes toward the embodied outgroup (Fini et al., 2013; Peck et al., 2013; Farmer et al., 2014).

To explain these effects of *body swap illusions* on social cognition, Maister et al. (2015) and Tsakiris (2017) recently hypothesised a connection between body perception and higher-level cognition. In particular, Maister et al. (2015) propose that the mental representation of "me" contains both a representation of the body as well as more abstract facets of the Self, such as attitudes, beliefs, and relations to social in- and outgroups. While several experiments have shown that body swap illusions can affect (implicit) attitudes toward an outgroup (see e.g., Banakou et al., 2013; Peck et al., 2013; Tajadura-Jiménez et al., 2017a), there is less research on how to facilitate the changes in the self-concept and identification with social groups. Banakou et al. (2013) and Tajadura-Jiménez et al. (2017a) found that embodying a child avatar in VR increased implicit associations between the Self and child-like attributes which provides evidence for a link between the self-concept and the embodied group after experiencing a body swap illusion. With respect to gender identity, Tacikowski et al. (2020a) found that body swap illusions with an avatar of a different sex cause a more balanced gender identification with male and female gender.

While these studies focus on a complete alteration of the body taking place by embodying another person's body, a connection between direct changes of one's own actual body and the Self remains to be investigated. Our research addresses this gap by focussing on subtle *own body illusions* induced through auditory feedback from body-environment interactions and investigates their effect on the self-concept and the feeling of belonging to a social group. The effects of direct alterations of one's own actual body perception are particularly relevant because this perception (and the body itself) might naturally change throughout life. If one's body perception is related to one's self-concept and social cognition, then these could situationally differ depending on the current state and perception of one's body.

In a recent study, Tajadura-Jiménez et al. (2019) had found that auditory information from footsteps did not only affect body size perception but also the perceived masculinity and femininity of the participants, hence, suggesting a change in the perception of the Self through a subtle own body illusion. Building on these earlier findings that footstep sounds can affect perceived masculinity and femininity (Tajadura-Jiménez et al., 2019), and that gender identity is temporarily malleable through body swap illusions (Tacikowski et al., 2020a), here, we investigate whether altered footstep sounds could induce a "gender illusion" during which participants identify more strongly with their respective gender outgroup. Thereby, we understand gender as "*the meanings ascribed to male and female social categories within a culture*" (Wood and Eagly, 2015, p. 461) and adopting those cultural meanings into one's own personality results in one's gender identity. Gender identity is a multifaceted concept evolving through a combination of biological, cognitive, and social factors (Wendy and Eagly, 2009) and appears to be closely linked to one's body perception (Tacikowski et al., 2020a).

One theory for explaining a possible influence of direct changes of one's own actual body perception on gender identity is the predictive coding account (Clark, 2013; Apps and Tsakiris, 2014). From this theoretical lens, a gender illusion would be expected to occur as follows: while walking, the brain constantly predicts the sensory input it will receive, including the well-known sound of one's own footsteps. The frequency components in the footstep sounds of female and male walkers are distinct and people can distinguish genders based on these sounds (Li et al., 1991; Giordano et al., 2014). Low frequency footstep sounds are typically associated with a more masculine, heavy walker, and with wearing flat shoes, while high frequency footstep sounds are typically associated with a more feminine, light walker, and with wearing high heels (Li et al., 1991). For most female individuals, the brain is therefore expected to predict more high frequency footstep sounds during walking. However, if the frequency components of footstep sounds are altered experimentally to emphasise the lower frequency bands, the perceived walking sounds differ substantially from the predicted sounds. This mismatch between predicted high frequency sounds and heard low frequency sounds creates prediction errors. To resolve the conflict and to reduce the occurrence of prediction errors, the mentally represented body is hypothesised to update in a way to look relatively heavier and bigger in size, thus, creating the bodily illusion of being more like a stereotypical male and less like a stereotypical female (Apps and Tsakiris, 2014).

The hypothesised prediction error caused by bodily illusions, including footstep sound manipulations, are expected to then impact people's self-perception. Specifically, we hypothesise that bodily illusions from footstep sounds will blur the boundaries between Self and other (Paladino et al., 2010), increase self-association with the embodied outgroup member (Maister et al., 2015), and change higher-level concepts of the Self (Tsakiris, 2017). Therefore, we expect changes in implicit self-gender associations and explicit self-gender group identification following the induced *own body gender illusion*.

To investigate this idea, we report two experiments which altered footstep sounds in real-time to resemble more feminine or masculine footsteps during walking. We tested how these sounds change participants' self-concept and the relation to social groups for cisgender females (Experiment I) and cisgender males (Experiment II). The following three hypotheses were formulated.

H1: Altered footstep sounds will affect *body perception*, as quantified by changes in *bodily feelings* and *related motor behaviour*. Frequency components in footstep sounds are generally associated with the sex and weight of the walker (Li et al., 1991), and previous research has induced illusory changes of one's own actual body (i.e., own body illusions) through altering footstep sounds (Tajadura-Jiménez et al., 2015, 2019). Therefore, it was expected that participants will feel lighter and more feminine after walking with high frequency step sounds compared to low frequency step sounds as it was found in Tajadura-Jiménez et al. (2019). The previously found interaction effects also suggest a connection between footstep sounds and perceived strength (Tajadura-Jiménez et al., 2019). As lower strength is stereotypically associated with females, we also hypothesised that participants will feel relatively weaker after walking with high frequency step sounds compared to low frequency step sounds. The bodily feelings of perceived body weight, masculinity/femininity, and strength might jointly or interactively be related to the multifaceted concept of gender identity and were thus all considered in this study. The second part of the hypothesis builds on two observations in the literature. First, altering body representations during bodily illusions can change *motor behaviour*. For example, arm reaching movements (Tajadura-Jiménez et al., 2016) and step size (Tajadura-Jiménez et al., 2018) are adjusted together with experienced changes in arm/leg size; leg acceleration and foot-ground contact time are adjusted together with experienced changes in perceived body weight (Tajadura-Jiménez et al., 2015, 2019). Second, masculine and feminine gait differ in lateral hip and chest sway (Mather and Murdoch, 1994). Given these observations, it was hypothesised that the bodily illusion could cause participants to adjust their walking behaviour to resemble masculine walking patterns more closely in the low frequency condition and feminine walking patterns more closely in the high frequency condition.

H2: Altered footstep sounds will affect implicit *self-gender associations*. Bodily illusions are expected to affect the self-concept by increasing associations of the Self with the embodied group (Banakou et al., 2013; Maister et al., 2015; Tsakiris, 2017). Therefore, it was expected that high frequency footstep sounds will enhance self-female associations and that low frequency step sounds will enhance self-male associations.

H3: Altered footstep sounds will affect explicit *self-gender group identification*. Bodily illusions can increase identification with the embodied group (Maister et al., 2015; Tsakiris, 2017). Therefore, it was expected that high frequency footstep sounds will increase identification of the Self with the group of women, and that low frequency footstep sounds will increase identification of the Self with the group of men.

EXPERIMENT I: ALTERING IMPLICIT SELF-GENDER ASSOCIATION AND EXPLICIT SELF-GENDER GROUP IDENTIFICATION OF WOMEN

Method

Participants

26 cisgender women took part in the first experiment (M = 26.31 years, SD = 4.46 years). On average, they weighed 58.73 kg (SD = 9.71 kg) and were self-reportedly 164.6 cm (SD = 8.03 cm) tall. Body mass index (M = 21.65, SD = 3.06, Range = 17.51 – 29.39) was in the healthy range (18.5 – 24.9) according to the National Health Service in the UK[1] for 19 of the participants. Eligibility criteria included no history of hearing problems and no (history of) eating disorders, as previous research showed that individuals with a (history of) eating disorder differ in their body perception and sensitivity to bodily illusions (Eshkevari et al., 2012, 2014). Participants were recruited through an online subject pool, flyers, the researcher's social network, and by asking people on campus. Participants could choose to participate in a raffle for one of three £30 Amazon vouchers (20 participants), to recruit the experimenter for their own experiment (6 participants), or to receive one academic credit (0 participants).

Ethical approval was obtained by the UCL Research Ethics Committee (Project ID: UCLIC/1516/003/Staff). The study was performed according to institutional ethics and international standards for the protection of human participants. All participants provided written informed consent prior to participation and were fully debriefed.

Materials

Participants walked with two types of altered footstep sounds in one "walking phase" respectively. During these walking phases, participants wore a set of equipment in order to alter footstep sounds in real-time and to capture behavioural data. The full set-up is displayed in **Figure 1**. The experiment was conducted in a quiet room and participants walked on a 3.6 × 0.6 m wooden corridor (medium density fibre, 2.5 cm thick). Questionnaires and tasks were presented on a 14" laptop (Intel Core i7, 16 GB RAM).

Real-time sound alteration

The equipment for altering footstep sounds in real-time involved a pair of strap-sandals similar to the one used by Tajadura-Jiménez et al. (2015). These sandals had a hard rubber sole and produced clear contact sound on the wooden corridor during walking. In order to capture and consecutively alter the footstep sounds, a pair of small microphones (Core Sound) were attached to the sandals (one microphone on each). These microphones were connected to a preamplifier (FoneStar, TC-6M) to increase the loudness of the captured sounds. The preamplifier was connected to a stereo 9-band graphic equaliser (Behringer FBQ800) which allowed the enhancement or diminution of the loudness of certain frequency components in the sounds (see sound conditions in Experimental Design). During walking, the participants heard their altered footstep sounds through a pair of headphones (Sennheiser HDA 300) with high passive noise attenuation (>30 dBA) that muffled the actual sound of footsteps. The preamplifier and equaliser were fitted into a small backpack for the participant to carry (∼2 kg).

Measuring instruments

(a) *Bodily feelings and motor behaviour*. Analogous to previous work (Tajadura-Jiménez et al., 2019), bodily feelings were

[1] NHS healthy weight. URL: https://www.nhs.uk/live-well/healthy-weight/

FIGURE 1 | Equipment during the two walking phases. Participants wore strap-sandals with attached microphones (1), a small backpack containing a preamplifier and an equaliser (2), and headphones through which participants heard their altered footstep sounds (3). Black rubber bands with one of six Notch movement sensors (white triangles) each (4) were attached to the upper arms, chest, hip, and thighs.

measured with three statements on a 7-point Likert scale: I felt... (1) "light" to "heavy," (2) "weak" to "strong," and (3) "very feminine" to "very masculine." These self-report questions were used to measure whether the altered footstep sounds affected participants similarly as in previous research using altered footstep sounds, and hence, whether the bodily illusion was induced successfully. As perceived weight, femininity/masculinity, and strength all relate to the multifaceted concept of gender identity, we refer to this bodily illusion as a gender illusion. To measure typically masculine and feminine gait features (i.e., lateral hip and shoulder sway) each participant wore 6 Notch movement sensors[2] attached with rubber bands to their upper arms, thighs, chest, and hips. The movement data was recorded with the Notch Pioneer Motion Capture application (v. 1.10.0) on an Android Samsung Galaxy S7 Smartphone.

(b) *Implicit self-gender associations.* Implicit Association (IAT) (Greenwald et al., 1998) have been frequently used to assess changes in implicit racial bias (Farmer et al., 2012; Fini et al., 2013; Maister et al., 2013; Peck et al., 2013; Banakou et al., 2016) and gender bias (Lopez et al., 2019) after experiencing body swap illusions with an avatar from an outgroup. Banakou et al. (2016) argue that body perception influences implicit attitudes "*below the threshold of consciousness*" (p. 9) and although participants do not explicitly report that their bodies or attitudes changed, a change in the IAT score provides support for this relation. Therefore, similarly to Tacikowski et al. (2020a), we used an IAT pairing words describing *self, other, male*, and *female* to measure changes in implicit self-gender associations. The word stimuli were selected based on the gender IAT reported in Greenwald et al. (2002) and the order of the blocks was counterbalanced. The IAT was implemented in Qualtrics with the "iatgen" package (Carpenter et al., 2018) and participants pressed the keyboard keys "E" and "I" to sort stimuli to the left and right category respectively.

(c) *Baseline gender identity.* Besides self-categorisation measures such as the IAT, gender identity is often researched based on the association of an individual with stereotypical attributes or traits of males and females (Wood and Eagly, 2015). To provide richer insights into the gender identity of the sample, the Traditional Masculinity-Femininity (TMF) scale (Kachel et al., 2016) was administered which measures self-ascribed masculinity and femininity in relation to perceived gender roles and stereotypes (interests, attitudes, behaviour, and appearance). Thereby, the first two questions closely resemble the ones used by Tajadura-Jiménez et al. (2019), only asking "I would like to be..." instead of "I wish to be..." in the second question which allows for a better comparison with their sample. All questions are included in the **Supplementary Methods**.

(d) *Explicit self-gender group identification.* Identification with the group of women and the group of men was measured with a variation of the Inclusion of the Other in the Self (IOS) scale (Aron et al., 1992), one for each gender group respectively. The IOS is a pictorial measure of closeness. It consists of seven pictures, each displaying two circles of decreasing distance, and has been used for measuring identification with different social groups (Schubert and Otten, 2002), and also for assessing gender identification (Hundhammer and Mussweiler, 2012). In this experiment, one circle represents the Self and the other circle represents the group of women (IOS Women) or the group of men (IOS Men) respectively. Participants were asked to select the picture that represents their relationship to the respective group best. The closer the circles are to one another, the closer is the perceived relationship to the group.

[2]Notch Movement Sensors. URL: https://wearnotch.com

(e) *Emotional state.* Similar to previous work (Tajadura-Jiménez et al., 2019), emotional state was measured with self-assessment manikins (Bradley and Lang, 1994) on a 9-point scale, respectively, for valence, arousal, and dominance. Based on these questions, it was assessed whether the emotional experience of the participants differed between the sound conditions, as for example increased arousal can further enhance the dominant IAT response (Gawronski and Bodenhausen, 2006).

(f) *Shape and weight concerns.* Previous research has shown that individuals with a (history of) eating disorders differ in their body perception and sensitivity to bodily illusions (Eshkevari et al., 2012, 2014). Not having any (history of) eating disorders was part of the selection criteria for the participants. However, to assess differences in this dimension, participants were asked to answer two subscales of the Eating Disorder Examination Questionnaire (EDE-Q) for weight and shape concerns (Fairburn and Beglin, 1994; Fairburn, 2008).

The **Supplementary Methods** contain an overview of all questions, answer options, and tasks which were used in this experiment.

Experimental Design

We used a within-subject design with two sound conditions: high and low frequency footstep sounds. Participants heard their own altered footstep sounds through headphones. Identical to previous research (Tajadura-Jiménez et al., 2015, 2019), in the *high frequency* condition, frequencies in the range of 1–4 kHz were amplified by 12 dB and the frequencies in the range of 83–250 Hz were attenuated by 12 dB. Conversely, in the *low frequency* condition, frequencies in the range of 83–250 Hz were amplified by 12 dB and frequencies in the range of 1–4 kHz were attenuated by 12 dB. Note that there was no walking condition without sound modification. As this study focussed on the malleability of gender identity within each participant in response to the altered footstep sounds, we included the two extremes (high frequency condition/low frequency condition) to explore potential changes. Each participant completed one high frequency condition and one low frequency condition walking phase. Sound order was counterbalanced across participants.

Procedure

After arriving in the lab, participants received written information about the experiment, were given the opportunity to ask any questions, and were then asked to sign an informed consent form. Participants completed a computerised version of the IAT for implicit self-gender association and then answered a set of questions (TMF, IOS Women, IOS Men). These tests provided a baseline control pre-intervention measurement. Then, six Notch movement sensors were attached to the participant's body, and the participants put on the shoe prototype and backpack. The experimenter then attached one microphone each to the outside of the left and right sandal. Participants were then instructed to stand at the beginning of the wooden corridor and the Notch movement sensors were calibrated. Then, the experimenter gave the participant instructions for the walking phase and asked them to walk as if they would do normally. If there were no questions on the procedure the participants put on the headphones. After a visual starting signal, participants marched on the spot for 30 s and paused briefly after a visual stopping signal. Following a second visual starting signal, they walked down the corridor and paused at the end. The total exposure time to the altered footstep sounds was 35–40 s. Two separate recordings of movement data were collected in the Notch app, one for walking on the spot and one for walking down the corridor. After the walking was completed, participants took off the headphones, microphones, and backpack. They were then asked to sit down and complete the IAT task followed by IOS Women, IOS Men, bodily feelings, and SAM. This procedure was repeated with the second sound condition. There were approximately 8–12 min between the sound exposure in the two conditions. At the end of the experiment, participants answered additional questions on their weight and shape concern, thoughts on the purpose of the experiment, prior experience, and demographics. Finally, after taking off the Notch sensors and sandals, participants were asked about their body height and to step on a scale to measure body weight because previous work (Tajadura-Jiménez et al., 2019) identified body weight as a relevant factor for the effect of the sounds. All participants were fully debriefed. The total procedure took about 45 min.

Data Analyses

We report p-values smaller than 0.05 as significant. P-values in the range 0.05 to 0.1 are reported as marginally significant and corresponding trends are interpreted.

Body perception as quantified by bodily feelings and motor behaviour (H1)

Bodily feelings were evaluated using the three questions from the bodily feelings questionnaire. We compared the answers after walking in the high and low frequency conditions using non-parametric Wilcoxon signed-rank tests. To check for a potential effect of order of condition, the data was aligned rank transformed with the ARTool package (v. 0.10.6)[3] in R, which allows a consecutive analysis with a two-way mixed ANOVA with order as a between-subjects factor. To assess potential effects on motor behaviour, we extracted CSV files with lateral hip and chest angles from the Notch recordings during the walking phase on the corridor. An automatic annotation of steps was tested but assessed to be unreliable due to high variability and noise within the data. Therefore, angles were plotted in MATLAB and peaks and valleys were manually annotated and extracted with the "data cursor mode" (see **Figure 2**). The total number of steps differed due to step size of the participants and some steps were overlaid by noise. Only those steps with a reoccurring, regular pattern were annotated. The manually annotated peaks and valleys were then used to extract from each walking phase: the average difference between a consecutive peak and valley (i.e., sum of distances between a consecutive peak and valley divided by total number of peaks and valleys) and the maximal difference between a consecutive peak and valley. The resulting data was not normally distributed; therefore, Wilcoxon signed-rank tests were used for statistical analysis. In the analysis,

[3] ARTool: Aligned Rank Transform. URL: https://cran.r-project.org/web/packages/ARTool/index.html

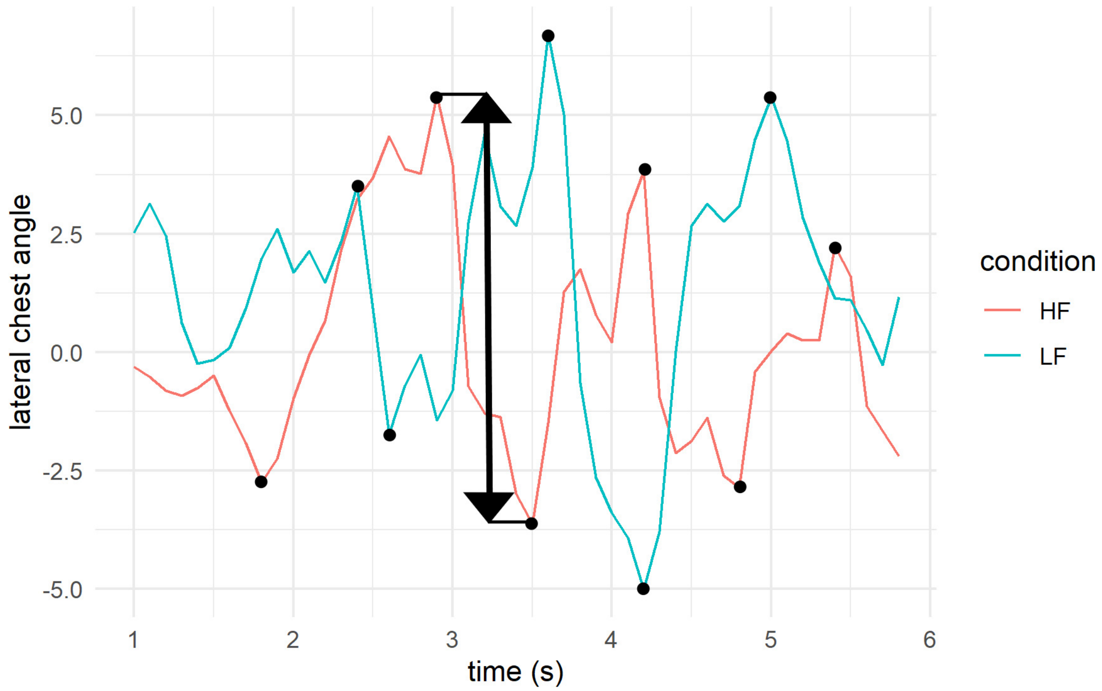

FIGURE 2 | Example plot of lateral chest tilt in high and low frequency. The black dots represent the manually annotated peaks and valleys. We calculated the absolute differences between a consecutive peak and valley (black arrow). Based on these distances, two values were extracted: the average distance (sum divided by the total number of peaks and valleys) and the maximal distance between consecutive peaks and valleys in a walking phase.

it became apparent that the results were strongly affected by the choice of metric (mean vs. maximal difference), included participants (with varying noise levels), and included number of steps. Given the high variability of signal-to-noise ratio between participants and pattern of statistical results depending on criteria, we decided to exclude the movement data from the reported analysis. Therefore, only the self-reported bodily feelings will be reported for H1.

Implicit self-gender association (IAT) (H2)

Implicit self-gender association was evaluated with the IAT, using the improved IAT scoring algorithm reported in Greenwald et al. (2003). A positive IAT score (0 to + 2] indicates an implicit self-female association; a negative IAT [−2 to 0) score indicates an implicit self-male association. After checking for normal distributions within each condition (Shapiro-Wilk test) and for sphericity (Mauchly's Test for Sphericity), a repeated measures ANOVA was used to compare IAT scores between pre-test baseline, after high frequency, and after low frequency. *Post hoc* comparisons were done using Bonferroni corrected paired *t*-tests. Also, a two-way mixed ANOVA with order as a between-subjects factor was calculated to check for a potential effect of order.

Explicit self-gender group identification (IOS) (H3)

Explicit self-gender group identification was measured using a coded (1–7) version of the IOS scale. Increasing numbers corresponded to a closer proximity between the circles. For both the IOS with the group of men and the IOS with the group of women, a non-parametric Friedman test was calculated to compare the pre-test baseline measurement with the results after the high, and after the low frequency condition. *Post hoc* tests were done using non-parametric Wilcoxon signed-rank tests with Bonferroni correction. Analogous to the bodily feelings data, the IOS data was aligned rank transformed and analysed with a two-way mixed ANOVA to check for a potential effect of order.

Baseline gender identity

The answers to the TMF scale were coded with numbers from 1 to 7 and mean scores were calculated for all six questions (Kachel et al., 2016). As a benchmark, Kachel et al. (2016) reported mean TMF values of 4.54 (SD = 1.15) and 5.36 (SD = 0.72) for, respectively, lesbian and straight women. As sexual orientation was not assessed during this experiment, a t-test was calculated to compare our measured mean TMF score with the average of Kachel's reported values for women (M = 4.95) to account for a potential diversity of sexual orientation in the sample. In addition, to allow a comparison with Tajadura-Jiménez et al. (2019), who only measured the first (masculine-feminine being) and second (masculine-feminine wish) question, we also analysed those questions individually. We compare our median scores to the medians reported in Tajadura-Jiménez et al. (2019).

Shape and weight concerns

We followed the coding instructions of Fairburn (2008), in which answers to the subscales are coded with numbers from 0 to 6. To allow a comparison of our observed scores with potential population scores, we compared the average shape and weight concern subscales with publicly available community norms for Australian undergraduate women (Mond et al., 2006).

Results

Questionnaire data of one participant were excluded due to indicators of *content non-responsivity* (Meade and Craig, 2012) (i.e., giving the same answer to many consecutive questions, suggesting that question content was not read). Hence, the analysis of questionnaire data (H1 and H3) is based on 25 participants. Additional information on the female sample and comparisons to existing norms, for example for shape and weight concerns, are provided in the **Supplementary Data S1**. *Post hoc* correlations of implicit and explicit measures of gender identity are provided in the **Supplementary Data S3**.

Bodily Feelings (H1)

After walking with high frequency step sounds, participants reported to feel significantly more feminine ($Z = -3.46$, $p < 0.001$, $r = 0.69$), lighter ($Z = -3.43$, $p < 0.001$, $r = 0.69$), and weaker ($Z = -2.21$, $p = 0.027$, $r = 0.44$) than after walking with low frequency step sounds. This trend is also reflected in the box-and-whisker plots in **Figure 3**. There was no significant interaction between the condition and the order of conditions for any of the bodily feelings ($p > 0.05$).

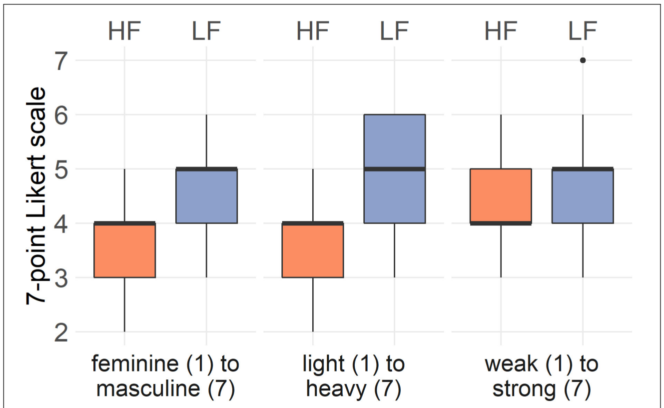

FIGURE 3 | Answers of the women ($n = 25$) to the bodily feelings questions on perceived masculinity and femininity, body weight, and strength in the high frequency and low frequency condition. Black horizontal line shows median score; lower and upper hinge correspond to the first and third quartiles (25th and 75th percentiles).

Implicit Self-Gender Association (IAT) (H2)

In the baseline measure, as expected, female participants associated themselves implicitly stronger with "female" than with "male" gender categories (IAT score: $M = 0.38$, $SD = 0.4$). The data was normally distributed within each point of measurement (Shapiro-Wilk test; baseline: $W = 0.971$, $p = 0.651$; high frequency: $W = 0.982$, $p = 0.904$; low frequency: $W = 0.97$, $p = 0.631$) and sphericity was not violated [$\chi^2(2) = 0.386$, $p = 0.824$]. Contrary to the formulated hypothesis, implicit self-gender association was not significantly affected by the walking sounds, $F(2,50) = 0.366$, $p = 0.695$, $n = 26$. There was also no significant interaction with the order of conditions [$F(2,48) = 0.812$, $p = 0.448$, $n = 26$)]. No further comparisons were calculated.

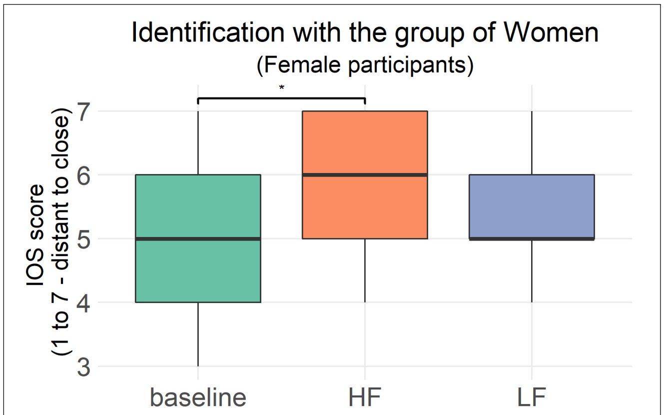

FIGURE 4 | Answers of the women ($n = 25$) to the IOS scale for the group of women at the three points of measurement. The horizontal bar represents the median IOS score. A higher score indicates a closer relationship between the self and the group of women. $^*p \leq 0.05$.

Explicit Self-Gender Group Identification (IOS) (H3)

In the baseline measure, as expected, women reported to feel significantly closer to the group of women ($M_{women} = 5.32$, $SD_{women} = 1.15$) compared to the group of men ($M_{men} = 3.68$, $SD_{men} = 1.28$; $Z = -3.77$, $p < 0.001$, $r = 0.75$). A higher mean indicates a closer proximity between the circles, that is a higher explicit self-gender group identification. As shown in **Figure 4**, there was a significant difference between the three points of measurement [baseline; after high frequency sounds; after low frequency sounds; $\chi^2(2) = 8.18$, $p = 0.017$, $n = 25$] with women reporting to feel closer to the group of women after walking with high frequency step sounds ($Z = -2.47$, $p_{adjusted} = 0.04$, $r_{adjusted} = 0.49$) compared to the baseline.

The relationship to the group of men (IOS Men) did not differ between the three points of measurement [$\chi^2(2) = 0.5$, $p = 0.78$, $n = 25$]. Both for IOS Women and IOS Men there were no significant interactions between the condition and the order of conditions ($p > 0.05$). No further comparisons were calculated.

Summary

Consistent with H1, the women in this experiment reported to feel lighter, more feminine, and weaker after walking with the high frequency step sounds compared to their perception after walking with low frequency step sounds. These findings align with previous work using altered footstep sounds (Tajadura-Jiménez et al., 2015, 2019) and confirm that the bodily illusion was induced successfully. The implicit self-association of women with "male" and "female" gender categories was not significantly affected by the altered footstep sounds (in contrast to H2). Consistent with H3, women indicated to feel closer to the group of women after walking with high frequency step sounds compared to the baseline measure. However, there were no differences in the reported identification with the group of men between the points of measurement.

EXPERIMENT II: ALTERING IMPLICIT SELF-GENDER ASSOCIATION AND EXPLICIT SELF-GENDER GROUP IDENTIFICATION OF MEN

Motivation and Method

The first experiment supported the idea that altered footstep sounds can induce a gender illusion (as indicated by changes in perceived weight, femininity/masculinity, and strength) and possibly affect explicit self-gender group identification (IOS) of women. To investigate whether similar effects would occur for men, we conducted a second experiment with cisgender males. 26 cisgender males took part (M = 33.62 years, SD = 12.87 years). On average, they weighed 74.04 kg (SD = 10.09 kg) and were self-reportedly 178 cm (SD = 6.2 cm) tall. Their body mass index (M = 23.37, SD = 2.99, Range = 17.63 – 30.64) was in the healthy range (18.5 – 24.9) according to the National Health Service in the UK (see text footnote 1) for 18 participants. The eligibility criteria were identical to Experiment I. As men tend to have larger feet than women, we additionally included a required shoe size below UK 10 (EU 44) to ensure a good fit of the shoes. Participants were recruited through an online subject pool and the researcher's social network. Each participant was compensated with £7 as an individual financial compensation.

Ethical approval was obtained by the UCL Research Ethics Committee (Project ID: UCLIC/1516/003/Staff). The study was performed according to institutional ethics and international standards for the protection of human participants. All participants provided their written informed consent prior to their participation and were fully debriefed.

The hypotheses were identical to those for Experiment I. All materials and procedures remained the same, only the order of the IOS scales was swapped, such that the male participants always answered the IOS for the group of men first. We also asked participants during debriefing whether they had noticed a difference between the sounds and – if so – how they would describe the difference. This was done to get more insight into participants' experience, as informal chats with the participants from Experiment I revealed that participants differed in their interpretation of the variation across the sound conditions, for example perceiving differences in volume or noise level. Finally, we also asked participants whether English was their native language, since it was suspected that the command of the English language could affect IAT responses.

The analysis was adjusted to compare baseline gender identity, and shape and weight concerns with respective values for the group of men. Specifically, a t-test was calculated to compare the mean TMF scores with the average (M = 3) of the reported TMF means for straight men at 2.51 (SD = 0.98) and for gay men at 3.49 (SD = 0.87) by Kachel et al. (2016) to account for potential diversity of sexual orientation in the sample. The shape and weight concerns were compared to the respective norms from undergraduate men in the US (Lavender et al., 2010).

Results

Additional information on the male sample and comparisons to existing norms, for example for shape and weight concerns, are provided in the **Supplementary Data S2**. *Post hoc* correlations of implicit and explicit measures of gender identity are provided in the **Supplementary Data S3**.

Bodily Feelings (H1)

After walking with high frequency step sounds, participants reported to feel significantly more feminine ($Z = -2.03$, $p = 0.042$, $r = 0.4$) than after walking with low frequency step sounds. There were no significant differences for light-heavy ($Z = -1.31$, $p = 0.19$, $r = 0.26$) or weak-strong ($Z = -0.53$, $p = 0.6$, $r = 0.1$) perception between high and low frequency step sounds (**Figure 5**). There was no significant interaction between the condition and the order of conditions for any of the bodily feelings ($p > 0.05$).

Implicit Self-Gender Association (IAT) (H2)

In the baseline measure, as expected, male participants associated themselves implicitly stronger with "male" than with "female" gender (IAT score: $M = -0.47$, $SD = 0.34$). The data was normally distributed within each point of measurement (Shapiro-Wilk test; baseline: $W = 0.98$, $p = 0.87$; high frequency: $W = 0.987$, $p = 0.977$; low frequency: $W = 0.969$, $p = 0.604$) and sphericity was not violated [$\chi^2(2) = 0.759$, $p = 0.684$]. The IAT scores differed significantly at the three time points [$F(2,50) = 8.688$, $p < 0.001$, $\eta_p^2 = 0.258$, $n = 26$]. Participants had significantly higher IAT scores after walking with the high frequency footstep sounds compared to the baseline [$t(25) = -4.00$, $p_{adjusted} < 0.001$], and compared to the IAT score after walking with low frequency step sounds [$t(25) = 3.02$, $p_{adjusted} = 0.012$]. Thus, participants implicitly associated themselves relatively less with "male" and

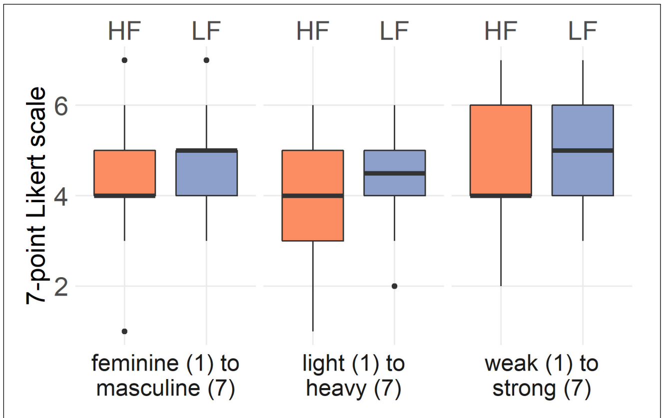

FIGURE 5 | Answers of the men to the bodily feelings questions on perceived masculinity and femininity, body weight, and strength in the high frequency and low frequency condition. Black horizontal line shows median score; lower and upper hinge correspond to the first and third quartiles (25th and 75th percentiles).

more with "female" after walking with high frequency step sounds compared to both baseline and low frequency step sounds (**Figure 6**). There was no significant interaction between the condition and the order of conditions [$F(2,48) = 0.587$, $p = 0.560$, $n = 26$].

Explicit Self-Gender Group Identification (IOS) (H3)

In the baseline measures for explicit self-gender group identification (IOS), as expected, men reported closer group identification with the group of men ($M_{men} = 4.96$, $SD_{men} = 1.82$) compared to the group of women ($M_{women} = 3.5$, $SD_{women} = 1.61$; $Z = -2.42$, $p = 0.016$, $r = 0.47$). A higher mean score represents a closer proximity between the circles, that is a closer explicit self-gender group identification. The group identification with the respective gender groups did not change in response to the altered footstep sounds, as there was no significant difference in the perceived closeness to the group of women [$\chi^2(2) = 1.77$, $p = 0.412$, $n = 26$] or the group of men [$\chi^2(2) = 1.45$, $p = 0.485$, $n = 26$] between the three points of measurement. Both for IOS Women and IOS Men there were no significant interactions between the condition and the order of conditions ($p > 0.05$).

We would have expected a change in explicit self-gender group identification (IOS) as the findings in the implicit self-gender associations (IAT) (H2) and the self-reported masculinity-femininity perception (H1) indicate a change in gender identity and this change is expected to affect explicit self-gender group identification (IOS) as well. Moreover, based on the mean IOS values, there was a tendency for men feeling closer to the group of women after walking in the low frequency condition compared to the other two conditions. As this is inconsistent with our hypothesis and the theory by Maister et al. (2015) and Tsakiris (2017), we examined the individual responses of the participants in more detail. Thereby, we noticed mismatches between the answers to the questions on perceived masculinity/femininity (TMF scale) and explicit self-gender group identification (IOS scales) for some of the participants (i.e., male participants 03 and 20; **Supplementary Data**). For example, male participant 20 indicated to be very masculine in the TMF scale [$M = 1.33$ on a scale from very masculine (1) to very feminine (7)] but then chose the most distant circles in the IOS for the group of men and the closest (i.e., completely overlapping) circles in the IOS for the group of women. One possible explanation for such mismatches could be that these participants misinterpreted the IOS scale to target *attraction toward* rather than *identification with* the respective gender group. Therefore, for some of the male participants, the IOS scale might have failed to capture the intended sense of belonging to the gender groups. For this reason, we decided not to interpret the IOS data from the second experiment further. We did not observe a similar pattern in the first experiment.

FIGURE 6 | Distribution of IAT scores (–2 to + 2) in the group of men. The black dot indicates the mean IAT score. A positive score indicates quicker association of "Self" and "Female." A negative IAT score indicates a quicker association of "Self" and "Male." *$p \leq 0.05$, ***$p \leq 0.001$.

COMBINED ANALYSIS

Although previous work did not find differences in sound perception based on sex (Tajadura-Jiménez et al., 2019), the results from the two presented experiments suggest slight differences between the male and female participants. For the women in Experiment I, altered footstep sounds affected perceived masculinity and femininity, body weight, and strength as well as self-identification with the group of women, but not self-association with gender categories. For the men in Experiment II, however, altered footstep sounds affected self-association with gender categories and perceived masculinity and femininity, but not perceived body weight. Thus, an additional combined analysis was performed to explore potential interactions between the effect of the sound conditions and the sex of the participant.

Combined Data Analyses

The ordinal data from the bodily feelings questions were aligned rank transformed with the ARTool package (v. 0.10.6) (see text footnote 3) in R, which allows a consecutive analysis with a two-way mixed ANOVA. The IAT data was not transformed and analysed with a two-way mixed ANOVA. Significant main effects were interpreted based on the interaction plots (see also **Supplementary Figure 1**) and for IAT data, a contrast analysis[4] was performed with the emmeans package (v. 1.4.2)[5] in R.

Results

Bodily Feelings (H1)

For the light-heavy perception, there was a significant main effect of sound condition [$F(1,49) = 17.29$, $p < 0.001$, $\eta_p^2 = 0.261$, $n = 51$], with participants feeling lighter after walking with the high frequency footstep sounds. The main effect of sex was not significant [$F(1,49) = 0.002$, $p = 0.965$, $n = 51$] but there was a significant interaction between sex and sound condition [$F(1,49) = 5.98$, $p = 0.018$, $\eta_p^2 = 0.109$, $n = 51$]. Visual inspection suggests that the change from high to low frequency was bigger for women than for men (**Figure 7A**).

[4]Contrast tests with ART. URL: https://cran.r-project.org/web/packages/ARTool/vignettes/art-contrasts.html

[5]Emmeans: Estimated Marginal Means, aka Least-Squares Means. URL: https://cran.rproject.org/web/packages/emmeans/

FIGURE 7 | Visualisation of the data from male and female participants after walking with high and low frequency step sounds. **(A)** Shows mean values of perceived body weight (n = 51). **(B)** Shows mean values of perceived masculinity and femininity (n = 51). **(C)** shows mean IAT scores where a higher score corresponds to a stronger association with "Female" (n = 52). Error bars show 95% confidence intervals.

For the masculine-feminine perception, there was a significant main effect of sound condition [$F(1,49) = 25.48$, $p < 0.001$, $\eta_p^2 = 0.342$, $n = 51$], with participants feeling more feminine after walking with the high frequency footstep sounds than with the low frequency step sounds. The main effect of sex was also significant [$F(1,49) = 9.1$, $p = 0.004$, $\eta_p^2 = 0.157$, $n = 51$] with women indicating to feel more feminine than men on average. The interaction between sex and sound condition was marginally significant [$F(1,49) = 3.49$, $p = 0.068$, $\eta_p^2 = 0.067$, $n = 51$]. Visual inspection suggests that the change from high to low frequency was bigger for women than for men (**Figure 7B**).

For the weak-strong perception, there was a significant main effect of sound condition [$F(1,49) = 4.17$, $p = 0.047$, $\eta_p^2 = 0.078$, $n = 51$], with participants tending to feel weaker after walking with the high frequency footstep sounds. Neither the main effect of sex [$F(1,49) = 1.1$, $p = 0.3$, $n = 51$] nor the interaction between sex and sound condition [$F(1,49) = 1.74$, $p = 0.194$, $n = 51$] was significant.

Implicit Self-Gender Association (IAT) (H2)

The requirements for the two-way mixed ANOVA were met as sphericity was not violated [$\chi^2(2) = 0.291$, $p = 0.865$], the variances were homogenous according to Levene's test (baseline: $p = 0.312$; after high frequency: $p = 0.312$; after low frequency: $p = 0.260$), and the data was normally distributed within each condition (see Shapiro-Wilk in analysis of H2 in Exp. I and II). The main effect of sound condition was significant [$F(2,100) = 5.744$, $p = 0.004$, $\eta_p^2 = 0.103$, $n = 52$] and the contrast analysis and visual inspection of the combined data in **Figure 7C** revealed a significantly stronger implicit self-female association after walking with high frequency step sounds compared to the baseline measure ($t = -3.08$, $p_{adjusted} = 0.01$, $n = 52$). The difference between the IAT scores after walking with high and with low frequency was significant as well ($t = 2.49$, $p_{adjusted} = 0.048$, $n = 52$). Both men and women implicitly associated themselves relatively less with "female" and more with "male" after walking with low frequency step sounds compared to high frequency step sounds. As expected, the main effect of sex was also significant [$F(1,50) = 75.644$, $p < 0.001$, $\eta_p^2 = 0.602$, $n = 52$], with women having stronger implicit self-female associations (higher IAT scores) than men. There was no significant interaction between sex and sound condition [$F(2,100) = 2.21$, $p = 0.115$, $n = 52$].

DISCUSSION

We studied the link between body perception and the self-concept through real-time alteration of footstep sounds. In two experiments, we replicated the finding that footstep sounds affect perceived masculinity and femininity during walking (Tajadura-Jiménez et al., 2019), suggesting that auditory feedback can induce a temporary gender illusion (H1). Further, men (Experiment II) experienced a temporary change in their self-concept as they associated themselves relatively more with "female" after walking with high frequency footstep sounds and relatively more with "male" after walking with low frequency footstep sounds (H2). This supports the theory that the self-concept is rooted in body perception and therefore malleable through bodily illusions (Maister et al., 2015; Tsakiris, 2017). Moreover, the results partially support the hypothesised connection between body perception and self-identification with social groups (Tsakiris, 2017), as women (Experiment I) reported to feel closer to the group of women after walking with high frequency footstep sounds (H3). We did not observe a "swap" in gender identity induced by the altered footstep sounds but a strengthened (Experiment I) or weakened (Experiment II) identification with one's own sex. Thus, our findings suggest the malleability of gender identity in response to an auditory-induced bodily illusion.

The combined analysis further strengthens the support for H1 and H2, hence, that altered footstep sounds affect perceived body weight, masculinity-femininity, and strength, as well as implicit self-gender association (IAT) of both males and females.

The combined analysis also revealed an interaction between the malleability of body weight perception and the sex of the participants, suggesting that the change in perceived body weight was stronger for women than for men. H3 is partially supported for the explicit self-gender group identification (IOS) with women feeling closer to the group of women after walking with high frequency footstep sounds. The changes in bodily feelings (perceived body weight, femininity/masculinity, strength) (H1) resemble and support earlier findings using the shoe prototype for altering footstep sounds to induce bodily illusions (Tajadura-Jiménez et al., 2015, 2019) and we thus expect that the bodily illusion was successfully induced similarly to previous experiments. The observed changes in implicit self-gender association (IAT) (H2) are consistent with the recent work from Tacikowski et al. (2020a) who showed that experiencing a body swap illusion with an avatar of a different sex causes temporary changes in the gender identity of the participants. We extend these findings by showing that subtle illusions of one's own actual body induced through auditory feedback can cause such changes in one's gender identity as well.

Illusory Changes of One's Own Actual Body Can Lead to Changes in the Self-Concept

Our findings contribute to the theoretical understanding of the connection between body perception and social cognition. Previous work showed that body swap illusions can affect implicit biases toward the embodied group (Maister et al., 2013; Peck et al., 2013), and the effect is theorised to occur through a change in the perception of one's own body and one's self-concept (Maister et al., 2015; Tsakiris, 2017). Specifically, it has been argued that attitudes and beliefs about the Self are linked to the representation of the body, and they will be adjusted in response to an altered body representation in order to maintain consistency between the Self and the body representation (Maister et al., 2015). Hence, body swap illusions are thought to first cause changes in the mental representation of one's own body and one's self-concept to incorporate more features of the embodied group, and thereby increase the identification with that group. The increased identification then causes a transfer of one's positive self-evaluation to the embodied group, which becomes apparent in the change in implicit associations (Maister et al., 2015; Tsakiris, 2017).

Our work addresses a gap in the literature of providing direct evidence for changes in the self-concept following direct changes of one's own actual body (i.e., own body illusions). There is some evidence from previous work that body swap illusions cause changes in the self-concept (Banakou et al., 2013; Tajadura-Jiménez et al., 2017a; Tacikowski et al., 2020a,b) but none of these showed these effects for own body illusions. Our findings support the hypothesised connection between body perception and the self-concept by demonstrating that subtle auditory-induced illusions of direct changes of one's own actual body can lead to temporary changes in gender identity, as reflected in changes in implicit self-gender associations (IAT) and explicit self-gender group identification (IOS).

It is noteworthy that the IAT which was used for this experiment measured implicit self-gender association with word stimuli. Hence, the IAT assessed an abstract, semantic conceptualisation of the Self. The observed change in the IAT score therefore suggests that the bodily illusion did not only affect participants' physical self-perception but also their higher-level conceptual Self. This is different from the majority of previous work on changes in the self-concept which assessed changes in implicit associations based on the sensory features that were manipulated during the bodily illusion. For example, Banakou et al. (2013) and Tajadura-Jiménez et al. (2017a) altered the physical appearance of participants by inducing a body ownership illusion of a child avatar in VR and used an IAT with *images* of adults and children to measure self-association with adults and children, hence, staying in the same sensory domain. Only the recent work by Tacikowski et al. (2020a) provides evidence for this transfer as they measured the effects of a body swap illusion with an IAT using semantic stimuli. We add to their work by demonstrating this effect for auditory-induced *own* body illusions.

Our findings also support the grounded or embodied approach to human cognition which assumes that our higher-level cognition is grounded in multimodal sensory experiences. In this approach, considerable attention is paid to physical sensations and the relationship between the body and the brain (Barsalou, 2008), exploring for example the influence of fluid movements on creativity (Slepian and Ambady, 2012). In the context of bodily illusions, previous research on body swap illusions found that embodying an Albert Einstein avatar can enhance performance in a cognitive task (Banakou et al., 2018) and that gender swap illusions in VR can improve performance in stereotype threatening situations [i.e., situations in which an individual's performance is affected by a negative stereotype: that the group is expected to perform worse (Peck et al., 2018)]. Future work should investigate whether auditory-induced illusions of one's own actual body can cause changes beyond the self-concept, for example alter one's performance in stereotype threatening situations or one's implicit attitudes toward others.

Why Might Changes in Implicit Self-Gender Associations (IAT) Be Less Pronounced for Female Participants?

In Experiment I, while the implicit self-association (IAT) of women with male and female gender (H2) followed the predicted trend, the differences were not significant. As the combined analysis revealed a significant main effect of footstep sounds for all participants (without an interaction with gender; see **Figure 7C**), we suspect that the effect was not as pronounced in the first experiment due to characteristics of the tested female sample. We discuss a stronger focus on body weight and shape in the female sample as a possible explanation.

The frequency components in the footstep sounds are not only indicators for sex, but also for the body weight of the walker (Li et al., 1991), and have been shown to affect body weight perception in previous experiments (Tajadura-Jiménez et al., 2015, 2019). As the shape and weight concerns were higher among the females compared to males (see **Supplementary Datas S1, S2**), females might have interpreted the sounds more strongly in relation to body weight than in relation to sex. This explanation is consistent with the findings in the bodily feelings questions, where women self-reportedly experienced a change in perceived body weight while the effect was not significant for men (H1). Accordingly, the combined analysis suggested that the effect of sound condition on perceived body weight was stronger for females than for males. As previous research did not find differences between sexes in footstep sound perception (Tajadura-Jiménez et al., 2019), the found differences might be specific to the tested sample. Possibly, the social stigma associated with weight and gender may make some women more susceptible to the illusion (Tiggemann, 1994). However, this relation needs to be confirmed in future research.

Implications for Research on the Malleability of Gender Identity

In addition to the implications for the connection between body and mind, our findings raise important questions about gender identity itself. While gender identity is generally considered to be stable for cisgender individuals, our experiments show that a short and subtle alteration of one's body perception can temporarily affect gender identity. Gender identity is complex and while it does not have to be aligned with the appearance of one's body, our results suggest that body-perception is at least an important facet in the perception of one's gender identity.

Our results support the idea that gender identity should be understood as a continuum rather than distinct categories. The reason being that participants did not fully shift for example from identifying with male gender to identifying with female gender, but their gender identity became more balanced. These findings are in line with the work from Tacikowski et al. (2020a) who discuss the malleability of gender identity in response to bodily illusions in more detail. The results from the combined analysis which are relevant to gender identity showed no interactions with the participant's sex and all trends (apart from the IOS Women scale) were identical in both experiments, which indicates that malleability of gender identity does not systematically differ between men and women.

Limitations and Future Work

One limitation of our work is that we could not provide insights on whether an auditory-induced gender illusion is reflected in movement behaviour (H1) as, due to a poor signal-to-noise ratio, we decided not to interpret our Notch movement data further. Given that other auditory bodily illusions have affected movement patterns (Tajadura-Jiménez et al., 2016, 2019), and that males and females have different walking styles (Troje, 2002), we consider it likely that the walking patterns change in response to a gender illusion. The Notch sensors were calibrated in the laboratory with all electronic devices present, however, it is possible that the *activity* of the electronic devices during the experiment (e.g., the program for data collection, the active shoe prototype, setup for sound alteration, and devices from the participants) interfered with the signal from the Notch sensors. Therefore, in future research, further reducing signal interferences where possible and measuring more steps with the sensors would allow a more reliable identification of the consistent features (and distinction from the noisy features) in the signal of the steps.

A second limitation is that we cannot conclusively answer whether changes in explicit self-gender group identification (IOS) also occurred for men (H3) as, due to a suspected misinterpretation of the IOS scale by at least two of the male participants, we decided not to interpret our IOS data from Experiment II further. To improve future research on explicit self-gender group identification using the IOS scale, we would recommend clarifying the instructions further, for example by adding that the scale does not target attraction. In addition, it would be interesting to explore alternative or implicit measures for self-gender group identification. For example, one simple modification could be to use a continuous scale with two circles instead of multiple images, asking participants to manually adjust the distance between the circles to reflect their sense of belonging. This could capture a more fine-grained and intuitive sense of group identification and prevent the response artefact of participants reselecting their previous answer option without considering their immediate experience.

Third, several women (Experiment I) had heard of the shoe prototype and its connection to body weight prior to their participation (**Supplementary Data S1**). Thereby, none of the women had listened to or experienced the sound alteration before taking part. Further, the differences between the conditions are quite subtle especially if they are not played seamlessly after one another. Thus, having heard about the prototype did not imply that participants were able to correctly identify the high ("light") and low ("heavy") frequency conditions. This is evidenced by the feedback provided by men in Experiment II: only six participants described the difference between the sound conditions in terms of light- or heaviness. As gender identity had not been linked to the altered footstep sounds in prior experiments, we do not expect that participants were able to allocate the conditions correctly. However, in future experiments, we would ask participants to describe explicitly how they perceived the respective conditions to gain a better understanding of their interpretation of the sounds.

Lastly, while our findings are consistent with the predictive coding account, both bottom-up (sensorimotor) mechanisms and top-down (stereotypes triggered by sounds) mechanisms could be playing a role in the fluidity of gender associations in response to footstep sounds. Thus, future experimental set-ups should include an additional asynchronous control condition in which the sounds are disassociated from the steps to disambiguate these mechanisms more clearly.

CONCLUSION

In sum, we showed that subtle illusions of direct changes of one's own actual body can cause temporary changes in the self-concept, in this case one's gender identity and relation to gender groups. Our findings support recent theories on the connection between body perception and social cognition (Maister et al., 2015; Tsakiris, 2017), and the notion that gender identity is at least partially rooted in physical experiences of one's body and therefore temporarily malleable through bodily illusions (Tacikowski et al., 2020a). As many people wear headphones in their daily lives, auditory information could potentially be used to induce bodily illusions in real-life situations without requiring a complex VR environment. Given that (strength of) gender identification influences self-stereotyping (Cadinu and Galdi, 2012), such an application could potentially alleviate the performance decrease of some women in stereotype threatening situations. Also, altered footstep sounds could be used to enhance body-sex change illusions in VR (Tacikowski et al., 2020a) and provide an interesting tool for individuals with gender dysphoria to explore the effects of an altered body perception on their gender identity and well-being.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding authors.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the UCL Research Ethics Committee (Project ID: UCLIC/1516/003/Staff). The participants provided their written informed consent to participate in this study. Written informed consent was obtained from the individual(s) for the publication of any potentially identifiable images or data included in this article.

AUTHOR CONTRIBUTIONS

AT-J developed the shoe prototype used in the experiments. SC designed and conducted the experiment and wrote the first draft of the manuscript. SC and AT-J analysed the data. All authors discussed the experimental design and the results, and contributed to and approved the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fnhum.2021.688170/full#supplementary-material

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Could Brain–Computer Interface Be a New Therapeutic Approach for Body Integrity Dysphoria?

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Patients suffering from body integrity dysphoria (BID) desire to become disabled, arising from a mismatch between the desired body and the physical body. We focus here on the most common variant, characterized by the desire for amputation of a healthy limb. In most reported cases, amputation of the rejected limb entirely alleviates the distress of the condition and engenders substantial improvement in quality of life. Since BID can lead to life-long suffering, it is essential to identify an effective form of treatment that causes the least amount of alteration to the person's anatomical structure and functionality. Treatment methods involving medications, psychotherapy, and vestibular stimulation have proven largely ineffective. In this hypothesis article, we briefly discuss the characteristics, etiology, and current treatment options available for BID before highlighting the need for new, theory driven approaches. Drawing on recent findings relating to functional and structural brain correlates of BID, we introduce the idea of brain–computer interface (BCI)/neurofeedback approaches to target altered patterns of brain activity, promote re-ownership of the limb, and/or attenuate stress and negativity associated with the altered body representation.

Keywords: apotemnophilia, body integrity dysphoria, body integrity identity disorder, body representation, brain–computer interface, neurofeedback, somatoparaphrenia, xenomelia

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INTRODUCTION

For most people, the thought of becoming physically disabled is troubling and something to be avoided at all costs. For patients suffering from body integrity dysphoria (BID) however, the desire to become disabled is characteristic, arising from a mismatch between the desired body and the physical body in terms of functionality or shape. In its most common variant, i.e., the desire for amputation, on which we focus here, the defining features include an intense feeling of inappropriateness concerning their current body configuration. BID patients desire to become physically disabled in order to feel "complete" and become the person they envisage themselves to be (First, 2005; White, 2014). Ironically, achieving this completeness often involves desiring to amputate an otherwise healthy and fully functioning limb, raising many ethical and medical considerations. In most reported cases, amputation of the rejected limb entirely alleviates the distress of the condition and engenders substantial improvement in quality of life (Noll and Kasten, 2014). Individuals with BID are non-psychotic and do not otherwise present major psychiatric or neurological disorders. Sufferers often describe themselves as being *trans*-abled, drawing a parallel with transgendered individuals.

Since BID can lead to life-long suffering, it is essential to identify an effective form of treatment that causes the least amount of alteration to the person's anatomical structure and functionality. Current forms of treatment such as amputation are extreme and lead to a permanent disability and presumably dependence on carers for activities of daily living. Other treatment methods such as medications, psychotherapy, and vestibular stimulation have proven largely ineffective (Ryan, 2008; Blom et al., 2012). In this article, we briefly discuss the characteristics, etiology, and current treatment options available for BID before highlighting the need for new, theory driven approaches. Drawing on recent findings relating to functional and structural brain correlates of BID, we introduce the idea of brain–computer interface (BCI)/neurofeedback approaches to target altered patterns of brain activity, promote re-ownership of the limb, and/or attenuate stress and negativity associated with the altered body representation.

CHARACTERISTICS AND ETIOLOGY OF BID

In order to provide an in-depth evaluation of BID and its manifestations, it may be helpful to first differentiate from other similar conditions such as body dysmorphic disorder (BDD) and somatoparaphrenia, among others (**Table 1**). BID shares similarities with BDD, because individuals with BID are also found to be preoccupied with certain aspects of their body (Grocholewski et al., 2018). However, there are some key differences. The dysphoria experienced by individuals with BDD is derived from their concerns over how a part of their body physically appears to others (First and Fisher, 2012). Specifically, individuals with BDD believe that some aspect of their physical appearance is defective and as such is a source of intense embarrassment, shame, and low self-esteem.

Somatoparaphrenia (SPP) is characterized by a denial of ownership combined with confabulatory signs (Gerstmann, 1942). It affects predominantly the left side of the body (McGeoch et al., 2011). Two main clinical features separate it from BID. First, while BID likely develops in childhood and may be related to amputation-related experiences (Barrow and Oyebode, 2019), SPP is an acquired condition in response to brain damage, typically of the right hemisphere, that typically also causes contralateral left limb paralysis. Moreover, while BID individuals recognize the unwanted limb as part of their current but undesired body, SPP is a disownership disorder, primarily characterized by a positive component, reflecting a "distorted mental representation of reality" (Bottini et al., 2009, p. 589), that is the delusional misattribution of the paralyzed limb to someone else (Gerstmann, 1942; Romano et al., 2014; Saetta et al., 2020). Another related clinical condition is asomatognosia, which is caused by a similar (more often a right lateral) cerebral lesion as SPP. In this condition, however, the limb is felt as non-existing rather than disowned (Critchley, 1954; Saetta et al., 2021).

Other conditions that have been discussed in relation to BID due to common features are alien hand syndrome and anarchic hand syndrome. For patients with alien hand syndrome, the motor control of the affected limb is disinhibited, and the limb executes smooth but non-volitional reflexive movements of grasping and compulsive manipulation of tools in the environment, i.e., utilization behavior (Doody and Jankovic, 1992; Feinberg et al., 1992). Typical damaged brain areas include fronto-mesial and anterior cingulate areas as well as the anterior corpus callosum (Feinberg et al., 1992). Anarchic hand syndrome (AHS) is a related disorder, which ensues from a relatively circumscribed lesion of the anterior corpus callosum (Feinberg et al., 1992, but see Pacella et al., 2021 for a more recent account). In this syndrome, the individuals' hands move outside of the volitional control as well (Della Sala, 2009; Jenkinson et al., 2015); however, intermanual conflicts are more typical than utilization behavior.

Gender incongruity/dysphoria (GD) is a condition in which there is a conflict between aspects of the physical body (sex) and the desired body, often leading to sex-reassignment through surgery and lifelong hormonal treatment. Before the release of the DSM-V, GD was referred to as "Gender Identity Disorder." The GD diagnosis separates this condition from sexual dysfunctions while framing it in terms of incongruence between phenomenological and assigned gender, instead of "cross-gender" identification disorder. Analogously, while BID has been previously defined as "Body Integrity Identity disorder" (First, 2005), the BID nomenclature focuses on the incongruence between the functionality and/or morphology of the current and assigned body. Conducting a direct comparison between attitudes of those with BID and GD (Ostgathe et al., 2014) revealed that both share similar onset (early childhood or adolescence), discontent in the individual with their identity, perceived reduction of desire post-surgical intervention, or through mimicking of desired identity such as cross-dressing in Gender Dysphoria and pretending of disability by using wheelchairs or crutches in BID. Comorbidity of BID with GID has been described in 19% of the cases (First, 2005; Lawrence, 2010). The groups differed, however, in the intensity of their aversion toward the unwanted body parts, with Gender Dysphoric individuals expressing an intense rejection or hatred, whereas BID individuals exhibited an indifference toward the limb. Remarkably, in both BID and GID individuals, the examination of reality is preserved in that the discomfort sensations are "illusions, not delusions" (Garcia-Falgueras, 2014; p. 161), and do not typically persist after surgical intervention (Garcia-Falgueras, 2014).

Before being recently included in the release of the 11th Revision of the International Classification of Diseases (World Health Organization, 2018) as a "disorder of bodily distress or bodily experience," BID has also been interchangeably referred to as xenomelia, apotemnophilia, and body-integrity identity disorder (BIID). While the lowest common denominator between these nomenclatures is the desire for amputation, each of them underlies a specific etiological hypothesis (Sedda and Bottini, 2014).

TABLE 1 | Taxonomy of disorders related to body integrity dysphoria.

Disorder	Key features		Implicated brain regions
Body integrity dysphoria (BID)	A "disorder of bodily distress or bodily experience" (World Health Organization, 2018). Desire to become physically disabled (e.g., blind, paralyzed, and amputated). Amputation variant includes (1) dysphoric feelings about a typical body morphology and/or functionality originating from a mismatch between the mental body image, i.e., the conscious representation of body size and shape, and the perceived body (Saetta et al., 2020), (2) lack of ownership over a limb, (3) excessive attention devoted to the limb, and (4) intact insight regarding the condition and its unusual nature (Giummarra et al., 2011). Most often left limb or both limbs (First, 2005). Typically observed in BID are also paraphilic interests, such as preferences for an amputated sexual partner and sexual arousal by the idea of being an amputee (Blom et al., 2017)		- Right superior parietal lobule (Ramachandran et al., 2009; McGeoch et al., 2011; Hilti et al., 2013; Saetta et al., 2020) - Left premotor ventral cortex (Saetta et al., 2020; van Dijk et al., 2013; Blom et al., 2016) - Right primary somatosensory and motor cortices (Hilti et al., 2013; Saetta et al., 2020) - Bilateral nucleus caudatus and putamen (Hänggi et al., 2016)
	Shared features with BID	Features distinct from BID	
Body dysmorphic disorder (BDD)	Preoccupation with certain aspects of the body (Grocholewski et al., 2018)	Dysphoria experienced by individuals with BDD is derived from their concerns over how a part of their body physically appears to others (First and Fisher, 2012). Specifically, individuals with BDD believe that some aspect of their physical appearance is defective and as such is a source of intense embarrassment, shame, and low self-esteem	- Reduced volume of the orbito-frontal cortex and the anterior cingulate, and larger volume of the thalamus (Atmaca et al., 2010) - Frontostriatal and temporoparietal occipital circuits for visual-spatial processing (Mufaddel et al., 2013)
Somatoparaphrenia	Denial of ownership over a limb (Gerstmann, 1942), and more often concerns the left body part (McGeoch et al., 2011).	Acquired condition in response to brain damage, typically right hemisphere, which may cause left limb paralysis. Characterized by delusional misattribution of the paralyzed limb to someone else (Gerstmann, 1942; Romano and Maravita, 2019)	- Right hemisphere subcortical white matter (Gandola et al., 2012; Moro et al., 2016) - Middle and inferior right frontal gyrus (Gandola et al., 2012) - Right hippocampus and amygdala (Gandola et al., 2012; Romano et al., 2014)
Asomatognosia	Disruption to right hemisphere influencing limb awareness Phenomenological similarities in 23% of the cases (Blanke and Metzinger, 2009)	Feeling that parts of the body are missing or have disappeared from corporal awareness (Arzy et al., 2006; Saetta et al., 2021)	Right temporo-parietal lobe, including the right superior parietal lobule (Saetta et al., 2021)
Alien hand syndrome	Disownership of the limb No traceable underlying cause for the perceived "disembodiment" of the limb (Müller, 2009)	Motor control of the affected limb is disinhibited and moves non-volitionally	- Primary motor cortex, premotor cortex, precuneus, and right inferior frontal gyrus (Schaefer et al., 2010) - Supplementary motor area, anterior cingulate gyrus, medial prefrontal cortex, and anterior corpus callosum (Feinberg et al., 1992)
Anarchic hand syndrome	Disembodiment of the limb Potential underlying mechanism relating to white matter disconnection and brain lesions (Pacella et al., 2021)	Motor control of the affected limb is disinhibited and moves non-volitionally No disownership of the limb	- Right inferior parietal lobe (Della Sala, 2009; Jenkinson et al., 2015) - White matter disconnection of antero-posterior, insular, and interhemispheric networks (Pacella et al., 2021) - Anterior corpus callosum (Feinberg et al., 1992)
Gender incongruity	Conflict between aspects of the physical body (sex) and the desired body. Onset (early childhood or adolescence), discontent in the individual with their identity, perceived reduction of desire post-surgical intervention or through mimicking of desired identity Comorbidity of BID with GID has been described in 19% of the cases (First, 2005; Lawrence, 2010) Preserved rationality and distress disappears after surgical intervention (Garcia-Falgueras, 2014)	Focus upon gender rather than upon a limb Intensity of rejection of body parts. Intense hatred in Gender incongruity vs. indifference in BID (Ostgathe et al., 2014)	- Bilateral superior parietal lobule and the primary somatosensory cortex (Lin et al., 2014) - Right insula (Nawata et al., 2010)

Apotemnophilia (from ancient Greek "love for amputation") proposes psychological or psychiatric features related to sexual disturbances to be the centerpiece of the disorder, whereas Xenomelia (from ancient Greek "foreign limb") put the disorder in the context of a neurological syndrome originating from alterations of the right parietal lobe (McGeoch et al., 2011). A lack of consensus regarding the nomenclature concerned with these conditions and their etiological basis is a topic of ongoing scientific debate.

Major characteristics observed in the amputation variant of BID include (1) dysphoric feelings about a normal body morphology and/or functionality originating from a mismatch between the mental body image, i.e., the conscious representation of body size and shape, and the perceived body (Saetta et al., 2020), (2) lack of ownership over a limb, (3) excessive attention devoted to the limb, and (4) intact insight regarding the condition and its unusual nature (Giummarra et al., 2011). Initial studies on BID have shown that in the case of a desire for amputation, most patients with BID desired amputation of either a left-sided limb or both limbs (First, 2005).

Ostgathe et al. (2014) found that justifications given by those with BID desiring an amputation included triggering childhood events, restoring a congruence between sentiment and body, feeling attracted by people with physical disabilities, a fascination for physically impaired people, as well as the perception of body impairment as a proper way of living. Typically observed in BID are also paraphilic interests, such as preferences for an amputated sexual partner and sexual arousal by the idea of being an amputee (Blom et al., 2017).

CURRENT APPROACHES TO TREATMENT FOR BID

Individuals with BID find symptomatic relief by spending substantial amounts of time engaged in so-called pretending behaviors in which they simulate the desired disability (e.g., walking with one's leg tied back, sitting in a wheelchair, using crutches, First, 2005). It is believed that the pretending behavior allows for the alignment of the perceived and desired body, reducing distress associated with the mismatch (Saetta et al., 2020).

While this provides some transient relief, the preoccupation with becoming disabled has harmful consequences. Time spent engaging in pretending behaviors interferes with the individual's productivity, leisure activities, and social functioning. In the case of desired amputation, pretending behaviors such as daily binding up of the leg can also cause injury over extended periods of time. At the most extreme end of the spectrum, attempts to actually achieve the desired disability can have catastrophic effects on the health of the individual, potentially putting their life at risk.

The only truly satisfying solution for BID sufferers seems to be the amputation of the rejected limb (Noll and Kasten, 2014). In most countries, this course of action will not be considered by physicians (Bayne and Levy, 2005) and is strictly illegal, knowing that it renders the individual with a new and unnecessary lifelong physical disability. Thus, alternative approaches targeting the comorbid anxiety and depression symptoms to reduce distress have been the key focus of treatment to date (e.g., Ryan, 2008; Blom et al., 2012). Psychotherapy has been shown to reduce psychological distress, but concurrently increase the individual's desire for amputation, most likely as a result of intense focus and discussion on the topic of their BID with the therapist (Kröger et al., 2014).

Reports of the effectiveness of pharmacological interventions are very limited, and sample sizes are small, often limited to single case reports. One such case report suggested a reduction of distress in one individual with BID from a course of selective serotonin reuptake inhibitors (SSRIs), and limited effects of psychotherapy (Braam et al., 2006). Another report with 25 BID patients found that 12 had been prescribed medications including antidepressants, neuroleptic drugs, and tranquilizers but with no positive effects on symptoms (Kröger et al., 2014).

Another potential treatment that received prior attention was artificial vestibular stimulation, initially proposed by Ramachandran et al. (2007). As disorders of the bodily self have been linked to the vestibular system for over a century (Bonnier, 2009), artificial vestibular stimulation (caloric or galvanic) has been shown to induce temporary remission of the denial of ownership over a limb in SPP (Lopez, 2013) and other bodily self disorders (Grabherr et al., 2015). Given the above-mentioned parallels between the BID and SPP clinical pictures, vestibular stimulation has been tentatively used to restore limb ownership in BID and thus to reduce the desire for amputation. Despite initial excitement and early adoption of the technique clinically, subsequent research studies have demonstrated that it provides no substantial benefit to individuals with BID (Lenggenhager et al., 2014).

Upon review of the available literature, it is evident that aside from amputation, existing treatment options are largely ineffective, and fresh approaches are required to alleviate distress for those with BID. Furthermore, persisting with the current ineffective treatment programs comes at a financial cost to the patients and healthcare providers. Amputation, although effective, carries the largest financial burden at an estimated $24,010 for the procedure itself with inpatient stay, and $878,927 in associated costs over the lifetime of the amputated individual (United States data according to health insurance claims, Lo et al., 2020). With advances in neuroimaging, the field of BID is set to undergo a paradigm shift, availing of new knowledge on brain structural and functional correlates of the disorder that may provide insights toward potential avenues for treatment exploration. In the next sections, we review recent developments for understanding the neurological mechanisms and consider how these may inform the inception of new theory driven approaches to treatment.

STRUCTURAL AND FUNCTIONAL CONNECTIVITY ABNORMALITIES IN BID

It has been well established since the mid 20th century that brain lesions in the right parietal lobe lead to altered perception and spatial awareness of body parts (Brain, 1941; Critchley, 1954). This area of the cortex is divided into the superior and inferior parietal lobules (the SPL and the IPL, respectively), with the latter being further subdivided into the supramarginal and angular gyri. Within the last decade, research specifically relating to structural and functional brain abnormalities in BID has emerged. In a recent review of all available neuroimaging evidence since 2012, Fornaro et al. (2020) reported that areas consistently found to be altered in xenomelia include right superior and inferior parietal lobule (rSPL and rIPL), premotor cortex, and right insula. A general pattern across studies emerged that cortical abnormalities tended to be right lateralized, whereas subcortical were left lateralized. Hänggi et al. (2016) specifically focused upon subcortical correlates of BID and found distinctive differences in the shape of several structures involved in somatotopic representation of the leg. Patients had thinner bilateral dorsomedial putamina, left ventromedial caudate nucleus, and left medial pallidum. This was accompanied by thicker bilateral lateral pallida and left frontolateral thalamus.

The aforementioned structural evidence is corroborated by data concerning functional connectivity between brain regions at rest in patients with BID compared to controls. In a relatively large and homogenous sample of BID patients who all desired amputation of the left leg, Saetta et al. (2020) found reduced functional connectivity between the primary sensorimotor area (S1) of the disowned leg and the rest of the brain, and the rSPL with the rest of the brain. Further, gray matter atrophy was evident in the rSPL of BID patients, and the extent of this atrophy correlated with desire for amputation and degree of engagement in pretending behaviors. These findings led Saetta et al. (2020) to suggest that the distressing feeling of non-acceptance of one's limb in BID might ensue from a discrepancy between preserved projections of somatosensory inputs from the limb to the respective primary cortical areas, and an impaired representation of the body at the highest level of integration, the so-called body image. The authors proposed that only a smooth interplay between sensory and higher level bodily processing may provide the phenomenal experience of a limb belonging to the body and the self. The previously identified neural network for (healthy) body image and ownership has been suggested to span a broad network involving primary sensorimotor, premotor, parietal, insular, and extrastriatal areas (see, e.g., Tsakiris, 2010; Grivaz et al., 2017; Park and Blanke, 2019; Seghezzi et al., 2019; Salvato et al., 2020; for reviews), which were, at least to some extent, also found to be altered in BID (Fornaro et al., 2020).

The presence of underlying neuroanatomical structural abnormalities is evidence that BID has both psychological and neurophysiological components, and that recovery may entail modifying hard wired brain circuitry. However, this does not necessarily imply permanency of the condition as both gray and white matter are highly neuroplastic and structural changes over time can be documented following treatment programs for other neuropsychological disorders including depression (Liu et al., 2015; Bouckaert et al., 2016) and alcohol addiction (Pfefferbaum et al., 2014). By altering functional connectivity using targeted therapeutic interventions to promote desired neural patterns, changes in brain structure often follow over time. For example, using brain–computer interfaces, functional and structural neuroplastic changes can be induced in regions specifically involved in the trained task (Ghaziri et al., 2013; Qian et al., 2018; Marins et al., 2019; Nierhaus et al., 2021; Sampaio-Baptista et al., 2020).

A NEW GENERATION OF RESEARCH INTO BID TREATMENT USING NEUROFEEDBACK/BRAIN–COMPUTER INTERFACE

Brain–computer interfaces and neurofeedback have been used in attempts to tune pathological brain rhythms or patterns of functional connectivity toward more neurotypical patterns (Ros et al., 2014). This is achieved by training individuals to use on-screen (or robotic) feedback of real-time brain activity to self-regulate some aspect of their own neural functioning. While BCI can come in a vast array of different arrangements using different neuroimaging modalities (see Simon et al., 2021 for a review), a commonly used setup involves recording electrical activity from the scalp using electroencephalography (EEG), and presenting feedback on screen in the form of a computer game. With this type of BCI, different aspects of brain activity can be targeted for modification depending on the method used to extract and present feedback. Positive outcomes using this method for symptom reduction have been demonstrated for ADHD (Qian et al., 2018), post-traumatic stress disorder (PTSD, van der Kolk et al., 2016; Banerjee and Argáez, 2017), and generalized anxiety disorder (GAD, Banerjee and Argáez, 2017; Mennella et al., 2017). In the case of BID, given that distinct functional connectivity patterns are evident involving S1, rSPL, and the rest of the brain (Saetta et al., 2020), there may be value in testing whether targeting this pattern using BCI would result in reduction of distress associated with the desire for amputation. For example, training could provide on-screen feedback in a computer game where rewards are achieved contingent on the strength of connectivity between the aforementioned nodes. Over multiple sessions playing the BCI game, strengthening of connectivity could be hypothesized as participants develop or refine mental strategies, and compared to a control condition where pseudofeedback is delivered. Experimental work would be essential to determine effective mental imagery strategies to recommend for participants (or alternatively whether to allow strategy-free implicit learning), and how many sessions of this type of feedback may be required in order to achieve symptomatic relief.

As Saetta et al. (2020) found that gray matter atrophy in BID correlated with the extent of pretending behaviors (such as binding up the leg and simulating amputation), and desire for amputation, it is also necessary to consider whether brain-related changes are a root cause of the disorder or an effect of the resultant coping behaviors. This too has implications for designing interventions based on structural or functional brain connectivity, as the intervention may be off target if focus is upon an epiphenomenal mechanism arising from the pretending behavior. Even if this is the case, however, BCI approaches to train functional connectivity patterns may still hold value. The simulation of the amputated state may in itself alter brain connectivity patterns for body representations, which may in turn enhance desire for amputation. BCI could be a means to disrupt this loop and find an alternative (less dangerous) method for symptomatic relief that does not perpetuate the altered activity in the brain's body representation regions.

An alternative but related approach would be to use BCI to implicitly promote re-ownership of the limb and engender more positive associations with it. In a study using a foot-specific variant of the rubber hand illusion, Lenggenhager et al. (2015) demonstrated that individuals with BID behaved similarly to healthy controls in that they could take ownership for a fake rubber foot. When stroked synchronously with their opposite foot, they reported sensations as if it were part of their own body. This implies that in the unwanted limb, not only are the basic senses functioning normally but also that the integration of visual, tactile, and proprioceptive information and visual capture is broadly intact. Thus, the authors suggested that behavioral training could be useful for those with BID based on the fact that they can feel ownership for an artificial limb and deny it for their own limb. Further, recent data from a small case study with two BID individuals revealed that augmented reality (AR) technology could successfully reduce symptoms by engendering the illusion that the unwanted limb is missing (Turbyne et al., 2021).

Some suggest that the desire to amputate arises from a failure to adequately represent the affected limb in the relevant area of cortex. For example, McGeoch et al. (2015) recorded somatosensory evoked fields using magnetoencephalography (MEG) during tactile stimulation of the feet of BID participants. They observed a significant reduction in activity over rSPL in the patients compared to controls. A BCI approach targeting this aspect of BID may involve neurofeedback of motor evoked potentials (MEPs) in response to transcranial magnetic stimulation (TMS). This TMS-NF approach has been shown to increase (or decrease) corticospinal excitability (responsiveness) of the pathways connecting brain to muscle, depending on whether rewarding feedback was provided for large or small MEPs (Ruddy et al., 2018; Liang et al., 2020). In a BID tailored variant of this, it may be possible to incorporate feedback of MEPs from TMS over motor cortical representations of both limbs into the computer game, but bias the feedback over time to gradually reinforce engagement of the unwanted limb. This could be achieved by providing larger or more frequent rewards for large MEPs from the targeted limb. As self-regulation of MEP amplitude is achieved *via* engagement of motor imagery strategies, over time this may promote re-integration of the limb into the mental schema of body representation/body image. Reducing the discrepancy between actual and desired body representation may subsequently engender more positive affect toward the unwanted limb, albeit implicitly.

CONCLUSION

As BID is a condition with both psychological and neurophysiological attributes, it is yet unclear whether interventions targeting one of these aspects in isolation can serve any benefit. Further, clarification of the relative mechanistic contribution of body ownership vs. disrupted integration of the limb into the body image will be necessary in order to accurately tailor interventions tackling these facets of the disorder. Upon reviewing the available evidence, what is known to date is that pharmacological and psychological therapies are largely ineffective, and that there are no known neurophysiological interventions that are sufficient to alleviate the suffering associated with the desire for amputation. Amputation itself is an extreme solution raising many ethical issues, and one that will not even be considered by most healthcare providers. Pretending behaviors adopted by BID patients as coping strategies raise health concerns and often have dangerous consequences. Thus, new theory driven approaches that leverage recent advances in neuroimaging and technology are greatly needed in order to improve quality of life for BID patients. Those presented here are intended to stimulate debate among those interested in working toward novel solutions, and may ultimately pave the way for a new dialog on approaches to tackle challenging neuropsychological phenomena.

AUTHOR CONTRIBUTIONS

SC wrote the first draft and edited the final draft. KR and SC conceptualized the idea for the manuscript. KR, SC, CS, BL, and GS worked on editing subsequent drafts of the manuscript and providing feedback. GS and BL significantly extended the sections of the manuscript. All authors reviewed the final version and were involved in discussions throughout.

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The Development of a Flexible Bodily Representation: Behavioral Outcomes and Brain Oscillatory Activity During the Rubber Hand Illusion in Preterm and Full-Term School-Age Children

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During childhood, the body undergoes rapid changes suggesting the need to constantly update body representation based on the integration of multisensory signals. Sensory experiences in critical periods of early development may have a significant impact on the neurobiological mechanisms underpinning the development of the sense of one's own body. Specifically, preterm children are at risk for sensory processing difficulties, which may lead to specific vulnerability in binding together sensory information in order to modulate the representation of the bodily self. The present study aims to investigate the malleability of body ownership in preterm (N = 21) and full-term (N = 19) school-age children, as reflected by sensitivity to the Rubber Hand Illusion. The results revealed that multisensory processes underlying the ability to identify a rubber hand as being part of one's own body are already established in childhood, as indicated by a higher subjective feeling of embodiment over the rubber hand during synchronous visual-tactile stimulation. Notably, the effect of visual-tactile synchrony was related to the suppression of the alpha band oscillations over frontal, central, and parietal scalp regions, possibly indicating a greater activation of somatosensory and associative areas underpinning the illusory body ownership. Moreover, an interaction effect between visual-tactile condition and group emerged, suggesting that preterm children showed a greater suppression of alpha oscillatory activity during the illusion. This result together with lower scores of subjective embodiment over the rubber hand reported by preterm children indicate that preterm birth may affect the development of the flexible representation of the body. These findings provide an essential contribution to better understand the processes of identification and differentiation of the bodily self from the external environment, in both full-term and preterm children, paving the way for a multisensory and embodied approach to the investigation of social and cognitive development.

Keywords: body ownership, multisensory integration, rubber hand illusion, development, preterm children, oscillatory activity

INTRODUCTION

The sense of body ownership, which is the feeling that our body belongs to ourselves, represents a central component of the developing sense of bodily self-awareness and the process of differentiation of the self from the others (Tsakiris, 2016). This implicit knowledge about our own body allows us to correctly identify and localize ourselves in the complexity of a multisensory environment, providing a reference for all experiences from the external world, thus it can be considered a prerequisite for the development of perceptual, cognitive, and social abilities. Normally, we take the experience of our body for granted, however the ability to perceive and recognize our body is a result of complex integration processes of signals coming from different sensory modalities (Ehrsson, 2012).

The ability to perceive spatio-temporal synchrony through the body lies at the core of the development of bodily self-awareness from infancy onwards. From a developmental perspective, bodily self-awareness emerges in parallel to the acquisition of somatosensory skills as infants develop an implicit knowledge of themselves by interacting with the surrounding environment (Riva, 2018). Sensorimotor exploration not only provides information about the external world but also includes the feeling of being the subject of a given experience, establishing a foundation for self-awareness. Empirical observations suggest that, from the first days of life, newborns already show an implicit sense of bodily self-awareness based on the integration of different sensory information (Rochat and Hespos, 1997; Rochat and Striano, 2000). This early ability to differentiate sensations originating from within or outside the body represents the most basic self-experience (Rochat, 2003), providing a foundation for the development of self-other interactions. Moreover, from 2-month of age infants start to systematically explore their own body and the perceptual consequences of self-produced actions, developing a sense of the bodily self as differentiated, situated, and agent in the environment (Rochat and Striano, 2000). Developmental studies have indeed demonstrated that infants differentiate sensations originating from within and outside the body, by showing the ability to discriminate visual-proprioceptive (Bahrick and Watson, 1985; Rochat and Morgan, 1995; Morgan and Rochat, 1997), visual-tactile (Zmyj et al., 2011; Filippetti et al., 2013, 2016; Della Longa et al., 2020) and visual-interoceptive contingencies (Maister et al., 2017). This suggests that implicit bodily self-awareness is based on multisensory integration of bodily signals and early detection of synchrony between vision and sensory feedback from the body.

The early ability to detect visual-tactile body-related contingencies paves the way to a protracted process of self-awareness. During the first years of life other abilities gradually emerges, such as mirror self-recognition (children begin to match their own facial and body movements with the image of themselves in a mirror), self-referential language (personal pronouns usage), emotions related to social contexts (embarrassment, guilt, pride; Lewis, 2011), suggesting toddlers begin to perceive themselves acting and interacting in the surrounding physical and social environment. The emergence of the representation of the body as an object in relation to other objects together with the sense of ownership over the body represents a central component of the developing bodily self-awareness, which underpins the acquisition of motor and socio-cognitive abilities. During childhood multisensory processes underlying the sense of body ownership gradually develop supporting children's ability to update the representation of a body that rapidly changes and grows. To the end of investigating the plasticity of body ownership, body illusions have been used in both adult and developmental populations.

The rubber hand illusion (RHI; Botvinick and Cohen, 1998) is a well-established paradigm to investigate the formation and modulation of the sense of body ownership based on the integration of multisensory information. In a typical RHI paradigm, the participant sees a rubber hand that lies in an anatomical plausible position, while the real hand is covered. The rubber hand, as well as the participant's own hand, are stroked synchronously, creating the multisensory conflict of seeing a touch that is felt at a different location. This multisensory conflict is resolved by incorporating the rubber hand in one's own body representation (subjective embodiment), as well as by relocating the perceived position of one's own hand towards the rubber hand (proprioceptive drift). These two correlates of the RHI reflect complementary mechanisms of body perception: the feeling of embodiment reflects the experience of body ownership, while the proprioceptive drift is related to the location of the body in space (Serino et al., 2013). The illusion indicates that body representation is continuously updated from sensory input and it can be modulated to include external objects.

Only a few studies have investigated the development of susceptibility to the RHI across childhood, showing preliminary evidence that children are able to flexibly modulate their body representation according to contingent visual-tactile input (Lee et al., 2021). All these studies consistently reported that children showed a stronger feeling of embodiment over the rubber hand during synchronous visual-tactile stimulation compared to the asynchronous condition, suggesting an early developing visual-tactile process underpinning the sense of body ownership (Cowie et al., 2013, 2016; Nava et al., 2017; Filippetti and Crucinelli, 2019). Importantly, the subjective experience induced during the illusion seems to be stable across different ages. By contrast, the findings regarding the perceived hand position in children are more complex. While some studies reported a greater proprioceptive recalibration towards the rubber hand in younger children, possibly indicating a strong reliance on visual information (Cowie et al., 2016), other findings failed to evidence the same developmental pathway (Nava et al., 2017; Filippetti and Crucinelli, 2019). Despite the fact that different methodological approaches make it difficult to compare results across studies (Lee et al., 2021), preliminary evidence suggests that the RHI has different psychological and physiological effects, which are experimentally dissociable and develop at different rates during childhood (Rohde et al., 2011; Abdulkarim and Ehrsson, 2016; Cowie et al., 2016). Further research is needed to better understand how multisensory integration processes underpinning body representations gradually develop. In particular, the neural mechanisms underpinning the processes of self-other differentiation are poorly understood from a developmental perspective. To our knowledge, no developmental studies have specifically investigated brain activity supporting the experience of body ownership during the RHI.

Considering the brain mechanisms underpinning the RHI, adult studies investigated somatosensory evoked potentials (SEP) showing an enhancement of late SEP components following synchronous tactile stimulation, which may reflect activation of premotor and parietal cortices (Press et al., 2008). These results are further supported by functional neuroimaging studies that evidenced a network of brain areas involved in the experience of body ownership, including the premotor cortex, sensorimotor cortex, intraparietal sulcus, temporoparietal junction, and insula (Ehrsson et al., 2004, 2005; Tsakiris et al., 2007; Tsakiris, 2010; Blanke, 2012). Moreover, studies of neural oscillation have also started to contribute to the understanding of the neural dynamics related to own-body perception. Neural oscillations in different frequency bands reflect separate mechanisms of multisensory processing, including local neural oscillations and functional connectivity between distant cortical areas (Keil and Senkowski, 2018). More specifically, bottom-up processing has been shown to engage local networks in high-frequency bands (>30 Hz), whereas top-down control through long-range integrative processing engages low-frequency bands (<30 Hz; Keil and Senkowski, 2018). In the context of the RHI, an increase of interelectrode phase synchrony in the gamma-band frequency has been evidenced over parietal regions, signaling crossmodal integration of visual and tactile signals during the induction of the illusion (Kanayama et al., 2007, 2009). Analysis of oscillatory activity also revealed that the emergence of the illusory sense of ownership over the rubber hand was related to modulation of oscillatory power in the alpha band during the RHI (Evans and Blanke, 2013; Rao and Kayser, 2017) as well as in the full body illusion (Lenggenhager et al., 2011) and in the somatic RHI (Faivre et al., 2017). These studies evidenced a relative decrease in alpha power over frontoparietal regions during the illusion, which is not associated with visual information or specific control condition, as it emerged from a combination of contrasts (spatial congruency/incongruency and temporal synchrony/asynchrony; Rao and Kayser, 2017), suggesting that modulation of alpha activity can be considered an important neurophysiological marker of body ownership during the induction of the RHI.

Therefore, the first objective of the present study is to explore EEG oscillatory activity related to visual-tactile integration processes that may represent the neurophysiological basis for the development of the sense of bodily ownership during childhood. To achieve this purpose, we use the RHI paradigm focusing on the classical behavioral measures (proprioceptive drift and subjective embodiment) as well as on the neural oscillatory activity, which may support the integration of multisensory signals in order to modulate body representation accordingly to the concurrent sensory input. More specifically, we decided to measure oscillatory activity during continuous visual-tactile stimulation, comparing the synchronous condition, which should induce the illusion, and the asynchronous condition, which prevents the integration of conflicting visual and tactile input. In contrast to event-related paradigms, continuous recording paradigms do not rely primarily on temporally defined events, thus they discard temporal information and focus instead on spectral information and their experimental induced changes (Gross, 2014). We hypothesized that synchronous visual-tactile stimulation would induce an increased activity in multisensory related brain circuits resulting in desynchronization of alpha oscillatory activity and thus a decrease of the power spectrum density.

A second purpose of the present study is to investigate possible differences in the modulation of body representation in full-term and preterm children. To our knowledge, no studies have specifically addressed the development of self-other differentiation and bodily awareness in children with multisensory processing vulnerability, such as children born preterm. Preterm birth is defined as a birth occurring before the 38th week of gestation and it is associated with increased risk for early brain damage due to hypoxia-ischemia and inflammation affecting in particular the cerebral white matter (Aarnoudse-Moens et al., 2009; Volpe, 2009). Moreover, detrimental environmental factors of the neonatal intensive care (NICU) may increase the vulnerability to develop neurodevelopmental difficulties (Anand and Scalzo, 2000; Mento and Bisiacchi, 2012). In NICU the pattern of sensory stimulation is radically altered, exposing preterm newborns to a stressful environment, which they are not developmentally prepared to handle. On one side, preterm newborns are presented with sensory overstimulation due to bright lights, noise, nursery handling, repetitive painful procedures (e.g., heel lancing, venipunctures, nasal suctioning). On the other side, preterm newborns suffer from sensory deprivation in terms of parental affective care (tactile, vestibular, and kinesthetic stimulation; Nair et al., 2003; Machado et al., 2017). This leads preterm infants to an increased risk for sensory processing dysfunctions, including the ability to integrate multisensory information (Mitchell et al., 2014; Machado et al., 2017). Sensory difficulties have been shown to persist in preterm school-age children affecting somatosensory and motor processing (Niutanen et al., 2020) with important implications for neurocognitive and behavioral outcomes (Bröring et al., 2017; Ryckman et al., 2017). However, multisensory integration and body processing in preterm children have not received much attention, with only a few studies suggesting that in infancy preterm children showed poor visual-tactile integration, atypical reactivity to tactile and vestibular stimulation (Bart et al., 2011; Lecuona et al., 2016) and reduced sensorimotor control (Delafield-Butt et al., 2018), which reflect a prerequisite for the emergence of an implicit sense of bodily self-awareness. Moreover, a recent study evidenced that preterm children showed difficulties in the visual perceptual processing of body representation as reflected by visuospatial judgments on body stimuli (Butti et al., 2020). This finding points to possible long-lasting consequences of preterm birth in children's ability to integrate multisensory information to create a representation of their body coherent with sensory input. For this reason, we proposed to include a group of children born preterm in order to examine possible differences in the susceptibility to the RHI between children born preterm and full-term. Considering that preterm birth is frequently associated with increased vulnerability for cerebral white matter damage (Volpe, 2009) together with inadequate early sensory experiences (Grubb and Thompson, 2004), it is plausible that preterm children might present difficulties in the ability to integrate multisensory bodily signals in order to develop a coherent and flexible representation of the bodily self. Thus, we hypothesized that preterm children would show atypical modulation of the sense of body ownership. More specifically, we expected that preterm children would be less sensitive to the RHI compared to children born full-term, showing difficulties in adapting their body representation to the available multisensory information.

MATERIALS AND METHODS

Participants

The study was conducted at the Department of Developmental Psychology and Socialization of the University of Padua. Forty children between the ages of 6 and 11 years old were included in the study (21 children born preterm and 19 children born full-term). Participants in the preterm group were recruited from the association "Pulcino" in Padua, a center for children born preterm that provides support for premature infants and their families from the earliest stages of development since later childhood. Participants in the control group were recruited from the local community. Participants' characteristics are summarized in **Table 1**. Parents gave written consent for their child's participation after being informed about the whole procedure. The local Ethical Committee of Psychological Research (University of Padua) approved the study protocol.

Stimuli and Procedure

In order to ensure comprehension of task instructions and comparable cognitive abilities between the two groups, each participant was asked to complete a cognitive assessment in the first session, and then he/she was presented with the RHI paradigm during high-density EEG (hdEEG) recording in a second session. We opted to carry out the cognitive assessment and the experimental task/hdEEG recording in two separate sessions in order to reduce testing time for children, thereby ensuring optimal performance.

In the first session, each participant was asked to completed the Raven's Colored Progressive Matrices (CPM; Raven, 1958) to evaluate abstract reasoning, the digit span test forward and backward (BVN 5–11; Bisiacchi et al., 2005) to estimate the working memory span, the Attention Network Task (ANT; Rueda et al., 2004), which provides a measure of three main components of attention (alerting, orienting, and executive control), and a computerized version of the Berg Card Sorting Test (BCST; Berg, 1948) for assessing cognitive flexibility. Moreover, parents were asked to fill some questionnaires to investigate the sensory, cognitive, emotional and behavioral functioning of children in everyday activities. Specifically, we included the Strengths and Difficulties Questionnaire (SDQ; Marzocchi et al., 2002), which investigate the presence of behavioral and emotional difficulties as well as prosocial behaviousr; the Emotion Regulation Checklist (ERC; Shields and Cicchetti, 1997; Molina et al., 2014), which investigate negativity and emotion regulation; Temperament in Middle Childhood Questionnaire (TMCQ; Simonds and Rothbart, 2004), which investigate the temperament of the child in the last 6 months; Behavioral Rating Inventory of Executive Function (BRIEF; Gioia et al., 2000), which investigates executive functioning. Finally, a purpose-built sensory questionnaire was used to explore children's sensory skills, focused on somatosensory and body-related processing. This questionnaire was specifically designed for the current research study in order to collect information about different areas of sensory processing involved in daily activities, including discriminative touch, affective touch, interoceptive sensitivity, proprioception, and body awareness.

In the second session, each participant was presented with the RHI paradigm, based on the procedure developed by Botvinick and Cohen (1998). Each child was seated in front of a table directly across from the experimenter. The participant placed his/her left hand on the table and was trained to slide his/her right index finger following a ridge under the table to find the point underneath the left index finger (pointing response task). After training, the participant was asked to repeat twice the pointing response task with eyes closed to estimate his/her baseline ability to localize the position of his/her own hand. Specifically, the baseline estimation error of hand position was calculated as the difference between mean pointing response and the actual hand position. Positive values indicate a shift towards the body midline from the actual hand position, whereas negative values indicate a shift away from the body midline. After that, a panel obstruction was placed on the table to prevent the participant from viewing his/her own hand and a fake rubber hand was placed on the table at a distance of 15 cm on the right from the actual hand position. A black cloth was placed around the child to cover part of both the real and the rubber arm. The trained experimenter stroked the participant's hand and the rubber hand with two identical brushes either synchronously or asynchronously. During the stimulation, the participant was asked to closely watch the rubber hand. Each participant was presented with two RHI blocks. In each block, the experimenter administered the same tactile stimulation twice (two trials), each time for 1 min. The tactile stimulation was manipulated between blocks, varying the synchrony between the touch on the real hand and the visual feedback on the rubber hand (synchronous—same time and same position- vs. asynchronous—different time and different position). The order of the experimental conditions was randomized between participants. As in the baseline, the same pointing response task was administered following each RHI trial. Therefore, the participant pointed four times for

TABLE 1 | Sample characteristics.

	Preterm children	Full-term children
N (%male)	21 (42.86%)	19 (31.58%)
Age (months)	103.9 (17.0); range 78–136	104.1 (15.2); range 81–139
Gestational age (weeks)	30.0 (3.27); range 24–36 Mild preterm (32–36 weeks) *N* = 8 Very preterm (28–31 weeks) *N* = 8 Extremely preterm (<28 weeks) *N* = 5	All >38
Birth weight (gram)	1,443.76 (622.69); range 512–2,500	All >2,500

each experimental condition. To measure the extent to which the proprioceptive perceived position of one's own hand was influenced by incongruent multisensory signals (induction phase of the RHI), proprioceptive drift was calculated by subtracting the mean baseline pointing response from the mean test pointing response for each experimental condition. After each RHI block, the participant was asked two questions, the first one concerned the sense of embodiment felt over the rubber hand "When I was stroking with the brush, did you feel like the rubber hand was your hand?"; the second one was a control question "When I was stroking with the brush, did you feel to have three hands?." A was designed to be easily understood by children: 1 = no, definitely not; 2 = no; 3 = no, not really; 4 = in between; 5 = yes, a little; 6 = yes, a lot; 7 = yes, lots and lots (**Figure 1**). Finally, we were interested in exploring the modulation of neural oscillations underpinning bodily illusion, thus we continuously record participants' hdEEG activity during the experimental session.

EEG Recording and Processing

During the entire RHI task, hdEEG data were continuously recorded. We used a Geodesic high-density EEG System (EGI GES-300) with a pre-cabled 128-channel Hydrocel Geodesic Sensor Net (HCGSN-128) and electrical reference to the vertex. The sampling rate was 500 Hz and the impedance was kept below 60 kΩ for each sensor. Signal pre-processing was performed through EEGLAB 14.1.2b (Delorme and Makeig, 2004). The continuous EEG signal was first segmented according to experimental conditions (synchronous vs. asynchronous visuotactile stimulation), resulting in two different 2-min experimental blocks for each participant. The EEG data from different recording blocks were pre-processed separately. The signal was downsampled at 250 Hz and then bandpass-filtered (1–40 Hz) using a Hamming windowed sinc finite impulse response filter (filter order 1/4 8250). Manual inspection was done for each subject in order to eliminate those segments of signal that presented huge artifacts amenable to body movements. Successively, data cleaning was performed by means of an independent component analysis (ICA; Stone, 2002) using the algorithm implemented in EEGLAB. The resulting independent components were visually inspected and those clearly related to eye blinks, eye movements, and muscle artifacts were discarded. Channels presenting artifactual activity were eliminated and their activity was reconstructed with spherical interpolation (Perrin et al., 1989; Ferree, 2006). Finally, the data were then re-referenced to the average of all electrodes. At this stage, EEG data were imported in Brainstorm (Tadel et al., 2011) to analyze the individual oscillatory activity for each experimental condition. We applied Welshed power spectrum density to decompose the raw EEG data into distinct frequencies from 1 to 40 Hz using the Brainstorm software. As we were mainly interested in changes of oscillatory activity in the alpha band, we considered the averaged power spectrum density between 8 and 12 Hz. We analyzed changes in this frequency band because alpha power has been associated with bodily self-awareness (Lenggenhager et al., 2011; Evans and Blanke, 2013; Rao and Kayser, 2017). No baseline normalization was performed but within-subject statistical comparisons were used (see below), which makes the subtraction of a common baseline unnecessary (Rao and Kayser, 2017).

Statistical Analyses

Behavioral Statistical Analyses

All statistical analyses were performed using R, a software environment for statistical computing and graphics (R Core Team, 2016). To test for group differences in the performance at the cognitive assessment and in the parent-reported questionnaires, we carried out *t*-tests; while to analyze data from the proprioceptive drift and the embodiment experience we used a mixed-effect model approach. The choice of using a mixed-effects model approach was determined by the possibility to take into account fixed effects, which are parameters associated with an entire population as they are directly controlled by the researcher, and random effects, which are associated with individual experimental units randomly drawn from the population (Gelman and Hill, 2007; Baayen et al., 2008). Akaike information criterion (AIC) model comparison has been used to compare a set of models fitted to the same data (Akaike, 1973; McElreath, 2016). The model that produces the lowest AIC value is the most plausible (Hopper et al., 2008). More specifically, to carry out mixed models, we used "lmer" from the "lme4" package (Bates et al., 2015). In order to compute R-squared for the models, we used "r.squaredGLMM" from MuMIn package (Barton, 2020), which takes into account the marginal R-squared (associated with fixed effects) and the conditional one (associated with fixed effects plus random effects). For each model, we reported the marginal R-squared. The p-value was also calculated using the "lmerTest" package (Kuznetsova et al., 2017).

EEG Statistical Analyses

To analyze oscillatory activity we implemented a two-level statistical approach. The first-level data analyses were carried out using a cluster-based procedure implemented in Fieldtrip, while in the second level of data analyses we performed mixed-effect models using R. More in detail, in the first-level analyses we decided to detect condition differences by employing an unbiased approach, testing for statistical effects across all electrode sites while controlling for multiple comparisons. Hence, we applied a whole-scalp cluster-based permutation analysis (Groppe et al., 2011) to identify illusion effects by comparing Synchronous vs. Asynchronous conditions. Specifically, a two-tailed paired *t*-test was performed for each electrode, and the cluster statistic was defined as the sum of the t-values of all spatially adjacent electrodes exceeding a critical value corresponding to an alpha level of 0.05, and a minimal cluster size of two (Maris and Oostenveld, 2007; Kayser et al., 2015). The cluster statistic was compared with the maximum cluster statistic of 1,000 random permutations, based on an overall *p*-value of 0.05. In the second-level analyses, the significant electrodes were grouped in clusters, defining three bilateral brain areas and we conducted mixed-effect model analyses on log-alpha power. The logarithmic transformation of the alpha power was used in order to improve the normality of the

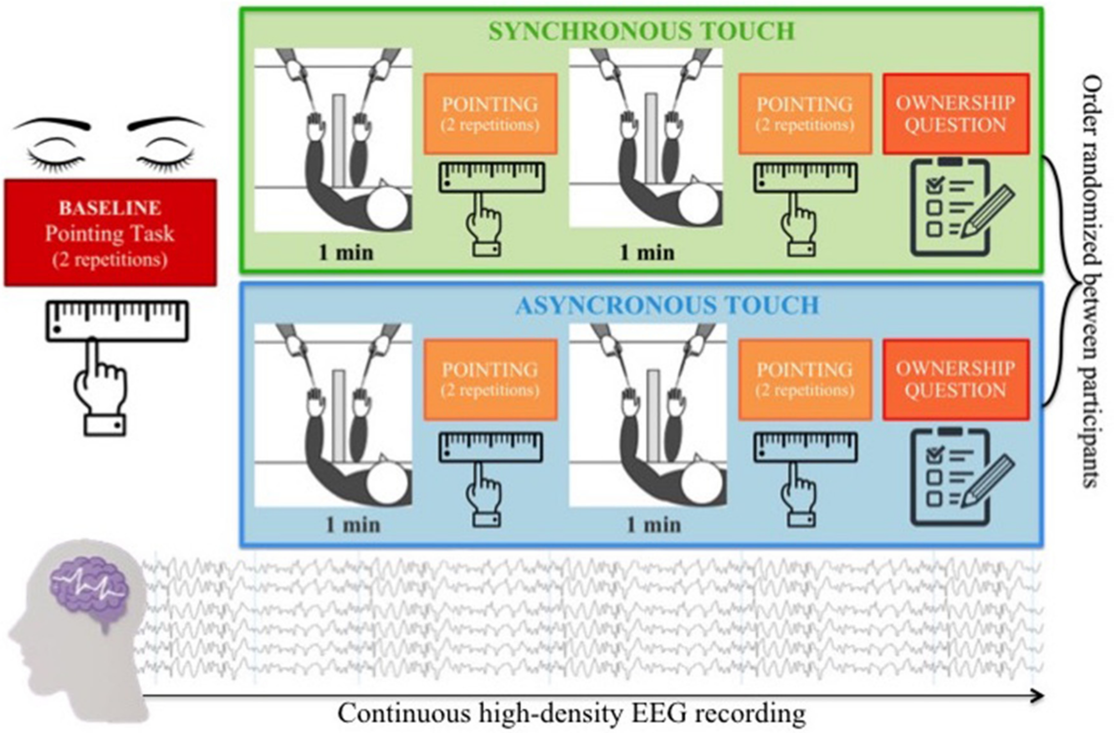


FIGURE 1 | RHI paradigm: each child was presented with two experimental blocks, varying the visual-tactile congruency (synchronous vs. asynchronous). Each block consisted of two 1-min visual-tactile stimulations immediately followed by a pointing task to measure the proprioceptive drift and a final question investigating the subjective feeling of ownership over the rubber hand. High-density EEG data were continuously recorded during the experimental session. RHI, rubber hand illusion.

power distribution (Oberman et al., 2005; Lenggenhager et al., 2011).

RESULTS

Cognitive Assessment

Paired t-tests were used to test for group differences in different cognitive tests that were selected to evaluate general cognitive abilities. No significant group difference was found for performance at the CPM ($t = -0.11$, $p = 0.915$, Cohen's $d = -0.04$), Digit Span forward ($t = 1.31$, $p = 0.201$, Cohen's $d = 0.43$) and backwards ($t = 1.49$, $p = 0.158$, Cohen's $d = 0.48$). Likewise, the two groups showed no difference in attentional skills, as measured by the three components of ANT: Alerting ($t = -0.08$, $p = 0.939$, Cohen's $d = -0.03$), Orienting ($t = -1.20$, $p = 0.241$, Cohen's $d = -0.43$) and Executive control ($t = -0.76$, $p = 0.452$, Cohen's $d = -0.25$). However, in a more complex task that assesses cognitive flexibility as a core executive function (BCST) a significant difference between groups emerged. The percentage of errors in the group of preterm children was significantly higher than in the control group ($t = -4.40$, $p < 0.001$, Cohen's $d = -1.42$). In particular, preterm participants made more perseverative errors than full-term participants ($t = -3.56$, $p = 0.001$, Cohen's $d = -1.15$), while no significant difference emerged between groups in respect of non perseverative errors ($t = -1.47$, $p = 0.152$; Cohen's $d = -0.50$; **Table 2**). It is important to note that non-perseverative errors are common after a rule change as a new association must be discovered using trial and error *via* feedback received after each card is sorted; however, perseverative errors identify impaired cognitive flexibility (Fox et al., 2013). Interestingly, correlations between gestational weeks and the performance at the BCST indicate that children born at lower gestational age showed higher number of errors ($r = -0.47$, $p = 0.035$) and perseverative errors ($r = -0.42$, $p = 0.067$; **Figure 2**).

Parent-Report Questionnaires

Paired t-tests were used to test for group differences in different parent-report questionnaires that were selected to evaluate children's cognitive, emotional and social functioning in everyday activities. No significant group difference was found in any subscale of the Strengths and Difficulties Questionnaire (SDQ; Marzocchi et al., 2002); the Emotion Regulation Checklist (ERC; Shields and Cicchetti, 1997; Molina et al., 2014); and the Temperament in Middle Childhood Questionnaire (TMCQ; Simonds and Rothbart, 2004). Behavioral Rating Inventory of Executive Function (BRIEF; Gioia et al., 2000), which investigate cognitive, behavioral, and emotional executive functioning, showed a significant difference between groups in the total score ($t = -2.07$, $p = 0.046$, Cohen's $d = -0.71$), and in particular in the subscale of cognitive control ($t = -2.75$,

TABLE 2 | Descriptives and tests for group differences for each cognitive test.

	Preterm children	Full-term children	Test for group differences
CPM (Z scores)	0.85 (0.66)	0.87 (0.71)	$t = -0.11$ $p = 0.915$
Digit span forward (Z scores)	−0.28 (0.78)	0.10 (1.01)	$t = 1.31$ $p = 0.201$
Digit span backwards (Z scores)	0.28 (0.70)	0.69 (1.00)	$t = 1.49$ $p = 0.158$
ANT	Alerting: 30.49 (50.62) Orienting: 39.23 (39.23) Conflict: 53.38 (61.96)	Alerting: 29.30 (41.04) Orienting: 15.51 (63.84) Conflict: 38.73 (51.84)	Alerting: $t = -0.08$ $p = 0.939$ Orienting: $t = -1.20$ $p = 0.241$ Conflict: $t = -0.76$ $p = 0.452$
BCST	Errors: 40.72% (10.81) Perseverative Errors: 22.81% (7.94) Non Perseverative Errors: 15.55% (5.68)	Errors: 26.86% (8.35) Perseverative Errors: 14.56% (6.14) Non Perseverative Errors: 12.30% (7.44)	Errors: $t = -4.40$, $p < 0.001$ Perseverative Errors: $t = -3.56$, $p < 0.001$ Non Perseverative Errors: $t = -1.47$, $p = 0.152$

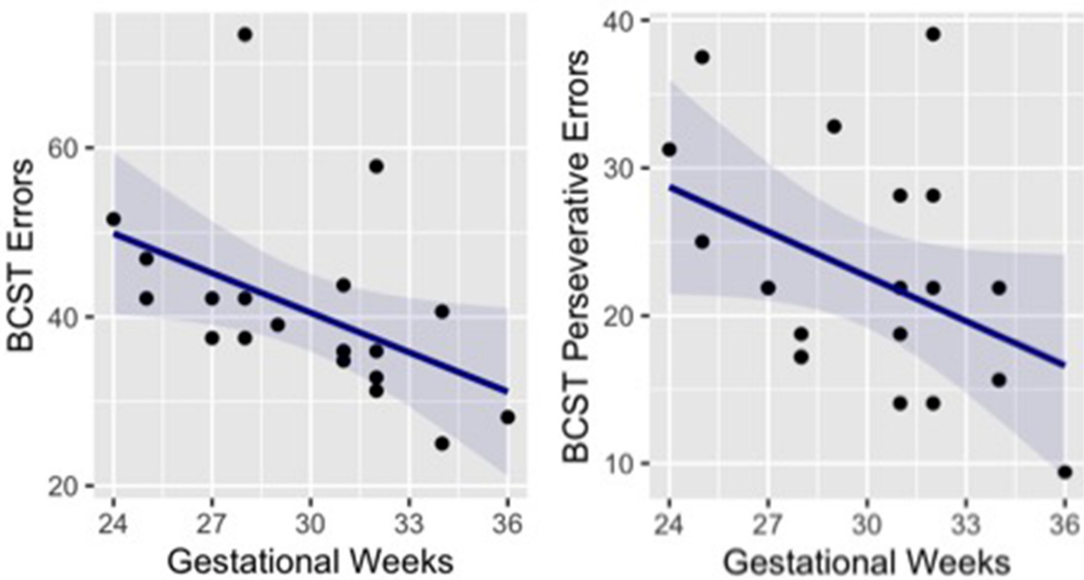


FIGURE 2 | Correlation between preterm children's gestational age and performance at the BCST (number of errors and number of perseverative errors). BCST, Berg Card Sorting Test.

$p = 0.010$ Cohen's $d = -0.93$). In order to deeper explore the risk for difficulties in executive functions in preterm children, we ran correlational analyses between the subscales of the BRIEF and neonatal information of the preterm group (gestational weeks and birth weight). The results revealed that parent-reported difficulties in executive functions are related to both lower gestational age ($r = -0.43$, $p = 0.072$) and birth weight ($r = -0.54$, $p = 0.021$) and more specifically cognitive aspects of executive function are related to lower gestational age ($r = -0.48$ $p = 0.044$) and lower birth weight ($r = -0.60$ $p = 0.009$), see **Figure 3**.

Finally, the sensory questionnaire revealed a significant difference between groups in the total score ($t = -2.14$, $p = 0.041$, Cohen's $d = -0.71$) and in particular in the subscale Discriminative Touch ($t = -2.94$, $p = 0.007$, Cohen's $d = -0.98$). Moreover, a trend for significant correlation between somatosensory difficulties (total score and subscale discriminative touch) and neonatal information (gestational weeks and birth weight) emerged in preterm children, showing that parent-reported sensory difficulties appear to be negatively related to both gestational age (Total score $r = -0.40$, $p = 0.240$; Discriminative Touch $r = -0.41$, $p = 0.093$) and birth weight (Total score $r = -0.29$, $p = 0.110$; Discriminative Touch $r = -0.46$, $p = 0.052$), see **Figure 4**.

Behavioral Results: Proprioceptive Drift

At first we ran some preliminary analyses on the baseline estimation error of hand position to the end of controlling whether the two groups were comparable in their proprioceptive ability to localize their own hand without any visuotactile

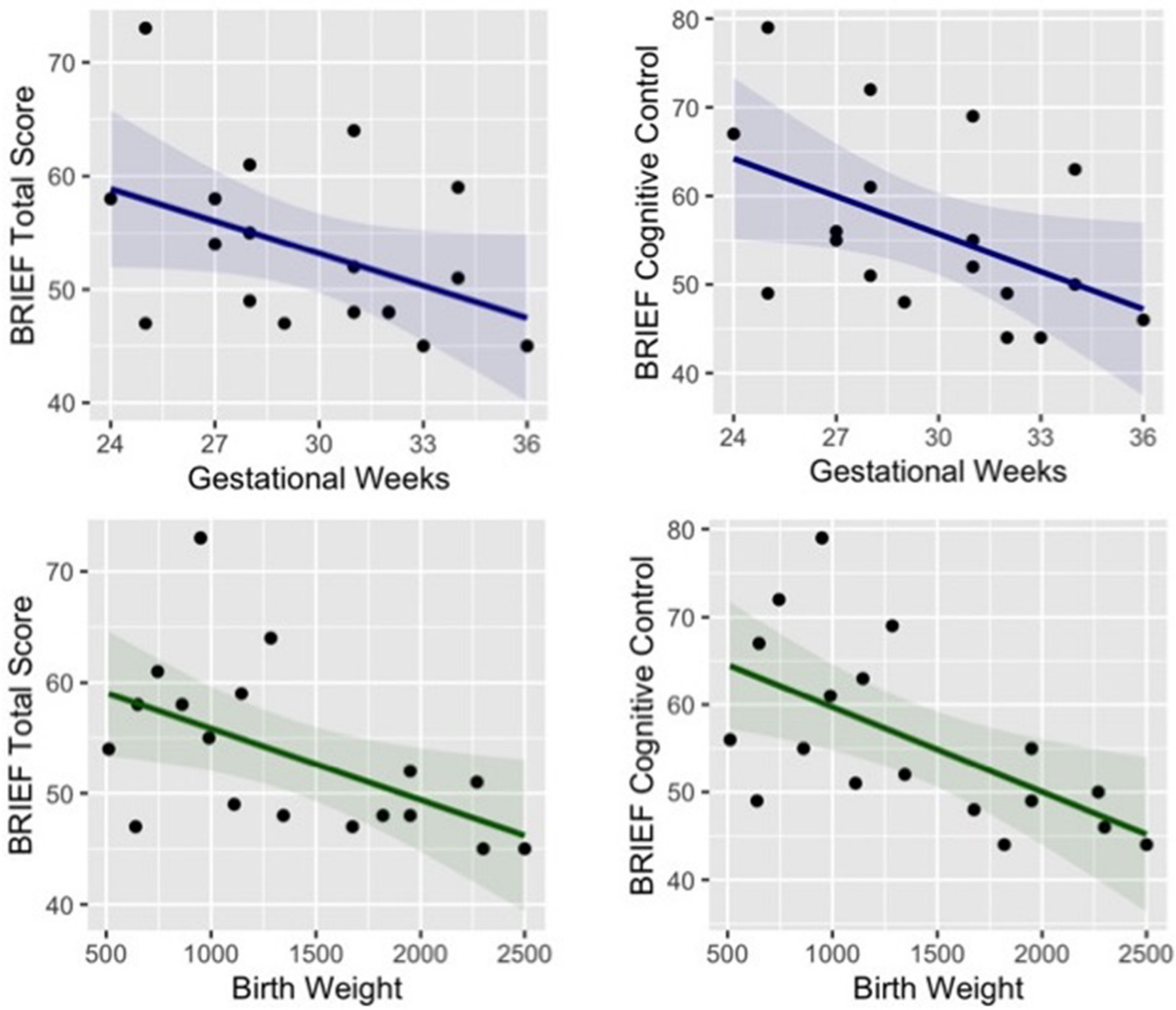


FIGURE 3 | Correlation between preterm children's gestational age (blue) and birth weight (green) and their parent-reported difficulties in executive functions (total score and subscale of cognitive control).

stimulation. In particular, estimation error was calculated as the difference between the mean pointing response before visual-tactile stimulation (baseline) and the actual hand position, in both groups of full-term and preterm children. The results revealed that all children were accurate in the localization of their own hand as suggested by simple *t*-tests comparing the baseline pointing with the real position of the hand (zero). Moreover, no significant difference emerged between groups (**Table 3**).

Then, we analyzed the proprioceptive drift, which was calculated as the difference between the perceived position of the hand after the visuotactile stimulation and the baseline location of the participants' hand. We used a mixed-effect model approach testing five nested mixed-effects models. In each model, proprioceptive drift was the dependent variable. The null model (Model 0) included only the random effect of Participants; the first (Model 1) included the experimental Condition (two levels; synchronous visuotactile stimulation vs. asynchronous visuotactile stimulation) as fixed factor and Participants as a random factor. Moreover, we were interested in investigating possible differences between preterm and full-term children; therefore, we tested two additional models including the Group (two levels; preterm vs. full-term children) as a fixed factor (Model 2) and the interaction effect (Model 3). Finally, we wanted to control whether developmental changes may influence the effects of the RHI, therefore we tested an additional model including age in months as a fixed factor (Model 4; **Table 4**).

The likelihood ratio test showed that Model 3 was the best at predicting the collected data and included the effect of visual-tactile Condition, the effect of Group, and the interaction effect Condition × Group. We selected this model, even though it did not reach statistical significance (p = 0.149) because it was associated with a smaller AIC indicating a better fit of the collected data and it increased the percentage of explained variance (6%). The main effect of Condition emerged as significant (B = 1.62, SE = 0.61, t = 2.63, p = 0.012). Moreover, the model showed a trend for the main effect of Group (B = 2.22,

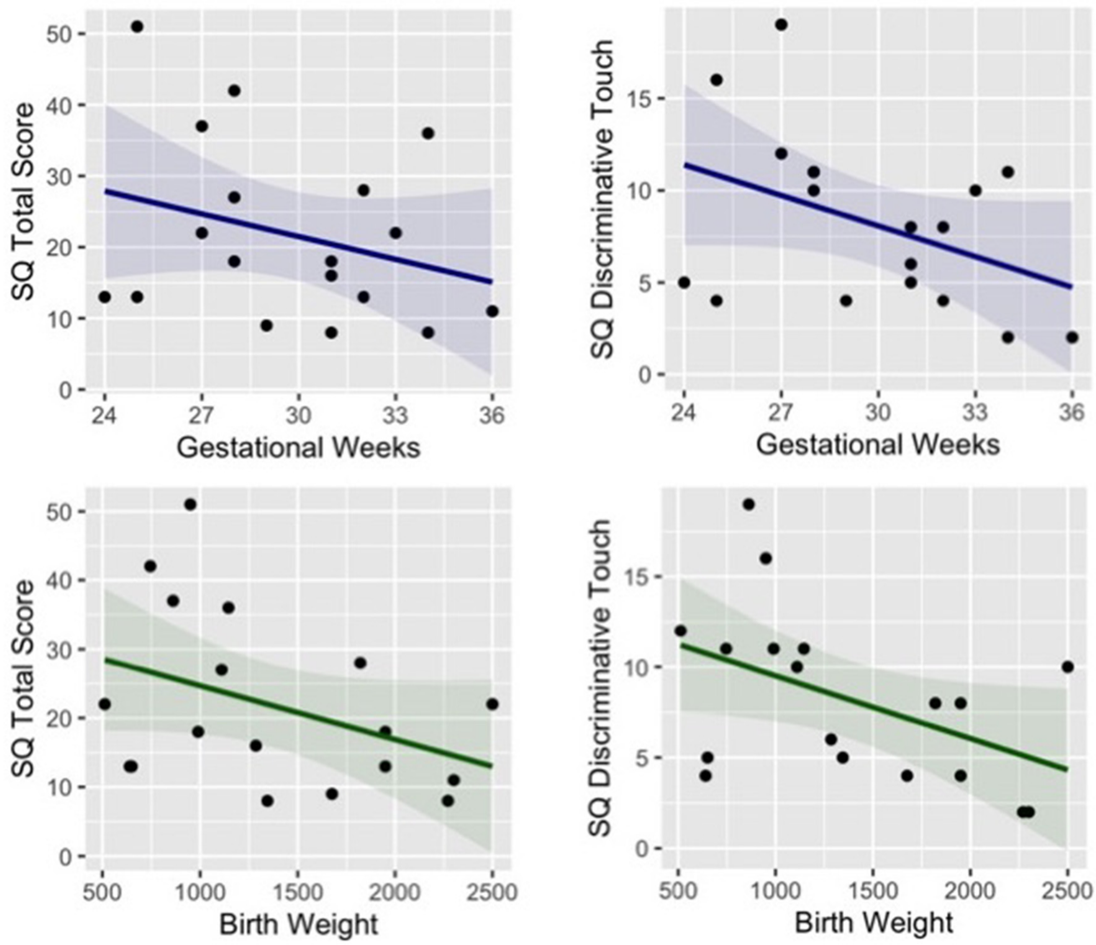


FIGURE 4 | Correlation between preterm children's gestational age (blue) and birth weight (green) and their parent-reported sensory difficulties (total score and subscale of discriminative touch).

TABLE 3 | Simple *t*-test comparing baseline pointing score with the real position of the hand (baseline estimation error in cm) and independent *t*-test testing the difference between groups.

	Preterm children	**Full-term children**
Baseline estimation error (cm)	−0.37 (3.45)	−0.93 (2.88)
Simple *t*-test (null level)	$t = -0.49$, $p = 0.629$	$t = -1.42$, $p = 0.174$
Independent *t*-test	$t = -0.56$, $p = 0.576$, Cohen's $d = -0.18$	

TABLE 4 | Comparison between models predicting proprioceptive drift.

Tested models	**Variables**	**AIC**	**Delta AIC**	**Marginal R^2**	χ^2	***p***
Model 0	Random effect of participants	419.01				
Model 1	+ Condition	415.94	3.19	0.016	5.06	0.024
Model 2	+ Group	415.86	2.11	0.058	2.09	0.149
Model 3	+ Condition × Group	415.78	1.52	0.064	2.08	0.149
Model 4	+ Age	417.70	−6.73	0.064	0.08	0.784

Note that smaller values of AIC indicate better fitting models.

SE = 1.21, $t = 1.84$, $p = 0.073$) and an interaction effect Condition × Group ($B = -1.21$, $SE = 0.85$, $t = -1.42$, $p = 0.163$), although statistical significance was not reached. These results indicate that when the touch applied on the participant's actual hand was asynchronous compared to the touch applied on the rubber hand, children showed a larger proprioceptive drift away from the real hand. This effect shows a different modulation in the two groups of participants (**Figure 5**).

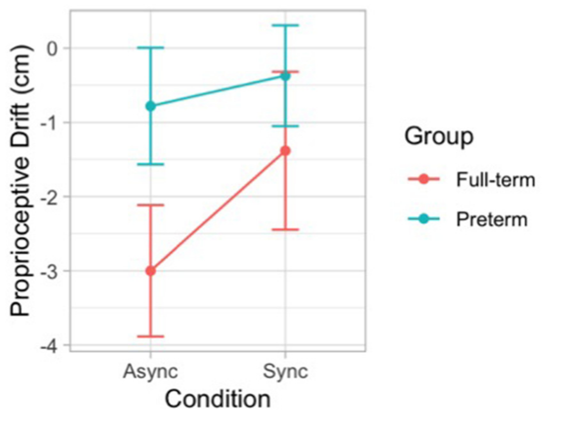


FIGURE 5 | Error bar graph of the mean proprioceptive drift following synchronous and asynchronous visuotactile stimulation in full-term (red) and preterm (blue) children. The graph shows the interaction effect between visual-tactile condition and group.

Behavioral Results: Embodiment

Then, we analyzed the subjective experience of feeling a sense of embodiment over the rubber hand after the manipulation of multisensory signals. A set of five nested mixed-effect models was tested including the same factors used to analyze proprioceptive drift (**Table 5**).

The likelihood ratio test showed that Model 2 was the best at predicting the collected data and included factors Condition and Group. The model explained 26% of the variance (p = 0.010). The main effects of Condition (B = 1.68, SE = 0.26, t = 6.40 p < 0.001) and Group (B = −1.34, SE = 0.51, t = −2.62, p = 0.013) emerged. These results indicate that children felt a stronger sense of ownership over the rubber hand when the touch was delivered synchronously on the participant's real hand and the rubber hand. This finding is in line with qualitative observations of children's behavior during the induction of the illusion, as many of them exhibited surprise and made spontaneous verbal comments about feeling the rubber hand as part of their own body. Moreover, preterm children reported lower scores in response to the ownership question in both conditions of the RHI. Notably, the same pattern of scores was shown for the control question with the important difference that in all experimental conditions the mean values were above 4, which corresponded to the middle value of the scale indicating uncertainty whether or not the illusory effect was applied (**Figure 6**).

EEG Results

In the first-level oscillatory analyses, we applied an exploratory analysis by testing the difference between experimental conditions (asynchronous vs. synchronous) considering the full sample of children (full-term and preterm). This first-level analysis was performed to individuate the electrodes showing any condition-related significant modulation. We used a cluster-permutation procedure to control for multiple comparisons (detailed parameters: 1,000 iterations, two-sided t-test at p < 0.05 on the clustered data, requiring a cluster size of at least 2 significant neighbors). The condition contrast applied to the power of oscillatory activity revealed a significant cluster of 22 electrodes over the right frontal, central and parietal areas, where alpha power (8–12 Hz) was lower in the synchronous condition compared to the asynchronous condition (**Figure 7A**). A second-level, confirmatory analysis was then performed, with the specific aim of assessing the presence of group-level significant differences. For this purpose, we selected three bilateral clusters of electrodes, covering frontal, central, and posterior parietal brain areas (**Figure 7B**). These clusters were identified according to both the exploratory analysis and previous literature (Evans and Blanke, 2013; Rao and Kayser, 2017).

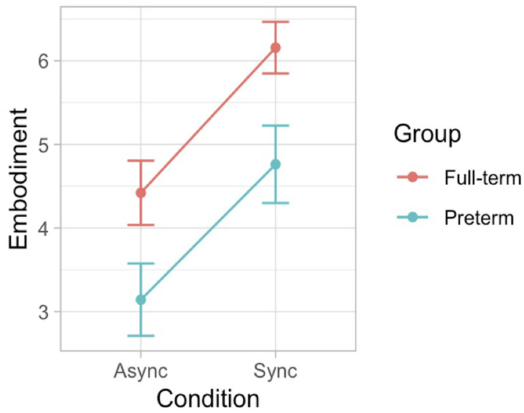
We then computed and averaged the mean power spectrum density of all the electrodes within each cluster, separately for the full-term and preterm groups of children. In this way, we obtained a single, averaged power density value per cluster and participant and entered these values into a mixed model approach. A set of seven nested mixed-effect models was tested considering the mean alpha power as our dependent variable. The null model (Model 0) included only the random effect of Participants; the first (Model 1) included Condition (two levels; synchronous visuotactile stimulation vs. asynchronous visuotactile stimulation) as fixed factor and Participants as random factor. Moreover, we were interested in investigating possible differences between preterm and full-term children; therefore, we tested two additional models including the Group (two levels; preterm vs. full-term children) as a fixed factor (Model 2) and the interaction effect (Model 3). Finally, we tested three additional models including Scalp area (3 levels; frontal vs. central vs. parietal, Model 4), Laterality (2 levels; right vs. left, Model 5), and their interaction (Model 6) as fixed factors (Model 5; **Table 6**).

The likelihood ratio test showed that Model 5 was the best model at predicting the collected data and included the factors Condition, Group, Condition × Group, Scalp area, and Laterality. The model explained 5% of the variance

TABLE 5 | Comparison between models predicting the subjective experience of embodiment over the rubber hand.

Tested models	Variables	AIC	Delta AIC	Marginal R^2	χ^2	p
Model 0	Random effect of participants	343.95				
Model 1	+ Condition	317.22	25.88	0.162	28.73	<0.001
Model 2	+ Group	312.60	4.94	0.261	6.62	0.010
Model 3	+ Condition × Group	314.55	−1.39	0.260	0.05	0.820
Model 4	+ Age	316.39	−8.25	0.258	0.15	0.696

Note that smaller values of AIC indicate better fitting models.



		Preterm Children	Full-term Children
Sync	Embodiment	4.76 (2.12)	6.16 (1.34)
	Control Question	3.19 (2.06)	4.00 (1.86)
Async	Embodiment	3.14 (1.98)	4.42 (1.68)
	Control Question	2.19 (1.29)	3.58 (1.84)

FIGURE 6 | Error bar graph of the mean embodiment score following synchronous and asynchronous visuotactile stimulation in full-term (red) and preterm (blue) children. The graph shows the main effects of condition and group.

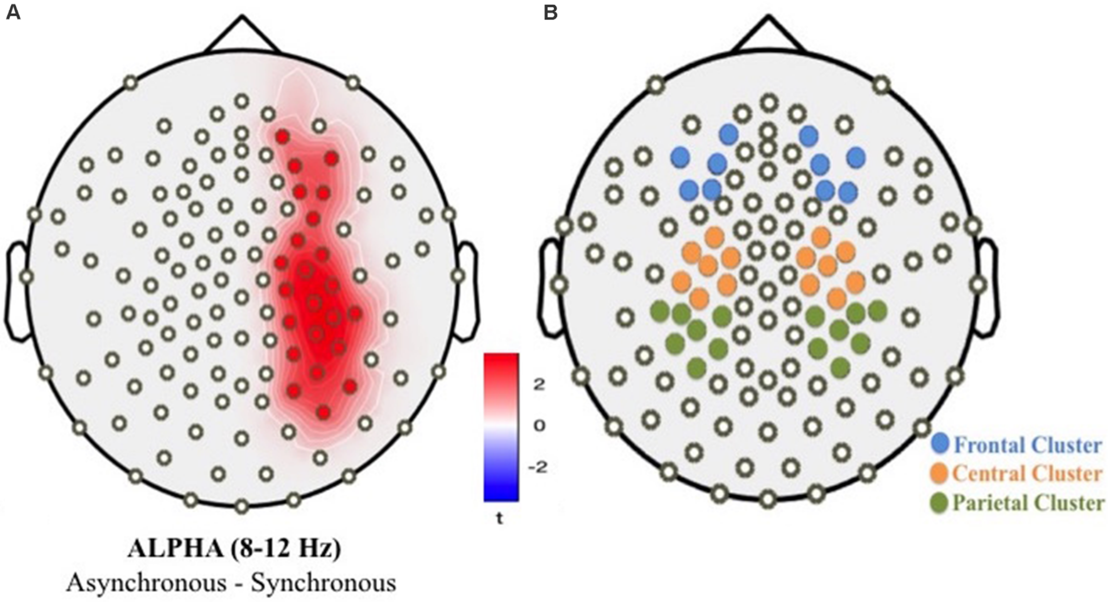


FIGURE 7 | Cluster of significant electrodes resulting from the first-level permutation analyses contrasting asynchronous vs. synchronous conditions **(A)**; bilateral areas of interest considered in second-level analyses **(B)**.

TABLE 6 | Comparison between models predicting oscillatory activity in the alpha frequency band.

Tested models	Variables	AIC	Delta AIC	Marginal R^2	χ^2	p
Model 0	Random effect of participants	−103.48				
Model 1	+ Condition	−138.77	28.91	0.022	37.29	<0.001
Model 2	+ Group	−137.49	−4.23	0.035	0.73	0.394
Model 3	+ Condition × Group	−139.76	−2.74	0.037	4.27	0.039
Model 4	+ Scalp Area	−148.52	−3.60	0.044	12.76	0.002
Model 5	+ Laterality	−166.77	11.61	0.055	20.25	<0.001
Model 6	+ Scalp Area × Laterality	−163.34	−13.04	0.055	0.58	0.750

Note that smaller values of AIC indicate better fitting models.

($p < 0.001$). The main effect of Condition ($B = -0.07$, $SE = 0.02$, $t = 2.91$ $p = 0.004$) and Laterality ($B = 0.07$, $SE = 0.02$, $t = 4.53$, $p < 0.001$) emerged. These results indicate that children displayed higher alpha desynchronization, as reflected by a decreased power, on the contralateral scalp side of stimulation and that they show a greater alpha

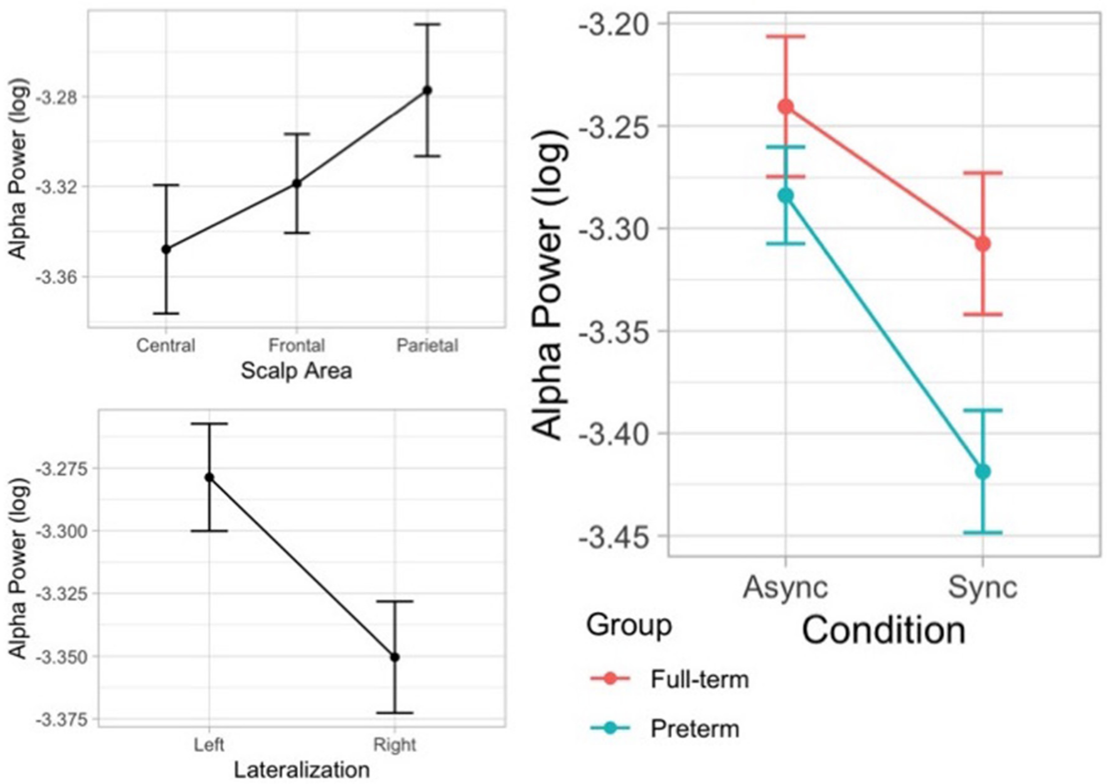


FIGURE 8 | Error bar graphs of the mean alpha power showing the main effects of scalp area, lateralization, and the interaction effect between visual-tactile condition (asynchronous vs. synchronous) and group (full-term vs. preterm).

suppression when the touch was delivered synchronously on the participant's real hand and on the rubber hand compared to the asynchronous condition. Moreover, alpha power density varied across regions on the scalp showing a higher alpha power over parietal area ($B = 0.07$, $SE = 0.02$, $t = 3.64$ $p < 0.001$). Finally, an interaction effect between visual-tactile condition and group emerged ($B = -0.07$, $SE = 0.03$, $t = -2.14$ $p = 0.033$), suggesting that preterm children showed a greater suppression of alpha oscillatory activity during the illusion (**Figure 8**).

Correlation Between Behavioral Measures and Alpha Power

Finally, we ran correlational analyses searching for a possible relationship between changes in EEG activity and changes of self-location at the individual level. Specifically, we calculated the difference (delta score) between the synchronous and asynchronous conditions in both proprioceptive drift and alpha power and we computed the correlation for these measures separately for each scalp area. The results revealed a positive correlation between the changes in proprioceptive drift and alpha power ($r = 0.43$ $p = 0.006$) over the right frontal cluster (**Figure 9**). The positive correlation indicates that participants with larger changes in the perceived position of their hand between the synchronous and asynchronous visual-tactile stimulation, showed larger modulation of alpha oscillatory activity in electrodes over the right frontal area.

DISCUSSION

During childhood, the body undergoes numerous changes, pointing to the need of constantly monitoring and integrating bodily signals in order to update the representation of one's own body, which mediates all interactions with the external physical and social world and represents a foundation for the development of individual psychological identity as separate from the others. Specifically, bodily self-awareness relies on the sense of body ownership, which refers to the feeling that our body belongs to ourselves, and the localization of our body in the environment, based on the experience that our body occupies a given location in space (Serino et al., 2013). The RHI paradigm allows investigating the flexibility of the sense of body ownership, as a result of multisensory processes that integrate the tactile input felt on the actual hand with the visual feedback seen on the rubber hand. The main correlates of the RHI are the experience of feeling a rubber hand as part of one's own body (subjective embodiment) and the misallocation of the own hand towards the rubber hand (proprioceptive drift). A primary aim of this study was to explore sensitivity to the RHI in childhood, focusing on the classical behavioral measures as well as on the oscillatory activity during synchronous

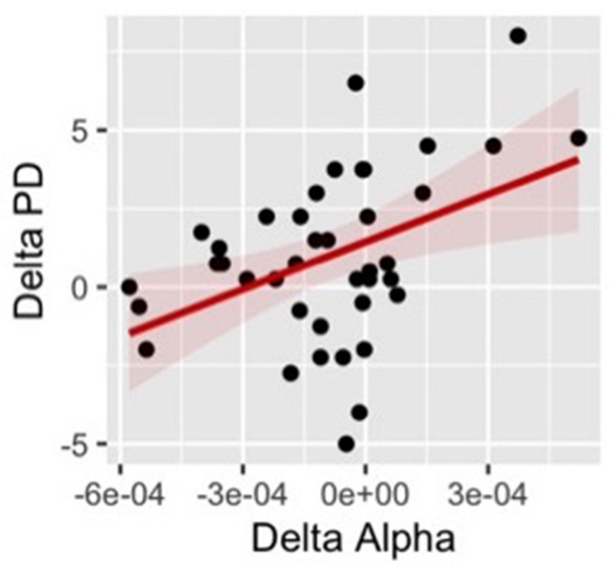


FIGURE 9 | Positive correlation between changes in proprioceptive drift and alpha power.

and asynchronous visual-tactile stimulation. Moreover, we were interested in investigating whether the deprivation of parent-infant bodily contact in the neonatal period, such as in the case of preterm birth, bears long-term negative consequences for the development of bodily self-awareness. Thus, a second purpose of the present study was to explore whether preterm children present less susceptibility to the RHI compared to full-term children, which may indicate atypical integration of multisensory bodily signals.

In order to achieve our objectives, we presented full-term and preterm school-age children with the RHI. The two groups of participants have been shown not to differ for abstract reasoning, as evaluated in performance at the Raven's Colored Progressive Matrices (CPM; Raven, 1958), short-term (forward digit span) and working memory (backward digit span; BVN 5–11; Bisiacchi et al., 2005) and attention skills, as measured by the Attention Network Task (ANT; Rueda et al., 2004). This general cognitive assessment was designed in order to ensure comparable cognitive levels between the two groups. Similarly, parent-report questionnaires indicated no difference in behavioral and emotional difficulties (SDQ; Marzocchi et al., 2002), emotion regulation (ERC; Shields and Cicchetti, 1997; Molina et al., 2014), and temperament (TMCQ; Simonds and Rothbart, 2004) between the two groups of children. However, in line with previous studies (Mulder et al., 2009), preterm children were found to have some difficulties in executive functioning as indicated by a lower performance at the Berg Card Sorting Test (BCST; Berg, 1948). In particular, preterm children showed a higher number of perseverative errors, whereas no difference emerged in the non-preservative errors, indicating that preterm children may present a specific impairment in inhibiting a prevalent response when they are challenged with a complex task. In line with this finding, parents of preterm children reported more difficulties in cognitive control during everyday activities compared to parents of full-term children, as measured by the Behavioral Rating Inventory of Executive Function (BRIEF; Gioia et al., 2000). Executive functions, which refer to the self-regulation processes involved in emotion, cognition, and goal-directed behavior (Diamond, 2013) are frequently compromised in preterm children, especially in those with more extreme prematurity (Taylor and Clark, 2016). Indeed, in the present study, correlational analyses revealed that children born at lower gestational age showed more difficulties in executive function, as measured by children's performance at the BCST and parents' reported scores in the subscale of cognitive control of the BRIEF. Furthermore, the sensory questionnaire revealed a significant difference between groups in the total score and in the subscale of Discriminative Touch. Notably, a trend for a significant correlation between somatosensory difficulties and neonatal information (gestational weeks and birth weight) emerged in preterm children, showing that parent-reported sensory difficulties are prevalent in children born at lower gestational age and birth weight. These results are in line with previous findings which suggest that sensory difficulties related to preterm birth persist during childhood with important implications for neurocognitive and behavioral outcomes (Bröring et al., 2017; Ryckman et al., 2017).

The behavioral measures obtained from the RHI task are in line with previous studies (Cowie et al., 2013, 2016; Nava et al., 2017; Filippetti and Crucinelli, 2019), revealing that school-age children are able to modulate their body representation based on the integration of visual-tactile information, as reflected by the higher subjective feeling of embodiment over the rubber hand in the synchronous compared to the asynchronous experimental condition. The illusion was often very vivid for the children who made spontaneous verbal comments and exhibited reactions of excitement or surprise. The visual-tactile synchrony, meaning the spatial and temporal consistency between the visual and the tactile information is a major factor underpinning the RHI that has been consistently reported in both adult and children studies (e.g., Botvinick and Cohen, 1998; Ehrsson et al., 2004; Bekrater-Bodmann et al., 2014; Cowie et al., 2016). The principles of spatio-temporal congruence constrain the selection of the multisensory signals that are to be combined. In the synchronous condition, participants integrate the tactile sensation felt on their actual hand with the visual information on the rubber hand and adjust their body representation in order to maintain a unitary representation of the self, resulting in an illusory sense of ownership over the rubber hand. By contrast, when the touch is administered on different fingers (spatial discrepancy) or asynchronously between the real hand and the rubber hand (temporal discrepancy), the illusion is abolished (Botvinick and Cohen, 1998; Kammers et al., 2009). More specifically, a strong sensation of the RHI occurs when the temporal discrepancy is 300 ms or less, while it decreases as the delay lengthens (Bekrater-Bodmann et al., 2014; Shimada et al., 2014). Similarly, the distance between the real hand and the rubber hand has proven to modulate the strength of the illusion (Erro et al., 2020), with a significant decrease of illusory effect after a distance of 30 cm (Lloyd, 2007). Notably, developmental studies investigating multisensory processes suggest that the spatial distance and the temporal window within which multisensory stimuli are likely to be integrated into a unitary experience narrows over childhood (Greenfield et al., 2017), suggesting that children might partially perceive the RHI even during asynchronous conditions. Future investigation should investigate this possibility by systematically manipulating the length of temporal delay and spatial distance between visual and tactile stimulations in an RHI paradigm.

We also found a shift of the children's proprioceptive perceived position of the real hand relatively closer to the rubber hand when the visual-tactile stimulation was synchronous compared to the asynchronous condition. It is important to notice that overall, values obtained from the pointing task indicate that children tended to localize their own hand away from the rubber hand, although this effect was reduced for the synchronous condition. One may find this result inconsistent with previous findings in developmental populations, which on the contrary reported a bias towards the body midline even without any stroking (Cowie et al., 2013, 2016; Nava et al., 2017; Filippetti and Crucinelli, 2019). This unexpected negative bias is not easy to interpret, however, given the fact that it appears to spread to all experimental conditions and in both groups of participants, it is still relevant to investigate whether children modulate the perceived hand position based on the integration of visual-tactile stimulation. Indeed, our results revealed a main effect of synchrony on proprioceptive drift resampling the classical effect that participants tend to localize their own hand closer to the rubber hand during the synchronous compared to the asynchronous stroking (Botvinick and Cohen, 1998). However, it has to be taken into account that developmental results regarding the proprioceptive drift in children are complex and they do not agree on the relationship with age. Indeed, all RHI studies consistently reported a stable and early developing subjective experience of ownership over the rubber hand in children from 4 to 13 years (Cowie et al., 2013, 2016; Nava et al., 2017; Filippetti and Crucinelli, 2019), but they showed different results concerning the recalibration of hand position. While in some studies young children showed a greater proprioceptive shift towards the rubber hand compared to older children and adults, suggesting a strong reliance on visual information (Cowie et al., 2016), other findings pointed to a different developmental pathway in the ability to localize one's own hand (Nava et al., 2017), yet another study failed to find any effect of recalibration of hand position towards the rubber hand (Filippetti and Crucinelli, 2019). Therefore, developmental research up to now seems to provide evidence in support of adults studies that found a dissociation between subjective (embodiment questionnaire) and behavioral (proprioceptive drift) measures of the RHI (Rohde et al., 2011; Abdulkarim and Ehrsson, 2016), raising the question about how multisensory processes underpinning different components within body ownership develop across childhood (Cowie et al., 2016; Filippetti and Crucinelli, 2019). More specifically, the subjective feeling of an embodiment is consistently sensitive to visual-tactile synchrony and it has been shown not to depend on changes in the hand position sense (Abdulkarim and Ehrsson, 2016). This effect emerges early in life as children of all ages appear to experience a sense of ownership over the rubber hand in much the same way as adults (Cowie et al., 2016). By contrast, proprioceptive drift relies on visuo-proprioceptive integration and it seems to be inhibited by asynchronous stroking (Rohde et al., 2011). The developmental trajectory of the effect of the RHI on proprioceptive hand position across childhood is still unknown, as different studies reported inconsistent results, possibly due to the variation in experimental paradigms. Indeed, significant differences in methodological approaches and conceptualization make it difficult to integrate findings across different studies, suggesting the need for a more coherent body of literature for developmental RHI studies (Lee et al., 2021).

In particular, a substantial lack of understanding concerns the neural signatures of the multisensory mechanisms underlying the development of body ownership. To our knowledge, no studies have yet examined neural responses during the RHI in the developmental population. Thus, an essential aim of this study was to fill this research gap investigating children's oscillatory activity in order to provide some insight into the multisensory processes underpinning the RHI. EEG oscillatory activity results suggest that in the synchronous condition all children showed a suppression of alpha frequency bands over the right frontal, central, and parietal scalp regions in respect to the asynchronous condition, pointing to an increased involvement of the brain network supporting multisensory body-related processing. More specifically, alpha band oscillations over central regions have been linked to sensorimotor processing (Pineda, 2005). Central alpha suppression, indicated by a decrease of spectrum power, is caused by neuronal desynchronization and reflects increased cortical activation in sensorimotor and premotor cortices (Oakes et al., 2004). Central alpha suppression has been linked to somatosensory stimulation and observation of touch of another person (Pfurtscheller, 1981; Cheyne et al., 2003) as well as action execution, observation, and imagery (Gastaut, 1952; Pfurtscheller and Neuper, 1997). Stronger activations in the synchronous visuotactile condition could be related to mechanisms of multisensory body processing, suggesting a greater engagement of cortical areas associated with visuotactile body-related integration. In support of this interpretation, functional neuroimaging studies supported the activation of a diffuse network of brain areas during the illusory self-attribution of a rubber hand (Ehrsson et al., 2004, 2005; Tsakiris et al., 2007; Tsakiris, 2010; Blanke, 2012). Different brain regions including premotor cortex (Ehrsson et al., 2004), sensorimotor cortex, intraparietal sulcus (Kammers et al., 2009), temporoparietal junction (Tsakiris et al., 2008), and insula (Tsakiris et al., 2007; Baier and Karnath, 2008) work in concert integrating vestibular, visual, and somatosensory signals providing a foundation for self-identification and self-location processes (Blanke, 2012; Limanowski and Blankenburg, 2015).

Another important finding of the present study is that a positive correlation emerged between modulation of alpha band power in the right frontal site and the shift of proprioceptive position of the hand after the illusory visuotactile stimulation. In line with previous results from adult research (Lenggenhager et al., 2011), this positive correlation links frontal oscillatory activity with self-location processes suggesting that participants with a stronger illusory misallocation of their own hand showed decreased frontal activation, as reflected by an increased alpha power. Indeed, activity in the medial prefrontal cortex has been associated with various aspects of the self, including linguistic self-reference (Esslen et al., 2008), memory for self-relevant personality characteristics (Macrae et al., 2004), and self-other discrimination (Heatherton et al., 2006). Notably, neurological patients with impaired frontal processing presented specific alterations of self-location and self-identification (Heydrich et al., 2010; Lopez et al., 2010). Therefore, it is reasonable that frontal activation may reflect the robustness of self-representation and consequently different susceptibility to body illusions. Accordingly, our results evidenced that, contrasting the synchronous vs. the asynchronous visual-tactile conditions, increased oscillatory power in a distributed network where frontal areas have a central role is associated with a stronger illusory bias in self-location. This result provides important insight into possible individual differences that may mediate the effect of the illusion. Notably, interoceptive predictive models provided enlightening evidence in this direction, suggesting that individuals who strongly rely on internal bodily signals presented a less malleable sense of body ownership. Specifically, individual differences in interoceptive sensitivity, measured as the ability to accurately detect the own heartbeat, has been shown to predict proprioceptive drift during the RHI (Tsakiris et al., 2011). A possible interpretation is based on the fact that during the RHI there is a conflict between the proprioceptive input about the hand position and the visual information about the location of the rubber hand and the tactile stimulation, thus the brain has to resolve uncertainty by weighting multisensory inputs in order to select some sources of information and down-regulate other conflicting somatosensory cues (Zeller et al., 2016). In order to minimize predictor errors, high-level body representation is also integrated and updated, resulting in a modulation of the sense of body ownership when the illusion occurs (Limanowski and Blankenburg, 2015). In this perspective, our results indicate that variation of activation of frontal areas, which is typically observed during self-referential processes, correlates with modulation of self-localization, possibly suggesting that participants who are able to inhibit a self-anchored representation of their body, are more likely to recalibrate their perceived hand position during the RHI.

Concerning the difference between preterm and full-term children, the results of the present study suggest that both groups of children showed sensitivity to the RHI, as they reported significantly higher scores of embodiment during synchronous visual-tactile stimulation compared to the asynchronous condition. Therefore, preterm children appear to be able to modulate the representation of their body on the basis of multisensory integration processes, as typically developmental children do. However, our results also indicate a main significant effect of the group, suggesting that overall preterm children reported lower scores of subjective embodiment over the rubber hand. A possible interpretation of this result is that preterm children may be more anchored on a stable representation of their body, thus showing more difficulty in modulating their bodily boundaries in order to include external objects as part of their own body, irrespective of the available multisensory information. This speculation is further supported by the data from the proprioceptive drift, which showed a different modulation of the proprioceptive perceived position in preterm and full-term children, although statistical significance was not reached. In particular, full-term children exhibited a greater recalibration of self-localization due to different visuotactile stimulation, whereas preterm children showed a more persistent response close to the initial proprioceptive perceived position. The reduced embodiment of the rubber hand and the accurate localization of the hidden hand could indicate a bias towards proprioceptive processing. It is possible that preterm children presented an unusual strong reliance on proprioception and atypical multisensory integration of other body-related cues. Notably, similar atypicalities in behavioral measures of the RHI have been found in children with autism spectrum disorder (ASD) who displayed a delayed susceptibility to the illusion after 6 min of stimulation and difficulty in differentiating their subjective experiences between asynchronous and synchronous stimulations (Cascio et al., 2012). Compared to children with typical development, both groups of autistic and preterm children showed a stronger tendency to focus on proprioceptive signals ignoring competing information from other sensory modalities, resulting in less susceptibility to the conflicting visual and tactile input during the induction of the RHI. By systematically varying the brushing period from 2 to 6 min, future studies could investigate the possibility that prolonged visuotactile stimulation may eventually lead to a remapping of the body representation in preterm children, as evidenced in children with ASD. Considering the neural measures, preterm children revealed a different modulation of alpha oscillatory activity compared to full-term children during the RHI. In particular, they showed a greater alpha suppression which may reflect a greater effort in integrating multisensory bodily signals. Taken together, our findings might suggest that although preterm children showed sensitivity to different visual-tactile stimulation suggesting the ability to integrate multisensory information, they also appeared to be more anchored to their own body and to place a greater reliance on internal proprioceptive information rather than external sensory cues. Indeed, they seem to be less likely to perceive the rubber hand as part of their own body irrespective of the visual-tactile stimulation, possibly indicating a more rigid representation of their own body.

Accurate integration of visual, tactile, and proprioceptive input underpins the sense of bodily self with important implications for identifying, differentiating, and comparing oneself with others (Meltzoff, 2007; Tsakiris, 2016). The malleability of the sense of body ownership allows a partial overlap of our body and those of others (Maister et al., 2015), as reflected by a shared representation of the self and the other in the brain, which may underpin the basis of social understanding and social connection (Brozzoli et al., 2013; Courtney and Meyer, 2020). Indeed, the multisensory representation of the body not only guides self-awareness and sensorimotor development, but also provides an interpretative framework for understanding the actions, goals, and psychological states of others, critically influencing the ability to successfully engage in social interactions (Ropar et al., 2018). It has been shown that the embodiment of a different body to one's own with respect to gender, age, or race changes the representation of one's own body through a process of self-other association that first takes place in the bodily domain (Maister et al., 2015). In tune, the perceived physical similarity between the self and another outgroup person extends to the socio-cognitive domain, resulting in a reduction of implicit biases against outgroup members and modulation of social cognition processing (Paladino et al., 2010; Farmer et al., 2014). Thus atypical body-related multisensory integration could affect the development of body ownership and the malleability of one's own bodily representation, impacting higher-order social and cognitive processes, including the understanding of others' actions and emotions (Ropar et al., 2018). In support of this, a recent study showed that lacking bodily contact in the first weeks of life due to prenatal birth affected mother-infant synchrony (Yaniv et al., 2021). However, if additional skin-to-skin mother-newborn contact was provided, an increased mother-child synchrony was observed across development impacting the brain's capacity to empathize with others in adulthood (Yaniv et al., 2021). These findings support that early sensory experiences shape the representation of one's own body as a point of reference for interactions with the external physical and social environment with cascading effects on socio-emotional and cognitive development. Thus, studying the integration of different sensory signals in the context of the RHI may have a crucial relevance for better understanding typical and atypical developmental trajectories, sharing light on the developmental processes of the acquisition of a sense of body ownership and differentiation of the self from the others as precursors to more complex social behaviors. Specifically, the results of the present study point to a possible less malleable representation of the body in preterm children that should be better investigated in light of neurobiological vulnerability and early exposure to a detrimental sensory environment in NICU. This will help to assume a more comprehensive perspective on sensory, cognitive, and social development, with the potential of refining assessment methods and developing multidimensional interventions that include multisensory body-related stimulation.

In conclusion, the development of bodily-related multisensory processing and integration represents important precursors of self-awareness processes that organize sensation from different sensory channels, modulating perception of the bodily self and others. In typically developing children visual-tactile synchrony provides the basis for updating the sense of body ownership, as reflected by behavioral measures and alpha oscillatory activity. Preterm children, who are typically exposed to a detrimental sensory environment in the neonatal period, showed to be able to integrate incoming multisensory information to update the representation of their body. However, they appear to be more self-anchored, as reflected by the overall lower feeling of embodiment over the rubber hand. The findings of the present study pave the way for a multisensory approach to the investigation of social and cognitive development, focusing on the bodily self as a point of reference for the integration of sensory experiences. We believe that this line of research provides an essential contribution to better understand the processes of identification and differentiation between the self and the external environment, in both typical and atypical development.

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 Comitato etico della ricerca psicologica Area 17 Department of Psychology, University of Padua. Written informed consent to participate in this study was provided by the participants' legal guardian/next of kin.

AUTHOR CONTRIBUTIONS

LD, TF, and GM discussed the project. LD and TF developed the hypothesis, designed the method, and prepared the materials. LD collected the data and GM supervised the data collection. LD analyzed the data and GM supervised EEG data preprocessing and oscillatory analyses. LD prepared the manuscript. All authors contributed to the article and approved the submitted version.

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BRIEF RESEARCH REPORT
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Effects of Symmetry and Apparent Distance in a Parasagittal-Mirror Variant of the Rubber Hand Illusion Paradigm

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When I see my face in a mirror, its apparent position (behind the glass) is not one that my own face could be in. I accept the face I see as my own because I have an implicit understanding of how mirrors work. The situation is different if I look at the reflection of my right hand in a parasagittal mirror (parallel to body midline) when my left hand is hidden behind the mirror. It is as if I were looking through a window at my own left hand. The experience of body ownership has been investigated using rubber hand illusion (RHI) paradigms, and several studies have demonstrated ownership of a rubber hand viewed in a frontal mirror. Our "proof of concept" study was the first to combine use of a parasagittal mirror and synchronous stroking of both a prosthetic hand (viewed in the mirror) and the participant's hand, with a manipulation of distance between the hands. The strength of the RHI elicited by our parasagittal-mirror paradigm depended not on physical distance between the hands (30, 45, or 60 cm) but on apparent distance between the prosthetic hand (viewed in the mirror) and the participant's hand. This apparent distance was reduced to zero when the prosthetic hand and participant's hand were arranged symmetrically (e.g., 30 cm in front of and behind the mirror). Thus, the parasagittal-mirror paradigm may provide a distinctive way to assess whether competition for ownership depends on spatial separation between the prosthetic hand and the participant's hand.

Keywords: body ownership, distance, mirror box, multisensory integration, parasagittal mirror, peripersonal space, rubber hand illusion, symmetry

INTRODUCTION

Looking at oneself in a mirror is an everyday example of altering bodily self-awareness. One's seen body and felt body no longer coincide in space. If I sit in front of a mirror and look at the reflection of my face, then the apparent position of the face that I see is behind the glass and the apparent orientation is toward me. No face that was really in that position and orientation could possibly be my own face. Nevertheless, around 18 months of age, we come to recognize the baby seen in the mirror as ourself (Amsterdam, 1972; Brooks-Gunn and Lewis, 1984).

Over time, ownership of our mirror image becomes automatic under normal conditions, though the sense of ownership is disrupted if, for example, the facial movements seen in the mirror are not synchronous with our active movements of the face (O'Sullivan et al., 2018). This ownership of the mirror image is not just a matter of recognizing oneself, as in a (mirror-reversed) photograph. We learn to use our reflection to guide actions such as combing our hair or adjusting our clothing. More generally, we learn to transform the visual information about apparent position and orientation, so that we can act fluently in mirrored-space – although incorrect beliefs about mirror reflections are widespread (Lawson and Bertamini, 2006).

As we age, mirrors can sometimes re-emerge as a challenge. Some patients with focal onset dementia actually believe that the person they see in the mirror is not them (mirrored-self misidentification; Breen et al., 2000, 2001). Thus, just as the way we view and interact with our environment may alter our perception of that environment (DiZio et al., 1993), so too may viewing and interacting with our body seen in a mirror – in varying ways across the lifespan – modulate our sense of body ownership.

The experience of body ownership has been investigated using the rubber hand illusion (RHI; Botvinick and Cohen, 1998). In the Classic-RHI paradigm, the participant places their left hand out of view, hidden behind an opaque divider, and is asked to look at a rubber left hand positioned in front of them and oriented *egocentrically* (i.e., with the fingers pointing away from them). The participant is able to *see* brush strokes on the rubber hand and able to *feel* (but not see) strokes on their own hand. When the seen strokes are synchronous with the felt strokes, the RHI is elicited. The participant reports their experience of the RHI, by rating their agreement with statements expressing three aspects of the illusion: *ownership*, *causation*, and *visual capture of touch* (VCT). The experimenter may also measure the *proprioceptive drift* of the hidden hand toward the seen rubber hand, by asking the participant to indicate the felt position of their hidden left hand before, and again after, stroking.

In RHI studies by Bertamini et al. (2011) and Kontaris and Downing (2011), participants either viewed a rubber hand directly (as in the Classic-RHI paradigm) or looked at the reflection of a rubber hand in a mirror in front of them (with the direct view of the rubber hand occluded). In the mirror-view condition, the apparent position of the seen rubber hand was behind the glass and oriented *allocentrically* (i.e., with the fingers pointing toward the participant). Bertamini et al. found that the RHI was just as strong (assessed by illusion ratings and proprioceptive drift) in the mirror-view condition as in the direct-view condition; and this finding (for illusion ratings) was replicated by Jenkinson et al. (2013). Kontaris and Downing also added an orientation manipulation, with the fingers of the rubber hand oriented egocentrically or allocentrically. They found that, in the direct-view condition, the RHI (assessed by illusion ratings and proprioceptive drift) was abolished in the allocentric-orientation condition, replicating earlier findings (Ehrsson et al., 2004; also see Jenkinson and Preston, 2015). In contrast, in the mirror-view condition, the RHI was elicited in both orientation conditions – though at a somewhat reduced level compared with direct viewing of a rubber hand oriented egocentrically. Using the moving RHI paradigm (Kalckert and Ehrsson, 2012), Jenkinson and Preston (2015) found *higher* ratings for the illusion of ownership of the rubber hand in mirror-view than in direct-view conditions.

When I see my hand or face in a mirror in front of me, its apparent position (behind the glass) is not one that my own hand or face could be in. I accept it as my own hand or face because I have an implicit understanding of how mirrors work. The situation is different when the mirror is placed in a parasagittal plane (e.g., to the left of body midline). If I sit with my right hand at midline and look to the left into the parasagittal mirror, then the hand seen in the mirror appears to be a left hand behind the glass. No such hand in that position could be my own right hand but it could be my own left hand. For a participant looking at the reflection of a right hand in the parasagittal mirror, it is as if they were looking through a window at their real left hand. Thus, when using a parasagittal mirror, the reflection in the mirror of a real (or rubber) *right* hand can be "superimposed" on a hidden *left* hand behind the mirror.

This specular superimposition has been used to "resurrect" a phantom limb in patients following upper-limb amputation and, in some patients, to relieve pain in the phantom limb (Ramachandran et al., 1995; Ramachandran and Rogers-Ramachandran, 1996). Parasagittal mirrors have also been used to: manipulate the visually perceived distance between participants' hands (Gallace and Spence, 2005); assess the influence of vision on proprioception (Holmes et al., 2006); investigate visual enhancement of touch (Ro et al., 2004; Longo et al., 2008a); compare tactile illusions in amputees' phantom limbs and healthy individuals' intact but untouched limbs (Giummarra et al., 2010); explore relationships between the illusion of ownership, proprioceptive drift, estimates of the hardness of a foam pad, and skin temperature on the hands (Sadibolova and Longo, 2014; Medina et al., 2015; Katsuyama et al., 2018; Crivelli et al., 2021).

For the Parasagittal-Mirror-RHI paradigm used in the present study, the participant placed their left hand out of view, hidden behind the non-reflective side of the parasagittal mirror, and was asked to look *in the mirror* at the reflection of a prosthetic right hand – which appeared as a left hand behind the glass (The participant's real right hand, which was not relevant to the paradigm, remained in their lap.) When the prosthetic hand and the participant's hidden hand were stroked synchronously, the participant reported their experience of the RHI by rating their agreement with three illusion statements: *ownership*, *causation*, and *VCT*.

Physical distance between the prosthetic hand and the participant's hidden hand, and symmetry of the two hands in front of and behind the mirror, were manipulated so that in symmetrical conditions the reflection of the prosthetic right hand was "superimposed" on the participant's hidden left hand. In two experiments, we used the Classic-RHI paradigm and the Parasagittal-Mirror-RHI paradigm to investigate the experience of the RHI.

Our first research question concerned the strength of the RHI in the parasagittal mirror. We predicted effects for

- Paradigm: The Parasagittal-Mirror-RHI paradigm would elicit higher illusion ratings than the Classic-RHI paradigm with a matched symmetrical arrangement of the prosthetic hand and the participant's hand in front of and behind the mirror or opaque divider.

Our second research question concerned the effects of distance and symmetry in the Parasagittal-Mirror-RHI paradigm. We predicted that the way in which the physical distance between the prosthetic hand and the participant's hand was divided either side of the mirror (prosthetic hand **X cm** in front of the mirror **+** participant's hand **Y cm** behind the mirror) would be critical. Specifically, we predicted effects for

- Symmetry: Higher illusion ratings would be elicited when the prosthetic hand and the participant's hand were positioned symmetrically either side of the mirror, even if the physical distance between the prosthetic hand and the participant's hand differed between 30 cm (15 cm + 15 cm) and 60 cm (30 cm + 30 cm); and
- Asymmetry: Lower illusion ratings would be elicited when the prosthetic hand and the participant's hand were positioned asymmetrically either side of the mirror, even if the physical distance between the prosthetic hand and the participant's hand remained constant at 60 cm (15 cm + 45 cm and 30 cm + 30 cm).

METHODS

Participants

Participants were recruited from the Australian National University, and received a small remuneration. Participants provided informed written consent in accordance with the ethics protocol (2015/397) approved by the Australian National University Research Ethics Committee.

In Experiment 1, 21 participants (Mean age: 25.6 years, SD: 8.67) were tested with the Classic-RHI paradigm (in which participants were instructed to look directly at the prosthetic hand) and the Parasagittal-Mirror-RHI paradigm (in which direct viewing of the prosthetic hand was not occluded but participants were instructed to look at the mirror reflection of the prosthetic hand). In both paradigms, the physical distance between the prosthetic hand and the participant's hand was 30 cm, divided symmetrically: 15 cm + 15 cm in front of and behind the opaque divider or mirror (see **Figures 1A,B**).

In Experiment 2, 24 new participants (Mean age: 23 years, SD: 1.49) were tested only with the Parasagittal-Mirror-RHI paradigm. There were two symmetrical conditions (physical distance divided 15 cm + 15 cm or 30 cm + 30 cm in front of and behind the mirror) and two asymmetrical conditions (15 cm + 30 cm or 15 cm + 45 cm in front of and behind the mirror), which resulted in three different physical distances (30, 45, and 60 cm) between the hands (see **Figures 1B–E**).

Apparatus and Procedure

The custom-built RHI testing unit consisted of two boxes – each 70 cm (L) × 70 cm (W) × 30 cm (H) – with a lid that slid across the top of the boxes and served to keep the prosthetic hand hidden from the participant's view between trials. A left prosthetic hand was used for the Classic-RHI paradigm and a right prosthetic hand was used for the Parasagittal-Mirror-RHI paradigm (because, when viewed in the mirror, a right prosthetic hand appears as a left prosthetic hand). In both experiments, the prosthetic hand was placed in the gap between the two boxes, and aligned with the participant's midline. In the Parasagittal-Mirror-RHI paradigm, a 70 cm (L) × 30 cm (H) mirror was attached to the outside wall of the left testing-box, which allowed the participant to view the reflection of the prosthetic hand. In the Classic-RHI paradigm, the mirror was removed so that the participant saw only the opaque divider (i.e., the wall of the left testing-box).

The participant was seated (across from the experimenter) in front of the testing unit with the box lid closed. The participant was asked to rest their right hand in their lap and place their left hand in the left testing-box. A black barber's cape was draped around their neck, and was stretched out and attached to both testing boxes to obscure visual feedback from the participant's body. Before the experiment began, the participant was shown the prosthetic hand and it was demonstrated, first how the index finger of the prosthetic hand, and then how the index finger of their own hand, would be stroked. The participant then practised rating the RHI by responding to nine statements (see **Table 1**; Botvinick and Cohen, 1998) using a digital touch-screen tablet.

Once the participant understood the procedure, the experimenter opened the box lid to reveal the prosthetic hand. A cloth was draped over the base of the prosthetic hand to give the impression that the prosthetic hand was attached to the end of the participant's arm under the barber's cape. The experimenter instructed the participant that, for the duration of the trial, they were to look either at: (i) the index finger of the prosthetic hand (Classic-RHI paradigm); or (ii) the mirror reflection of the index finger of the prosthetic hand (Parasagittal-Mirror-RHI paradigm). Two fine-haired paintbrushes were used to stroke both index fingers from the metacarpophalangeal joint to the tip of the finger. Stroking consisted of a random sequence of tapping interspersed with long and short brushstrokes, which were administered at a consistent pressure and speed. Stroking of the prosthetic hand and the participant's hidden hand could be: (i) synchronous (temporally congruent); or (ii) asynchronous (temporally incongruent). The two stroke types were pseudo-randomized to avoid order effects. Each stroke type was administered twice per participant for each experiment condition. In Experiment 1, there were eight trials (two synchronous and two asynchronous trials for each of the two paradigms: Classic-RHI and Parasagittal-Mirror-RHI) with a stroking duration of 120 s. In Experiment 2, there were 16 trials (two synchronous and two asynchronous trials for each placement of the two hands: 15 cm + 15 cm, 15 cm + 30 cm, 15 cm + 45 cm, 30 cm + 30 cm) with a stroking duration of 90 s.

At the end of each trial, the box lid was closed, and the participant was instructed not to move their left hand, and to use their right hand to respond to the nine statements. When they finished responding, they were asked to remove their left hand

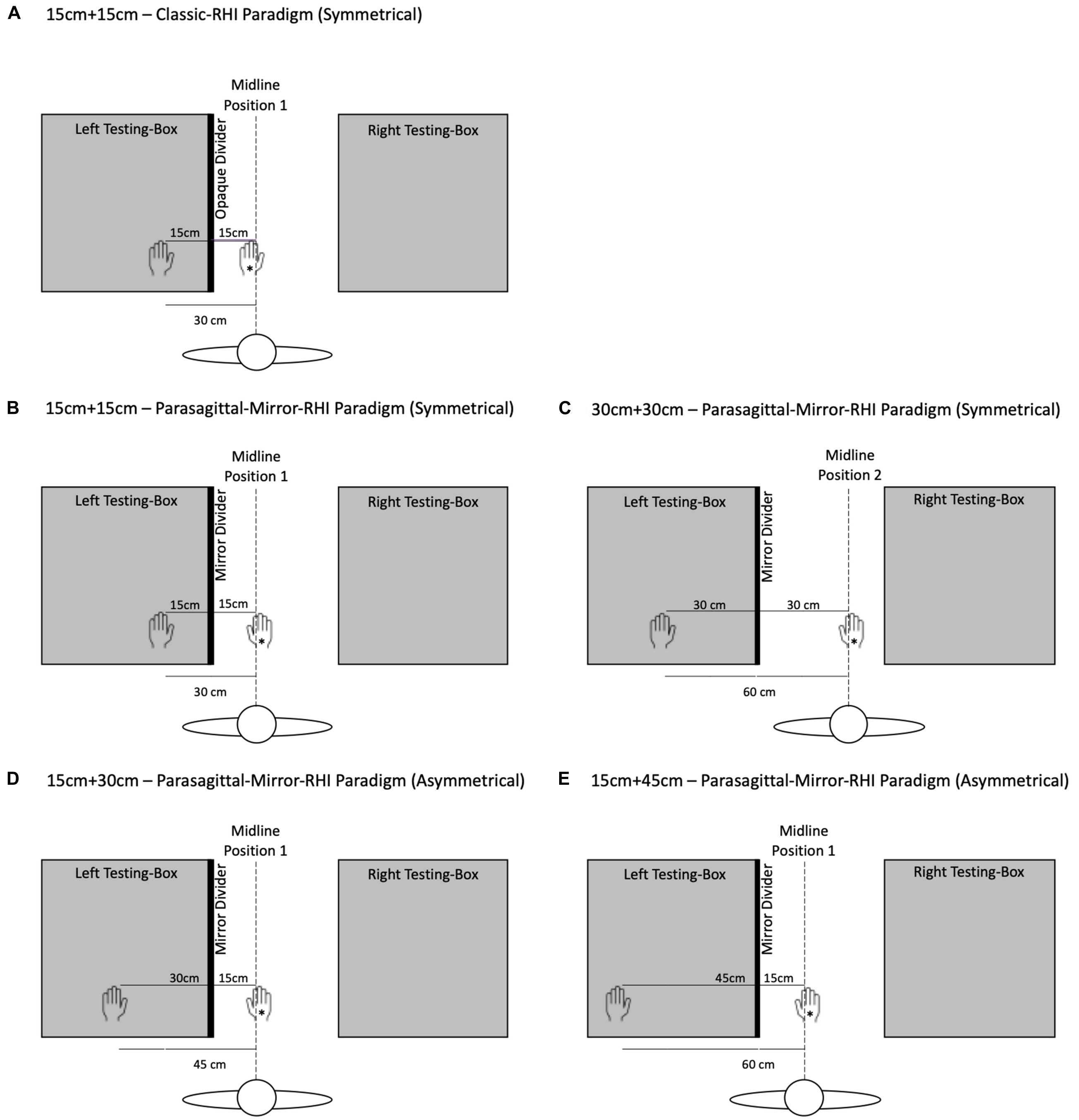

FIGURE 1 | Rubber hand illusion testing unit for the symmetrical placement of the prosthetic hand and the participant's hidden hand in the Classic-RHI paradigm, and the symmetrical and asymmetrical placements in the Parasagittal-Mirror-RHI paradigm. **(A)** Depicts the testing unit for the Classic-RHI paradigm (participants instructed to look at the index finger of the prosthetic hand), and **(B–E)** depict the testing unit for the Parasagittal-Mirror-RHI paradigm (participants instructed to look at the mirror reflection of the index finger of the prosthetic hand). In Experiment 1, Symmetrical condition **(A,B)**, the total distance between the prosthetic hand and participant's hand was 30 cm (divided 15 cm + 15 cm in front of and behind the opaque divider or mirror). In Experiment 2, (i) Symmetrical conditions **(B,C)**, the total distance between the prosthetic hand and participant's hand was either **(B)** 30 cm (divided 15 cm + 15 cm in front of and behind the mirror) or **(C)** 60 cm (divided 30 cm + 30 cm in front of and behind the mirror); (ii) Asymmetrical conditions **(D,E)**, the total distance between the prosthetic hand and participant's hand was either **(D)** 45 cm (divided 15 cm + 30 cm in front of and behind the mirror) or **(E)** 60 cm (divided 15 cm + 45 cm in front of and behind the mirror). In all conditions, the prosthetic hand, which is marked in the figure with an asterisk (*), was placed at the participant's midline (between the two boxes), and the participant's left hand was placed inside the left box (to the left of the participant's midline), at 15, 30, or 45 cm behind the opaque divider or mirror. There were two midline positions: Midline Position 1 (prosthetic hand positioned 15 cm in front of the mirror) and Midline Position 2 (prosthetic hand positioned 30 cm in front of the mirror).

TABLE 1 | Questionnaire for Assessing the Rubber Hand Illusion in the Classic-RHI Paradigm and the Parasagittal-Mirror-RHI Paradigm: Three Illusion Statements (S1–S3) and Six Control Statements (S4–S9).

Statement #	Illusion versus Control Statements	Statements
S1	Ownership	I felt as if the rubber hand were my hand
S2	Causation	It seemed as though the touch I felt was caused by the paintbrush touching the rubber hand
S3	Visual Capture of Touch	It seemed as if I were feeling the touch of the paintbrush in the location where I saw the rubber hand touched
S4	Control	It felt as if my (real) hand were drifting towards the right (towards the rubber hand)
S5	Control	It seemed as if I might have more than one left hand or arm
S6	Control	It seemed as if the touch I was feeling came from somewhere between my own hand and the rubber hand
S7	Control	It felt as if my (real) hand were turning "rubbery"
S8	Control	It appeared (visually) as if the rubber hand were drifting towards the left (towards my hand)
S9	Control	The rubber hand began to resemble my own (real) hand, in terms of shape, skin tone, freckles or some other visual feature

Nine statements (three illusion statements and six control statements) were presented in randomized order at the end of each trial. Participants responded on a visual analog scale, with indicative marks at only the two end points of the scale: 0 "Not at all" and 6 "Very strongly agree". Participants used a slider on a digital touch-screen tablet, with 0 and 6 serving to provide the participant with reference points when selecting the point along the line that best indicated their rating of the RHI. In Experiment 1, participants used a Samsung Galaxy 10 inch Tablet with a stylus, and in Experiment 2, participants used an 8 inch iPad Tablet and their finger.

from the testing unit and to flex and extend their fingers before beginning the next trial.

Statistical Analysis Plan

Mixed-effects beta regression with a logit link function was used to analyze the ratings (0–6) for the experiment statements (Illusion, Control) – the continuous doubly-bounded variable. The beta distribution supports continuous variables within the (0,1) range, but is undefined at the boundary values of zero and one; therefore, all of the raw ratings were divided by six and were shrinkage-transformed to move the boundary values slightly away from the boundary. See Equation 1 (Smithson and Shou, 2020, p. 51) for the formula in which N is the sample size.

$$y_{shrink} = \frac{y\,(N-1) + 0.5}{N} \tag{1}$$

Ratings for each illusion statement (Ownership, Causation, VCT) were analyzed separately with the averaged ratings for the control statements (Averaged-Control ratings). For Experiment 1, three within-subject predictors – Stroke (synchronous, asynchronous); Statement (Ownership/Causation/VCT, Averaged-Control); Paradigm (Classic-RHI, Parasagittal-Mirror-RHI) – were entered as fixed effects and random slopes that captured the dependencies in the repeated-measures design (Barr et al., 2013). For Experiment 2, three within-subject predictors – Stroke (synchronous, asynchronous); Statement (Ownership/Causation/VCT, Averaged-Control); Distance (15 cm + 15 cm, 15 cm + 30 cm, 15 cm + 45 cm, 30 cm + 30 cm) – were entered as fixed effects, but only Stroke and Statement were entered as random slopes[1]. For both experiments, Participant was entered as the random intercept.

All analyses were carried out in R (version 4.0.5) with the "*glmmTMB*" package for mixed-effects beta regression, "*car*" package for Type-III analysis-of-variance tables with Wald chi-square tests, and "*emmeans*" package for *post hoc* pairwise comparisons with Tukey-corrections for *p*-values.

RESULTS

Stroke and Statement Effects

For both experiments, there were significant main effects for Stroke and Statement, and a significant Stroke × Statement interaction. *Post hoc* pairwise comparisons indicated there were higher ratings for synchronous compared with asynchronous stroking for each of the illusion statements (Ownership, Causation, VCT). There were no synchronous versus asynchronous differences for the Averaged-Control ratings.

- Experiment 1 (see **Figure 2A**)

Main effects: Stroke [Ownership, χ^2 (1) = 15.17, $p < 0.001$; Causation, χ^2 (1) = 23.95, $p < 0.001$; VCT, χ^2 (1) = 63.10, $p < 0.001$] and Statement [Ownership, χ^2 (1) = 9.93, $p = 0.002$; Causation, χ^2 (1) = 15.91, $p < 0.001$; VCT, χ^2 (1) = 43.85, $p < 0.001$].

Stroke × Statement interaction [Ownership, χ^2 (1) = 17.36, $p < 0.001$; Causation, χ^2 (1) = 65.15, $p < 0.001$; VCT, χ^2 (1) = 145.15, $p < 0.001$].

Post hoc pairwise comparisons for synchronous versus asynchronous stroking: Illusion ratings (Ownership, $b = 0.86$, 95% CI [0.46, 1.27], $t(316) = 5.53$, $p < 0.001$; Causation, $b = 1.70$, 95% CI [1.15, 2.24], $t(316) = 8.00$, $p < 0.001$; VCT, $b = 2.74$, 95%

[1]Experiment 2: When Stroke, Statement and Distance were entered as random slopes, the model did not converge (the algorithm failed to reliably detect the maximum of the log-likelihood function); this problem could not be resolved by restarting, increasing iterations, or changing optimizers. In cases of convergence failure, it is sometimes necessary to simplify the random effects structure (Barr et al., 2013). Distance was removed from the random slopes to achieve convergence.

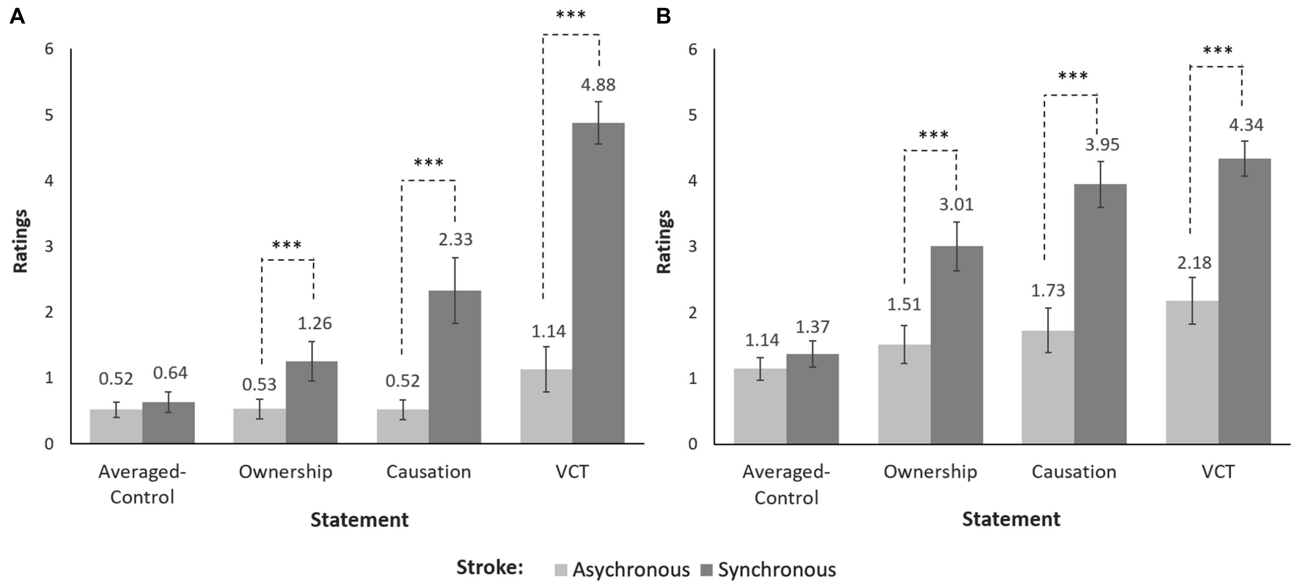

FIGURE 2 | Stroke and Statement effects for Experiment 1 and Experiment 2. The back-transformed means and within-subject standard errors for illusion ratings (Ownership, Causation, VCT) and Averaged-Control ratings are illustrated for Experiment 1 **(A)** and Experiment 2 **(B)**. Separate analyses of ratings for each illusion statement (Ownership, Causation, VCT) with the Averaged-Control ratings indicated that synchronous stroking elicited significantly higher illusion ratings than asynchronous stroking, whereas the Averaged-Control ratings for synchronous and asynchronous stroking were not significantly different. The estimated marginal means and within-subject standard errors of shrinkage-transformed ratings were obtained from the "*effect*" package in R and were back-transformed to the original scale (0–6). ***$p < 0.001$.

CI [2.17, 3.30], $t(316) = 12.57$, $p < 0.001$) and Averaged-Control ratings (all $ps \geq 0.53$).

- Experiment 2 (see **Figure 2B**)

Main effects: Stroke [Ownership, χ^2 (1) = 24.70, $p < 0.001$; Causation, χ^2 (1) = 32.46, $p < 0.001$; VCT, χ^2 (1) = 27.02, $p < 0.001$] and Statement [Ownership, χ^2 (1) = 32.22, $p < 0.001$; Causation, χ^2 (1) = 23.85, $p < 0.001$; VCT, χ^2 (1) = 42.26, $p < 0.001$].

Stroke × Statement interaction [Ownership, χ^2 (1) = 56.35, $p < 0.001$; Causation, χ^2 (1) = 115.79, $p < 0.001$; VCT, χ^2 (1) = 108.07, $p < 0.001$].

Post hoc pairwise comparisons for synchronous versus asynchronous stroking: Illusion ratings (Ownership, $b = 1.04$, 95% CI [0.69, 1.39], $t(745) = 7.60$, $p < 0.001$; Causation, $b = 1.49$, 95% CI [1.07, 1.90], $t(745) = 9.23$, $p < 0.001$; VCT, $b = 1.46$, 95% CI [1.01, 1.90], $t(745) = 8.49$, $p < 0.001$) and Averaged-Control ratings (all $ps \geq 0.43$).

Research Question 1. Paradigm Effects – Classic-RHI Paradigm and Parasagittal-Mirror-RHI Paradigm

For Experiment 1 (see **Figure 3A**), there was a significant main effect for Paradigm (Classic-RHI, Parasagittal-Mirror-RHI) for each of the illusion statements (Ownership, Causation, VCT). For Causation and VCT, these main effects indicated there were higher overall ratings for the Parasagittal-Mirror-RHI paradigm compared with the Classic-RHI paradigm.

- Main effect: Paradigm [Ownership, χ^2 (1) = 12.93, $p < 0.001$; Causation, χ^2 (1) = 7.65, $p = 0.006$; VCT, χ^2 (1) = 5.09, $p = 0.02$].
- Paradigm × Statement interaction [Ownership, χ^2 (1) = 13.48, $p < 0.001$]. There were no other significant two- or three-way interactions with Paradigm for the three illusion statements (all $ps \geq 0.13$).

Post hoc pairwise comparisons indicated that for Ownership there were higher illusion ratings for the Parasagittal-Mirror-RHI paradigm compared with the Classic-RHI paradigm, $b = 0.83$, 95% CI [0.40, 1.26], $t(316) = 4.98$, $p < 0.001$, but there were no paradigm differences for the Averaged-Control ratings, $p = 0.54$.

Research Question 2. Symmetry and Asymmetry Effects in Four Distance Conditions

For Experiment 2 (see **Figure 3B**), there was a significant main effect for Distance (15 cm + 15 cm, 15 cm + 30 cm, 15 cm + 45 cm, 30 cm + 30 cm), and a significant Distance × Statement interaction for Ownership and Causation, but not for VCT.

- Main effect: Distance [Ownership, χ^2 (3) = 12.80, $p = 0.005$; Causation, χ^2 (3) = 11.26, $p = 0.01$; VCT, $p = 0.57$].
- Distance × Statement interaction [Ownership, χ^2 (3) = 10.46, $p = 0.02$; Causation, χ^2 (3) = 9.81, $p = 0.02$;

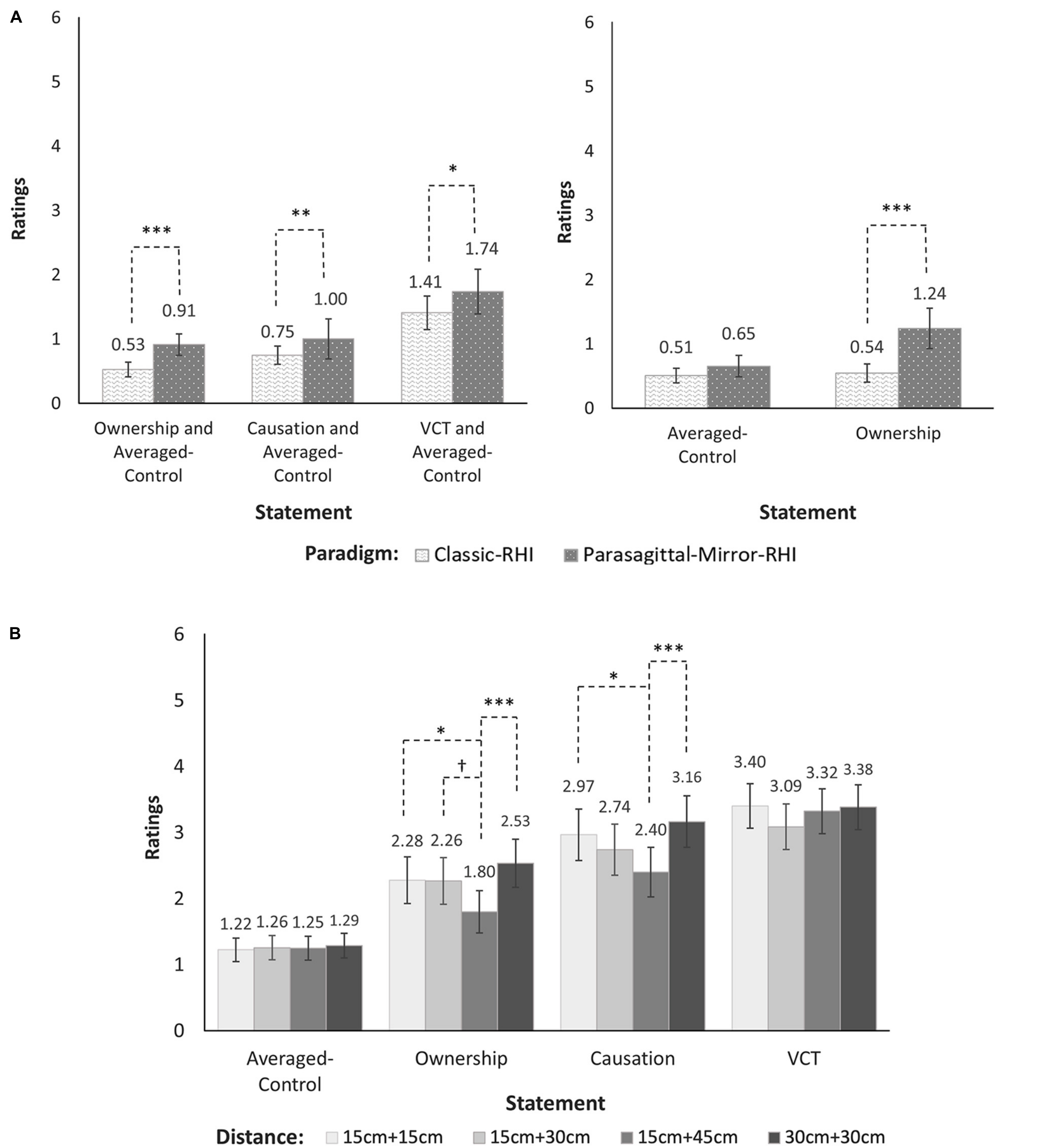

FIGURE 3 | Paradigm effects (Experiment 1), and symmetry *versus* asymmetry effects in four distance conditions (Experiment 2). The back-transformed means and within-subject standard errors for illusion ratings (Ownership, Causation, VCT) and Averaged-Control ratings are illustrated for **(A)** the effects of Paradigm (Experiment 1) and **(B)** the effects of Distance (Experiment 2). For Experiment 1 **(A)**, separate analyses of ratings for each illusion statement (Ownership, Causation, VCT) with the Averaged-Control ratings demonstrated significant main effects for Paradigm (left side) and, for the Ownership-illusion statement, there was a significant Paradigm × Statement interaction (right side). This interaction indicated that the Ownership-illusion ratings were significantly higher for the Parasagittal-Mirror-RHI paradigm compared with the Classic-RHI paradigm, whereas there was no significant difference between paradigms for the Averaged-Control ratings. For Experiment 2 **(B)**, separate analyses of ratings for each illusion statement (Ownership, Causation, VCT) with the Averaged-Control ratings demonstrated significant main effects for Distance, and significant Distance x Statement interactions for the Ownership-illusion and Causation-illusion statements, but not for the VCT-illusion statement. These interactions indicated there were no significant differences in illusion ratings between the two Symmetrical conditions (15 cm + 15 cm versus 30 cm + 30 cm), and there were higher illusion ratings for each of these symmetrical conditions compared with the asymmetrical 15 cm + 45 cm condition. The estimated marginal means and within-subject standard errors of shrinkage-transformed ratings were obtained from the "*effect*" package in R and were back-transformed to the original scale (0–6). *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, and †$p = 0.0502$.

VCT, $p = 0.48$]. There were no other significant two- or three-way interactions with Distance for the three illusion statements (all $ps \geq 0.32$).

Post hoc pairwise comparisons indicated that for Ownership and Causation there were no significant differences in illusion ratings between the two symmetrical conditions (15 cm + 15 cm versus 30 cm + 30 cm; both $ps \geq 0.76$), and there were higher illusion ratings for each of these conditions compared with the asymmetrical 15 cm + 45 cm condition:

- 15 cm + 15 cm versus 15 cm + 45 cm (Ownership, $b = 0.34$, 95% CI [0.02, 0.66], $t(745) = 3.18$, $p = 0.03$; Causation, $b = 0.37$, 95% CI [0.03, 0.70], $t(745) = 3.30$, $p = 0.02$);
- 30 cm + 30 cm versus 15 cm + 45 cm (Ownership, $b = 0.51$, 95% CI [0.18, 0.83], $t(745) = 4.76$, $p < 0.001$; Causation, $b = 0.49$, 95% CI [0.15, 0.83], $t(745) = 4.39$, $p < 0.001$).

There were no differences in illusion ratings between other pairs of conditions (all $ps \geq 0.21$) with one exception that was of interest, the comparison between 15 cm + 30 cm and 15 cm + 45 cm (Ownership, $p = 0.0502$). The Averaged-Control ratings did not differ for any Distance comparisons (all $ps \geq 0.99$).

DISCUSSION

Our study is the first, as far as we know, to combine use of a parasagittal mirror, and synchronous stroking of both a prosthetic hand (viewed in the mirror) and the participant's hand, with a distance manipulation (see **Supplementary Material D1**). The main aim of the current research was to investigate the Parasagittal-Mirror-RHI paradigm systematically.

First, we demonstrated that the Parasagittal-Mirror-RHI paradigm elicits the RHI. Participants' ratings for the Ownership-, Causation-, and VCT-illusion statements (but not their Averaged-Control ratings) were higher following synchronous stroking than following asynchronous stroking. Second, we compared the strength of the RHI elicited by the Classic-RHI and Parasagittal-Mirror-RHI paradigms using a matched symmetrical set-up (Experiment 1). The findings supported our prediction, in that the Parasagittal-Mirror-RHI paradigm elicited higher illusion ratings than the Classic-RHI paradigm for the Ownership-illusion statement, and higher overall ratings.

Third, we manipulated distance and symmetry in the Parasagittal-Mirror-RHI paradigm (Experiment 2), and our predictions were supported. In contrast with findings of reduced illusion ratings with increased distance for the Classic-RHI paradigm (Lloyd, 2007; Aimola Davies et al., 2013; Preston, 2013; Kalckert et al., 2019), the distance effect for the Parasagittal-Mirror-RHI paradigm was clearly *not* driven by differences in the *physical* distance between the hands. In the two symmetrical conditions (15 cm + 15 cm, 30 cm + 30 cm), the physical distance between the hands was different (30 cm *versus* 60 cm) while the apparent distance was the same (0 cm) – and the illusion was equally strong. In the symmetrical 30 cm + 30 cm condition compared with the asymmetrical 15 cm + 45 cm condition, the physical distance between the hands was the same (60 cm) while the apparent distance was different (0 cm *versus* 30 cm) – and the Ownership-illusion and Causation-illusion ratings were reduced (though the illusion was not abolished) in the 15 cm + 45 cm condition. Thus, the RHI can be elicited using the Parasagittal-Mirror-RHI paradigm, both when the prosthetic hand (viewed in the mirror) is apparently superimposed on the participant's hidden hand and when it is apparently separated from the participant's hand by 15 or 30 cm. The strength of the illusion depends on the apparent distance between the prosthetic hand (viewed in the mirror) and the participant's hand, rather than on the physical distance between the hands (see **Supplementary Material D2**).

The Parasagittal-Mirror-RHI paradigm differs from both the Classic-RHI paradigm and the Frontal-Mirror-RHI paradigm, in that it allows the *apparent* position of the prosthetic hand (when viewed in the parasagittal mirror) to coincide with the *physical* position of the participant's real hand. This superimposition would explain the stronger illusion ratings in the Parasagittal-Mirror-RHI paradigm compared with the Classic-RHI paradigm (Experiment 1) and in the symmetrical conditions compared with the asymmetrical conditions (Experiment 2).

Future Directions

Many RHI studies collect data on proprioceptive drift as well as illusion ratings but, in our "proof of concept" study, we prioritized illusion ratings. When a parasagittal mirror is used to superimpose the reflection of a prosthetic hand on the participant's hidden hand, there is a strong illusion of ownership of the prosthetic hand viewed in the mirror, and no scope for proprioceptive drift of the participant's hand toward the apparent position of the prosthetic hand (Hohwy and Paton, 2010). When a distance manipulation is included, however, there is scope for proprioceptive drift in at least some conditions (see Medina et al., 2015). It would thus be of interest to investigate the relationship between illusion ratings and proprioceptive drift in the Parasagittal-Mirror-RHI paradigm.

It would also be of interest to use illusion statements that reflect loss of the sense of ownership of a body part ("disembodiment": Longo et al., 2008b; Romano et al., 2021) to investigate whether ownership of a prosthetic hand is accompanied by disownership of the participant's real hand (Lane et al., 2017). The Parasagittal-Mirror-RHI paradigm may allow us to assess whether competition for ownership between the prosthetic hand and the participant's hand depends on spatial separation between the hands or results from a "no more than two hands" constraint imposed by a body model (see de Vignemont, 2011).

Finally, and more generally, similarities and differences between parasagittal-mirror viewing and frontal-mirror viewing are not yet fully understood (see **Supplementary Materials D3, D4**). One of several questions that warrant further investigation is whether images in *parasagittal* mirrors are just as "immediately and effortlessly" related to the objects from which they originate as images in *frontal* mirrors are (Bertamini et al., 2011, p. 1114).

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding authors.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Australian National University Human Research Ethics Committee. The participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

AA, JS, MD, RW, and SI devised the experiment and contributed to the design of the study. JS and SI collected the data. AA, HC, and JS analyzed the data. AA, JS, and MD drafted the manuscript. All authors contributed to editing and revision of the manuscript and approved the final version for submission.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fnhum.2021.718177/full#supplementary-material

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The Relative Contributions of Visual and Proprioceptive Inputs on Hand Localization in Early Childhood

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Forming an accurate representation of the body relies on the integration of information from multiple sensory inputs. Both vision and proprioception are important for body localization. Whilst adults have been shown to integrate these sources in an optimal fashion, few studies have investigated how children integrate visual and proprioceptive information when localizing the body. The current study used a mediated reality device called MIRAGE to explore how the brain weighs visual and proprioceptive information in a hand localization task across early childhood. Sixty-four children aged 4–11 years estimated the position of their index finger after viewing congruent or incongruent visuo-proprioceptive information regarding hand position. A developmental trajectory analysis was carried out to explore the effect of age on condition. An age effect was only found in the incongruent condition which resulted in greater mislocalization of the hand toward the visual representation as age increased. Estimates by younger children were closer to the true location of the hand compared to those by older children indicating less weighting of visual information. Regression analyses showed localizations errors in the incongruent seen condition could not be explained by proprioceptive accuracy or by general attention or social differences. This suggests that the way in which visual and proprioceptive information are integrated optimizes throughout development, with the bias toward visual information increasing with age.

Keywords: multisensory integration, sensory processing, vision, proprioception, development

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INTRODUCTION

The ability to locate our body parts in space is fundamental for successful interaction with the environment and plays a vital role in developing a sense of the bodily self. In order to understand and interact with the environment around the body, the brain must integrate information from multiple sensory modalities to construct unified representations of the bodily self and the world around it. The integration of proprioceptive, somatosensory and visual inputs specifically underpins the subjective sense of self and body ownership (Makin et al., 2008), which in turn are important for the development of self-awareness and social cognition (Schütz-Bosbach et al., 2006).

How the brain integrates sensory information in order to make sense of the body has been studied extensively in adulthood. Studies (e.g., Alais and Burr, 2004; Trommershauser et al., 2011) show that the degree to which adults integrate sensory inputs can be quantitatively predicted by a Maximum-Likelihood-Estimate (MLE) model of optimal integration (van Beers et al., 1996;

Ernst and Banks, 2002). For example, when judging the size of an object, estimates of size derived from each sense are averaged and combined to construct a coherent percept. These estimates are prone to variance but, by averaging the estimates, the brain can reduce the noise in the overall percept (Landy et al., 1995). Specifically, a greater weighting will be given to estimates with less variance, since these are deemed as more reliable. The degree of variance in an estimate is dependent on both bottom-up processes (i.e., the incoming sensory information) and top-down processes (derived from prior knowledge and experience).

In support of this model, research finds that in adults no single sense totally dominates bodily experience; instead the experimental context and prior information predicts which sense is treated as more reliable and hence given a greater weighting (van Beers et al., 2002). For example, proprioceptive inputs are weighted more strongly when adult participants actively move the hand compared to when it is passively placed by another person (Mon-Williams et al., 1997) because active movement provides richer and more reliable sensory information about limb position. Similarly, while visual cues are relied on more than proprioceptive information when perceiving limb position (Hay et al., 2014), the reverse is found when visual information is limited to a small light attached to one finger (Plooy et al., 1998). In addition, simply looking toward an unseen hand can change the weighting of sensory information and improve proprioceptive localization (Newport et al., 2001). Together, these findings support the argument that adults integrate information from multiple modalities in a statistically optimal way by taking into account the precision of inputs in different circumstances (van Beers et al., 1999). However, it is not clear when this ability to optimally integrate visual, proprioceptive and tactile information underlying body representation develops in children.

Though studies in early to late childhood have been conducted, a review on the development of multisensory integration abilities concluded that the age at which optimal integration occurs is still unclear (Dionne-Dostie et al., 2015). Charting the development of visuo-tactile-proprioceptive integration in children is important because it has been suggested that typical integration is necessary for higher order processes such as body ownership and social skills (Gallese, 2003; Gallese et al., 2004; Chaminade et al., 2005). A wide body of research has established that both a sense of self (Rochat, 2010; Lewis, 2011) and social processing skills (Merrell and Gimpel, 2014) develop and mature with age. Furthermore, research working with autistic children has indicated a relationship between atypical visuo-proprioceptive integration and the severity of social difficulties (Cascio et al., 2012). Investigating the integration of these inputs in typical development can increase our understanding of the mechanisms underlying the development of social behaviors and provide a comparison point to assess the nature of atypical multisensory integration in neurotypical conditions.

Based on adult research, a common method used to investigate how children combine multisensory information is by introducing conflict between cues from different senses. Research using preferential looking paradigms has demonstrated that infants even a few months old can detect temporal delays between visuo-tactile inputs (Zmyj et al., 2011; Filippetti et al., 2013, 2014; Freier et al., 2016) and visuo-proprioceptive information related to their bodies (Bahrick and Watson, 1985; Rochat and Morgan, 1995; Schmuckler, 1996; Morgan and Rochat, 1997). However, although these findings suggest that infants may be sensitive to visuo-tactile and visuo-proprioceptive contingencies, it cannot tell us if they actually derive a sense of bodily self or body ownership from this (Bremner et al., 2012). Moreover, preferential looking studies cannot assess the relative weighting given to different senses and thus whether infants integrate multisensory information in an optimal, adult-like manner. Research examining the development of postural control has shown that children as young as 4 years old are able to integrate sensorimotor signals and re-weight these in response to changing sensory environments; however, the magnitude of this re-weighting increases with age over childhood and does not become adult-like until around 12 years of age (Barela et al., 2003; Bair et al., 2007; Polastri and Barela, 2013).

Other studies which have also found evidence for a protracted period of development for sensory integration have employed the rubber hand illusion (RHI) (Cowie et al., 2013, 2016). In the RHI a fake hand is embodied following simultaneous felt and seen touch applied to an individual's unseen hand and a fake hand, respectively. Estimates of body ownership of the fake hand are assessed through explicit questions of body ownership and through hand localization via pointing to the position of their unseen hand. In Cowie et al.'s (2013) study, when visual-tactile inputs were synchronous, both adults and children aged 4—9-years-old estimated the location of their unseen hand to be closer to the fake hand than in pre-touch baseline conditions—an indication that multisensory integration had taken place. However, unlike adults, even when visual-tactile inputs were asynchronous, 4–9 year old children's made estimates were also closer to the fake hand than in baseline conditions which might suggest either that visual capture by the fake hand dominates proprioception or that the temporal binding of visuo-tactile sensory information is not as tightly constrained in younger children as it is in older children and adults (Greenfield et al., 2015, 2017). Therefore, the involvement of temporal processing in the RHI paradigm, makes it more difficult to determine the weighting of different sensory inputs.

Other research which has been able to more clearly assess the relative weighting of specific sensory inputs in early childhood have used hand localization tasks. King et al. (2010) used a sensory conflict paradigm to assess visuo-proprioceptive integration in 7-13-year-olds. Children pointed to a visual or a proprioceptive target (the unseen finger of their other hand), with or without the addition of a visual marker (i.e., circle), which was either congruent or incongruent with the location of the unseen finger. When congruent visual and proprioceptive information was available, children's estimates were more reliable than in conditions when information from only one modality is present. This indicates that 7–13-year-olds are able to flexibly re-weight sensory information according to the task demands. However, in an incongruent condition in which the visual marker and proprioceptive target (the unseen finger) were in conflicting locations, older children increased the weighting given to proprioceptive inputs while younger children utilized visual information more. In a younger cohort, Bremner et al. (2013) tested reaching accuracy in 5–7-year-olds using a mirror illusion that placed proprioceptive and visual cues to arm location in conflict. The results showed evidence of visual capture of perceived hand location which increased up until 6 years of age.

In summary, although this body of research points to a maturation of sensory integration skills during childhood, the age at which children are reported to become adult-like in flexibly re-weighting sensory inputs appears to vary considerably. This could be due to the extent that the task relies on motor skills (i.e., pointing to the target/hand), temporal processing and/or working memory, all of which improve significantly over childhood (Takahashi et al., 2003; Gathercole et al., 2004; Barkley et al., 2014; Greenfield et al., 2015, 2017).

As previous studies have demonstrated (van Beers et al., 1996, van Beers et al., 1999; King et al., 2010), the relative weighting of visual and proprioceptive sensory information is best determined by the presentation of incongruent input. However, it should also be noted that overcoming experimentally induced visuo-proprioceptive conflict through sensory integration mechanisms is not an instantaneous process; integration mechanisms have been shown to be incomplete or less tightly constrained in children than in adults (Cowie et al., 2013; Greenfield et al., 2015). Nonetheless, research employing mediated reality methods, have been successful in demonstrating that seeing one's hand in one location while feeling it in another will rapidly alter the perceived location of that hand (e.g., Newport and Preston, 2011; Preston and Newport, 2011; Greenfield et al., 2015; Bellan et al., 2015). The current study therefore investigated the development of optimal integration in children by characterizing the developmental trajectory of sensory weighting in a task that promoted the integration of visual and proprioceptive information concerning hand position. Unlike King et al. (2010), who used a localization task, with different targets for vision and proprioception (circle vs. own hand), here we employ a hand localization task in which a virtual image of the participant's own hand serves as the incongruent visual "target" as well as the proprioceptive "target" using a mediated reality device called MIRAGE (Newport et al., 2010). Seeing the actual body is more analogous to real life and provides more salient information compared to a visual target that merely signals the position of the body, which may affect the extent to which visual information is weighted. Furthermore, so that a measure of purely visuo-proprioceptive integration could be obtained, without the confound of movement as in previous research, hand localization in the current study was measured using a perceptual judgment task rather than a pointing task. The task required children to locate their right index finger after being exposed to either congruent or incongruent visuo-proprioceptive information regarding hand position. Age-related differences in unimodal accuracy were assessed by asking children to estimate the location of their unseen hand after viewing congruent information. The same task was completed after presenting children with incongruent visual and proprioceptive information to measure the developmental trajectory of optimal sensory integration and to assess age related differences in the degree that one or other sense dominated. A similar paradigm used by Bellan et al. (2015) found that the presence of incongruent visual information significantly affects hand localization, with estimates biased toward the visual location of the hand. Overall, adults weighted visual and proprioceptive information at approximately 60 and 40%, respectively. Based on previous observations that suggest young children are more driven by visual information during visuo-proprioceptive conflict in hand localization tasks (King et al., 2010; Cowie et al., 2013), we hypothesized that the weighting of proprioceptive information under conditions of visuo-proprioceptive conflict would increase with age. Due to inconsistent methodology and findings in the literature, it is difficult to make predictions about the precise age children are able to integrate and flexibly reweight sensory information, however, most research has indicated that children under 10 years tend to favor one sensory modality, usually vision, more strongly.

MATERIALS AND METHODS

Participants

Seventy-five children aged 4-11 years (M = 8.44, SD = 1.94, 43 females, 8 left-handed) participated as part of a Summer Scientist Week event held at The University of Nottingham for which children were invited to complete short experiments. Children came from mid-to high socioeconomic backgrounds. Parents of all children completed the Social Aptitudes Scale (SAS; Liddle et al., 2008), which measures social skills, and the Strengths and Weaknesses of ADHD symptoms and Normal behavior rating scale (SWAN; Swanson et al., 2012), which measures positive attention and impulse control. Ratings on the SAS and SWAN are made by parents based on how they think their child compares in relation to peers of the same age. On the SWAN a rating of 0 is exactly average while any rating above average gains a negative value and below average is given a positive value (SWAN; Swanson et al., 2012), On the SAS a validation study carried out by Liddle et al. (2008) with 7,977 participants yielded a mean score of 24.6 and similar distributions across different age ranges (5–8; 9–12; 13–16) each with a modal score of 20. The British Picture Vocabulary Scale III (BPVS III; Dunn and Dunn, 2009), was used to assess verbal mental age and administered to ensure none of the children had a developmental delay. Handedness was determined by the hand with which a child used for writing/drawing.

Data from 11 children were excluded: nine children did not keep their hands still during the task, one (aged 4 years) did not want to complete the task, and age data for one child was missing, leaving 64 children (40 females, 7 left-handed) who were included in the analysis (**Table 1**). The remaining participants included: 5 (aged 4–5 years); 12 (aged 6–7 years); 29 (aged 8–9 years); and 18 (aged 10–11 years). In this final sample, data were missing for three participants on the SAS, three on the BPVS and four on the SWAN. However, no children were reported to have a clinical diagnosis of a developmental disability. The parents of all children gave written informed consent prior to testing and ethical approval for the experiment was granted by the University of Nottingham, School of Psychology Ethics Committee and

TABLE 1 | Descriptive statistics for the sample.

Statistic:	Mean	*SD*	Min	Max
Age in years	8.78	1.79	4.51	11.95
BPVS raw score	120.72	21.21	59	156
BPVS standardized score	105.05	11.4	72	131
Social Aptitudes Scale	25.31	6.19	6	39
SWAN	−21.64	9.68	−74	43
SWAN inattentive subscale	−6.22	9.09	−24	21
SWAN hyperactive subscale	−7.38	9.68	−27	15

Age statistics are reported for the whole sample (N = 64). For the remaining measures statistics are reported for the number of participants it was available for. BVPS, British vocabulary picture scale; SAS, Social Aptitudes Scale; SWAN, Strengths and Weaknesses of ADHD Symptoms and Normal Behavior Scale. Higher SWAN scores indicate more inattention and hyperactivity.

was conducted in accordance with the ethical standards of the Declaration of Helsinki.

Experimental Setup

Children knelt or sat on a chair to allow them to view their hands when placed on the work surface of the MIRAGE mediated reality device (Newport et al., 2010). The MIRAGE uses a rectangular horizontal mirror, suspended equidistant between the worksurface below and a computer screen above, to reflect live camera images of the hands displayed on the computer screen. These appear in the same physical location as the real hands with a minimal delay (∼16 ms) (see **Figure 1**), thus giving the child the impression that they were viewing their own hand, in its real location, in real time.

A black bib attached across the length of the mirror was tied comfortably around the participant's shoulders to obscure a direct view of their upper arm. At the start of the task, a glove tip was placed on the child's right index finger. This was referred to as "the finger with the hat on" so that there could be no confusion about which finger was being referred to during the experiment.

Procedure

The basic task required children to make judgments about the location of their seen or unseen finger by verbally directing an arrow to be in line with their index finger after exposure to congruent or incongruent visuo-proprioceptive sensory input about the location of the hand. All participants were tested individually and took part in three conditions completed in the following order: congruent with vision of the hands (congruent seen; included to verify children understood the task and were competent in making verbal judgments of their hand position), congruent without vision (congruent unseen) and incongruent without vision (incongruent unseen). This particular order of conditions was important to ensure children were familiar with the MIRAGE system and understood how to judge the position of their hand before taking part in the more challenging incongruent condition.

In the two congruent conditions, the participant placed his or her hands on the worksurface of MIRAGE and watched as the experimenter moved their hands to a specified position. Both the left and right seen hands were in the same location as the real left and right hands, respectively. In the incongruent condition, before the experimenter placed the participant's hands on the worksurface the individual took part in a visual adaptation procedure. The participant placed his or her hands in MIRAGE and held them approximately 5 cm above the workspace and were instructed to not touch blue bars which could be seen to box in each hand to the left and right (see **Figure 1**). The blue bars were graphically superimposed on the visual workspace and expanded slowly over the course of 25 s so as to constrict the space in which the hands could be positioned. During this period the spatial relationship between the seen location of the right hand and its real location was manipulated using an adaptation procedure modified from Newport and Gilpin (2011) and similar to that used in Bellan et al. (2015). This was achieved by moving the image of the right hand smoothly and incrementally leftwards at a rate of 4.5 mm/s. Thus, in order to keep the right hand in the same visual location the participant had to move their hand rightwards at the same rate with the result that after 25 s the seen hand was viewed 11.25 cm to the left of its true location. During the same period, the visual image of the left hand oscillated slowly leftwards and rightwards at an average velocity of 4.5 mm/s but ended up in the same location as it had started (i.e., with the seen left hand in the same location as the real left hand). This oscillation was included so that the movement of the image relative to the hand, and the tracking of that movement by the real hand, was equivalent across both hands. It is very rare for people to notice the movement of either hand relative to its seen image and conscious awareness of this has never been observed under experimental conditions (see Newport and Gilpin, 2011; Bellan et al., 2015). Once the adaptation procedure was complete, the participant's hands were placed back down onto the worksurface of MIRAGE prior to them making judgments about the position of their right index finger.

After this initial period, the participant's hands either remained visible (in the congruent seen condition) or were immediately occluded by replacing the visual scene with a blank image (in the congruent unseen and incongruent unseen conditions). Thus, the participant could either: see and feel the location of the hand simultaneously (congruent seen), only feel the location of the hand (congruent unseen) or feel the location of the hand having previously seen it in an incongruent location (incongruent unseen). The participant then estimated the location of the right index finger using the following procedure. For location judgments, the participants saw a red arrow (reflected from the computer screen above) traveling laterally across the MIRAGE workspace where his or her hands were located and said "Stop" when they thought that the arrow was directly in line with the finger wearing the hat (the right index finger). This would prompt the experimenter to immediately release a button on the computer keyboard immediately stopping the arrow from moving. The position of the arrow was then recorded in pixels along the x-axis. Each measurement was taken twice for each condition, once with the arrow traveling from right to left and once from left to right (order counterbalanced across conditions and participants). In all conditions, the hands were resting on the worksurface of the MIRAGE throughout the duration of the judgment task. The total duration of the

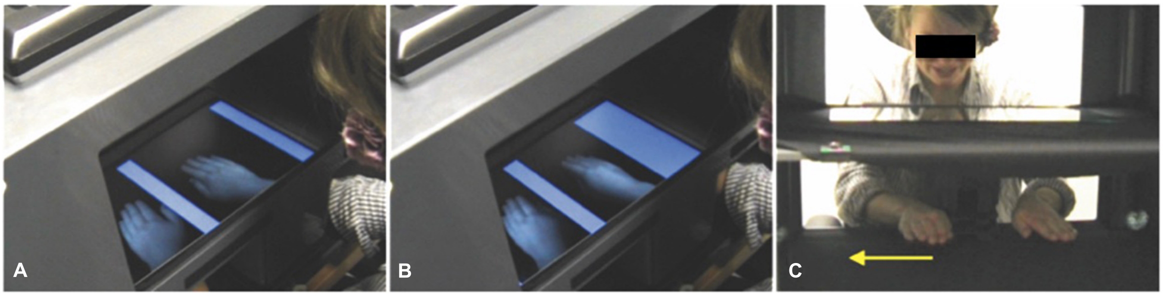

FIGURE 1 | (A) At the start of the adaptation procedure, the seen location of the right hand matches its real location (note the alignment of the seen right hand and participant's real arm). **(B)** Over the course of the adaptation procedure, the superimposed blue bars slowly expand to constrict the hand space. At the same time and without the participant's awareness, the image of the right hand is shifted slowly leftwards so that in order to keep the hand visible between the blue bars, the participant must move their hand rightwards. This results in a separation between the seen and real location of the right hand (note the misalignment of the seen right hand and the participant's real arm). In the actual experiment, a bib occluded the participant's view of their arms. **(C)** The MIRAGE worksurface and participant's hands from the experimenter's viewpoint. The yellow arrow indicates the direction in which the right hand moves during the adaptation procedure. See electronic Supplementary Material 1 of Bellan et al. (2015) for a video of the MIRAGE adaptation procedure (incongruent condition).

experiment, including set-up and explanation of the task, was approximately 10 min.

Statistical Analysis

Localization error scores were calculated for each participant for each of the three conditions in the following way. For each trial the *x*-axis co-ordinate of the position of the tip of the right index finger was recorded in pixels (100 units equates to 7.5 cm). For each condition, the average of the two estimates of finger position was calculated and subtracted from the actual finger position to give an estimate of localization error. A score of zero would represent a completely accurate estimate of hand location. Positive values indicated estimates to the right of the actual finger location and negative values indicated estimates to the left (i.e., closer to the midline). In the incongruent unseen condition, the hand was seen 11.25 cm to the left of the real location; thus, a score of zero in this condition would represent total reliance on proprioception, a score of −11.25 would represent total reliance on vision. Scores in between these values indicate the level of weighting given to proprioception and vision, respectively, with −5.625 having equal weighting.

A developmental trajectory analysis was conducted to address the main research questions which involved two steps. Firstly, the within-subjects effect of condition on localization error was explored using a one-way repeated measures ANOVA. This allowed us to directly investigate the influence of incongruent visual information on proprioception in comparison to conditions when visual and proprioceptive information are congruent. Next to assess developmental change in localization error and importantly how it interacts with performance on the different conditions the analysis was re-run as an ANCOVA with rescaled age entered as a covariate in accordance with a developmental trajectory approach (Thomas et al., 2009). Investigating the main effect of condition separately from the condition by age interaction is recommended (Thomas et al., 2009) because the addition of a covariate changes the main effect of the within-subjects factor leading to an overly conservative estimate of the effect (Delaney and Maxwell, 1981).

In addition to our main analyses, further regressions were carried out to explore secondary questions in regards to other factors that might influence performance based on previous research. As previous research (King et al., 2010) found a positive relationship between proprioceptive accuracy and weighting of proprioceptive inputs over and above the effect of age a regression analysis was conducted. This analysis was only carried out on the congruent unseen condition which gave an estimate of baseline proprioceptive accuracy and the incongruent unseen error which measured proprioceptive weighting. Specifically, a hierarchical regression model was used to control for age effects on performance by entering it at the first step so the relationship between proprioceptive accuracy and proprioceptive weighting could be explored independently. A second hierarchical regression was also conducted to explore whether general attentional skills (as measured by the SWAN) and social skills (as measures by the SAS) influenced localization accuracy on the incongruent unseen condition. Age and congruent unseen scores were entered at the first step, with SWAN and SAS scores entered at the next step.

RESULTS

Figure 2 shows performance in each condition across the whole sample. The one-way repeated measures ANOVA revealed a main effect of condition on localization error, $F(1, 63) = 151.70$, $p < 0.001$, $\eta_p^2 = 0.716$. Pairwise comparisons (Sidak adjustment for multiple comparisons) revealed no significant difference in accuracy between the congruent seen and congruent unseen conditions ($p = 0.159$) but significant differences were found when incongruent unseen was compared to the congruent seen and congruent unseen conditions (both $p < 0.001$). Children were highly accurate at locating their index finger when congruent visual and proprioceptive information was available, indicating that they all understood the task. Accuracy

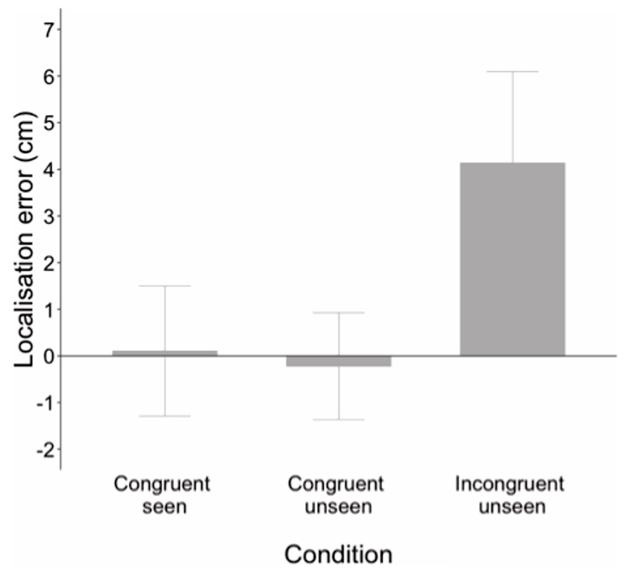

FIGURE 2 | Localization error in cm for each condition across the whole sample. Positive values represent mislocalization to the left of the real hand; negative values represent error to the right of the real hand. Error is low in both congruent conditions, but significantly increased when visual and proprioceptive inputs were incongruent. Error bars ± 1 SD.

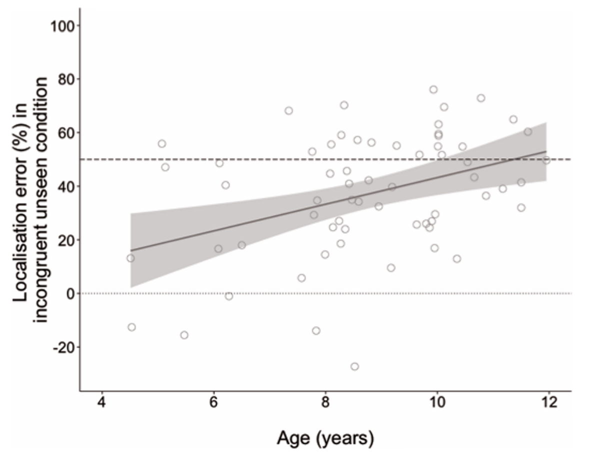

FIGURE 3 | Localization error as a percentage of distance between seen and actual hand locations in the incongruent unseen condition in which the seen and real hands were in different locations. The dashed line at 50% indicates equal weighting of vision and proprioception; the dotted line at zero indicates complete reliance on proprioception. Negative values indicate estimates beyond the real hand location. Shaded region shows 95% confidence interval.

remained high in the congruent unseen condition, when only proprioceptive inputs were present at judgment. However, as predicted, accuracy was significantly reduced in the incongruent condition compared to both congruent conditions.

An ANCOVA was performed entering age as a covariate to compare developmental change in localization error between conditions. This analysis revealed a main effect of age, $F(1, 62) = 7.64$, $p = 0.007$, $\eta_p^2 = 0.110$, but also a significant condition by age interaction, $F(1, 62) = 12.77$, $p = 0.001$, $\eta_p^2 = 0.171$. Parameter estimates showed that age did not predict performance in the congruent seen, $B = -0.004$, $t(62) = 1.64$, $p = 0.106$, or congruent unseen conditions, $B = -0.008$, $t(62) = -1.11$, $p = 0.272$. However, age was a significant predictor of performance in the incongruent unseen condition, $B = -0.046$, $t(62) = -3.34$, $p = 0.001$. As age increased, localization estimates were increasingly further from the actual hand and closer to the seen hand. Age explained 15% of the variance in accuracy scores in the incongruent unseen condition ($R^2 = 0.153$). **Figure 3** displays the developmental trajectory for this condition, with localization error converted into a percentage of the distance between the seen and actual hand locations to demonstrate how the weighting of vision and proprioception changed with age.

Regression Analyses

A hierarchical regression was conducted with age (in months) entered at the first step and congruent unseen error (absolute value) entered next as a predictor with incongruent unseen error (i.e., percentage of distance between seen and unseen hand) as the outcome variable. Congruent unseen error was not a significant predictor of accuracy in the incongruent unseen condition, $B = -5.63$, $t(62) = -1.54$, $p = 0.129$.

To investigate whether general attentional or social skills predicted accuracy (i.e., error as distance percentage) of estimates in the incongruent unseen condition, age and congruent unseen accuracy scores were added as predictors into the first block of a hierarchical regression model, with SAS and SWAN inattentive subscale scores entered in the second block. Seven participants (10.94%) were excluded from the regression due to list-wise missing data across measures. Neither SAS [$B = 0.48$, $t(59) = 0.84$, $p = 0.40$] or SWAN [$B = 0.13$ $t(59) = 0.93$, $p = 0.36$] scores predicted localization error on the incongruent unseen condition.

DISCUSSION

The present study investigated the relative contributions of visual and proprioceptive inputs on the development of body localization in primary school-aged children. When given incongruent visual and proprioceptive information about the location of the hand, younger children (<10 years) favored proprioceptive input more than older children who weighted vision and proprioception more equally. The developmental trajectory for multisensory integration in this task was not affected by variability in social skills or inattention.

As expected, all children were highly accurate in locating the finger in the congruent seen condition (see **Figure 2**), indicating that they understood the task and could easily indicate the location of their seen hand by 4 years of age. Children's estimates were also accurate in the congruent unseen condition, when congruent vision of the hand had been removed and only proprioceptive information was available. Again, performance did not improve with age suggesting that younger children are equally good at using proprioceptive information as older children to localize the hand when this is not aided by visual inputs. One might argue that in the congruent unseen condition visual information about the location of the target had recently been available so it is possible that children could have used a memorial representation, or visual trace, of the hand's visual location in this condition. However, if this were the case then we would have also found visual anchoring in performance on the incongruent unseen condition, but instead location estimates were in between the seen and real location of the hand. Furthermore, estimates for younger children were shifted more toward the proprioceptive (true) location. Younger children appeared to rely more on proprioception to locate their unseen finger while older children weighted visual inputs more strongly. The nature of this sensory integration was not related to proprioceptive accuracy in the congruent unseen condition and did not appear to be influenced by variability in social aptitude or inattention.

It is interesting that these results appear to contradict previous research that observed greater weighting of visual over proprioceptive information in early childhood. For instance, in the hand localization task conducted by King et al. (2010) it was found that older children upweighted proprioceptive information (i.e., actual finger location) more than younger children. Although the discrepancy between visual and proprioceptive information was smaller in King et al. (2010), the abrupt onset of the incongruent visual indicator (i.e., a target circle) in a different location than the proprioceptive target (i.e., unseen finger) may have made the disparity more salient. Thus, older children may have actively discounted the visual information and instead favored the more reliable proprioceptive information. In the current study, by contrast, the separation of visual and proprioceptive information was gradual and constant during the adaptation process allowing hand location to be recalibrated without reaching conscious awareness. Secondly, the nature of the visual information in the current study, being a live image of the participant's own hand, was much more likely to be embodied as pertaining to the body than a target circle representing finger location in King et al.'s (2010) study. In everyday life, visual cues of limb localization originate from vision (and proprioception) of the body rather than from visual targets signaling body position. This argument is supported by research which has shown body ownership of a virtual hand is stronger for images that look more like one's actual hand (Ratcliffe and Newport, 2017; Pyasik et al., 2020). Thus, the current experimental conditions were perhaps more likely to induce sensory integration of signals related to the body due to the use of a virtual image of the participant's own hand.

Nonetheless, the current results also contrast with other research findings where an image of a hand was used as the visual representation. A stronger reliance on vision in younger children was observed by Bremner et al. (2013) in a task requiring a visually driven response under conditions of visuo-proprioceptive conflict. Visual and proprioceptive information about the limb were placed in conflict by reflecting the left hand in a mirror located asymmetrically between the hands so that it appeared (visually) to be the right hand but was not in the same physical location as the real right hand (which was hidden behind the mirror). The task involved pointing to a visual target with the unseen hand while the reflected left hand was in view and, presumably, perceived to be the right hand due to the nature of the illusion. Vision dominated (or captured) subsequent processing of limb position with children tending to point from the seen position of the hand rather than the felt position. Since the task necessitated visually guided reaches with the seen (albeit incorrectly positioned) hand to a visual target, this was a primarily visual-driven task and, as such, vision might be expected to dominate. The current task conducted in MIRAGE by comparison was primarily proprioceptive in nature (verbally guiding an arrow to the felt location of the unseen hand). If vision and proprioception are not integrated effectively at a young age, but instead are either processed independently or are treated such that one sense is strongly dominant over the other, then a task which favors the processing of proprioceptive inputs might produce outcomes with a strong proprioceptive bias. Under this hypothesis, children are still integrating information probabilistically, as suggested by King et al. (2010), but the weighting of sensory information is heavily influenced by the development of multisensory integration abilities rather than (or as well as) the development of unisensory capabilities. Importantly, an immature development of this integration process, could lead to a bias in processing either visual, proprioception, or another sensory input depending on which is the most salient in a given task.

In a previous study using a similar task in adults, Bellan et al. (2015) found that localization errors in the incongruent condition were consistent with a bias toward visual information, which was given a weighting of approximately 60%. In the current study, the performance of the older children was approaching this adult benchmark, with 10–11-year-olds (n = 18) judging the real hand to be ~50% of the distance to the seen hand. By contrast the youngest children, 4–6-year-olds (n = 11), judged the distance at less than 30% toward the seen hand. We contend, therefore, that the results of this experiment demonstrate that visuo-proprioceptive integration develops throughout childhood from very little integration at 4 years to almost adult-like at 11.

In the current study, the three conditions were presented to participants in a fixed order—congruent seen, congruent unseen and incongruent unseen. This was done to ensure that the children understood the task and were able to complete the non-illusory conditions first before completing the critical illusory trials (incongruent unseen). It is important to note that children were not given any feedback about their accuracy so as not to influence their performance in the subsequent conditions. The duration of the experiment was relatively short, taking a total of less than 10 min. Therefore, it is unlikely the age-related differences observed in the incongruent unseen condition are due to fatigue; if this were the case, we would expect the performance of younger children to be random. However, the results indicate a systematic difference in the way in which younger children integrate visual and proprioceptive inputs, with a clear developmental trend in performance on this task.

The experiment only measured localization of the right hand, which was the dominant hand for the majority of children in this sample. In future work, it might be interesting to investigate whether similar effects are observed for localization of the non-dominant hand. Studies have found an attentional bias for the dominant side of space (Rubichi and Nicoletti, 2006), which could have an effect on the extent to which visual information is prioritized during integration during body localization.

In summary, developmental trajectory analysis of a hand localization task in primary school age children suggests that while localization of the seen and unseen hand in children is consistently good, when visual and proprioceptive input are incongruent, localization estimates reveal differences in the integration of multisensory information related to the body which younger children appear to integrate less optimally than older children.

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 School of Psychology Ethics Committee at the University of Nottingham. Written informed consent to participate in this study was provided by the participants' legal guardian/next of kin. Written informed consent was obtained from the individual(s) for the publication of any potentially identifiable images or data included in this article.

AUTHOR CONTRIBUTIONS

NR, KG, DR, and RN developed and planned the study. NR, KG, and EH collected data. NR and KG analyzed the data and wrote the first draft of the manuscript. NR, KG, EH, DR, and RN edited and developed the manuscript. All authors contributed to the article and approved the submitted version.

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Body Ownership of Anatomically Implausible Hands in Virtual Reality

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Manipulating sensory and motor cues can cause an illusionary perception of ownership of a fake body part. Presumably, the illusion can work as long as the false body part's position and appearance are anatomically plausible. Here, we introduce an illusion that challenges past assumptions on body ownership. We used virtual reality to switch and mirror participants' views of their hands. When a participant moves their physical hand, they see the incongruent virtual hand moving. The result is an anatomically implausible configuration of the fake hand. Despite the hand switch, participants reported significant body ownership sensations over the virtual hands. In the first between-group experiment, we found that the strength of body ownership over the incongruent hands was similar to that of congruent hands. Whereas, in the second within-group experiment, anatomical incongruency significantly decreased body ownership. Still, participants reported significant body ownership sensations of the switched hands. Curiously, we found that perceived levels of agency mediate the effect of anatomical congruency on body ownership. These findings offer a fresh perspective on the relationship between anatomical plausibility and assumed body ownership. We propose that goal-directed and purposeful actions can override anatomical plausibility constraints and discuss this in the context of the immersive properties of virtual reality.

Keywords: body ownership, virtual reality, body representation, visuomotor interaction, anatomical plausibility, volition, immersive virtual reality

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INTRODUCTION

Our body is the source of our experienced sensations and the target of our voluntary actions. Its character is possessive, and we perceive it as our own through self-attribution (Gallagher, 2000; Tsakiris et al., 2006). This phenomenon, termed body ownership, can extend beyond our physical self. For example, synchronous stroking of a hidden hand and a visible rubber hand creates an ownership illusion of the fake hand (Botvinick and Cohen, 1998). These illusions manipulate sensory and motor cues to prompt ownership of artificial bodies, like mannequins (Botvinick and Cohen, 1998; Ehrsson et al., 2004, 2007; Tsakiris and Haggard, 2005; Tsakiris et al., 2006; Lloyd, 2007; Petkova and Ehrsson, 2008; Dummer et al., 2009; Guterstam et al., 2011; Kalckert and Ehrsson, 2012, 2014; Ide, 2013; Erro et al., 2020) or virtual avatars (Petkova and Ehrsson, 2008; Slater et al., 2009, 2010; Sanchez-Vives et al., 2010; Yuan and Steed, 2010; Kilteni et al., 2012; Won et al., 2015). In particular, they show that we can take ownership of a fake body that is in a different spatial location than our body (Botvinick and Cohen, 1998; Ehrsson et al., 2004, 2007; Blanke and Mohr, 2005; Tsakiris and Haggard, 2005; Lloyd, 2007; Riva et al., 2007; Petkova and Ehrsson, 2008; Dummer et al., 2009; Guterstam et al., 2011; Kalckert and Ehrsson, 2012, 2014; Ide, 2013; Kilteni et al., 2015; Erro et al., 2020). The illusion is possible so long as the location and orientation of the fake body part are anatomically plausible (Kilteni et al., 2015). Applying a rotation to the false body part in an anatomically implausible configuration, such as rotating the hand 180°, reduces the illusory experience (Ehrsson et al., 2004; Kalckert and Ehrsson, 2012; Ide, 2013). There is a significant drop in sensations of ownership when the location of the fake body part is far from the real body part (Lloyd, 2007; Sanchez-Vives et al., 2010; Erro et al., 2020) and beyond its anatomical reach. Last, the illusion does not occur with an anatomically incongruent fake body part (Graziano et al., 2000; Tsakiris and Haggard, 2005; e.g., a fake right-hand in a left-hand illusion), which defies the anatomical configuration of the joints.

Yet, participants in these RHI studies had limited interaction with their external environment. The experiments use passive touch (Tsakiris and Haggard, 2005; Lloyd, 2007; Guterstam et al., 2011; Ide, 2013; Kalckert and Ehrsson, 2014; Erro et al., 2020) or restrict actions to a narrow range of predetermined movements (Kalckert and Ehrsson, 2014) such as finger tapping with little goal-direct movement. These interactions consist of a narrow set of sensorimotor cues compared to the complex ways we use our body and take ownership of it. Although the RHI provides an easy and replicable way to study body ownership, there is a need for an ecological and realistic environment to examine anatomical plausibility constraints. In the current study, we use immersive virtual reality to challenge previous assumptions on anatomical plausibility. We chose virtual reality to precisely manipulate the illusion and control experimental conditions in a way that would hardly be possible in real life (Bohil et al., 2011).

In the virtual environment, hand movements were visually switched and mirrored. Hand movements result in visual feedback of the other hand's analogous movements (**Figure 1**). We thus applied three anatomically implausible transformations to the fake hands—their location constantly changes and can be far from the real hands (distance constraint), they are at a wide-angle to the real hands (angle constraint), and their physical attributes are incongruent with the real hands (anatomical incongruency constraint). We developed two interactive playing scenarios where participants use their switched hands to hit and lift virtual balls in an office-like setting (**Figure 1**). In experiment 1, one group of participants performed the scenarios while their real hands were incongruent with the virtual hands. Another group participated in the same experiment while their real hands were congruent with the virtual hands. After the virtual reality, participants from both groups completed a questionnaire on their subjective sense of body ownership, agency, and self-location (Gonzalez-Franco and Peck, 2018). In experiment two, participants performed both the incongruent and congruent conditions (in random order). Participants answered the questionnaire at the end of each condition. We hypothesize that purposeful tasks in an immersive setting would increase the level of ownership towards the virtual avatar (Slater et al., 2009; Sanchez-Vives et al., 2010; Yuan and Steed, 2010; Won et al., 2015) even when there are vast anatomical discrepancies between the real and fake hands (Slater et al., 2010; Feuchtner and Müller, 2017). We further predict that sensations of ownership and agency will not depend on the perceived location of the avatar, similarly to previous studies (Kilteni et al., 2015; Gonzalez-Franco and Peck, 2018). In addition, such a result would demonstrate that the fake hand's location does not have to follow strict anatomical constraints, as previously assumed (Kilteni et al., 2015).

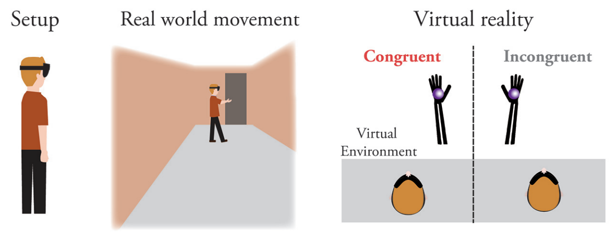

FIGURE 1 | Experimental setup and virtual environment. Participants wear a head-mounted display with a sensor that tracks both hands. They can move freely within the room, using their hands to play with a virtual ball (right hand in the figure). In virtual reality, the avatar hands can be congruent with the real hands or switched and incongruent. The figure on the right shows the virtual display of a participant's right arm in congruent and incongruent conditions. In each experimental condition, both hands were either congruent or incongruent.

MATERIALS AND METHODS

Participants

A total of 49 healthy participants took part in experiment 1 (age 28.2 ± 7.2, average and standard deviation; 30 females; 49 right-hand dominants); 29 performed the virtual reality incongruent condition with switched hands, the other 20 performed the congruent condition (**Figure 1**). Another 20 more participants took part in experiment 2 (age 27.1 ± 5.4, average and standard deviation; six females; 20 right-hand dominants). We counterbalanced the condition order in experiment 2, with 10 participants starting with the congruent condition and 10 with the incongruent condition. All participants reported normal or corrected-to-normal vision with no known neurological deficits.

Materials

We developed the virtual environment using the Unity 3D engine (Unity Technologies). We used the VIVE Pro head-mounted display (HTC Corporation) to convey the virtual environment (**Figure 1**) and a LeapMotion sensor (Ultrahaptics) to track participants' hand gestures. To switch participants' hands, we developed a real-time algorithm that receives the hands' location from the sensor, transposes the hands' coordinates, and displays the transposed figures as avatars. All the visual assets in VR are of our creation and made for this study.

Procedure

We first instructed participants about the experiment and informed them, if needed, about the incongruent condition. The virtual environment is a 2.5 by 3 meters virtual office space with an 'r-shaped' desk and a blue curtain. In the congruent condition, participants view a virtual representation of their hands that overlaps with their real hands. In the incongruent condition, we switched participants' hands. When participants move their hands, they see the opposite virtual hand moving (**Figure 1**). Participants in experiment 1 completed one condition, while participants in experiment 2 completed two conditions. Each condition includes two consecutive scenarios—(a) A bowl stands in the middle of the virtual desk with a single ball on each side. In each trial, the participant picks up a ball with one hand and places it in the bowl. In experiment 1, the scenario ends when the participant completes 16 successful tries or 5 min have elapsed. In experiment 2, the scenario ends after 3 min; (b) We remove the bowl while two balls remain on the desk. In each trial, the participant tries to push a ball off the desk following an auditory cue. The cue consists of instructions on which virtual hand to use (left or right) and the proceeding action (push the right or left ball). The scenario includes 40 trials in experiment 1 and 20 trials in experiment 2. The trials were equally divided between the four hand and ball combinations, with an inter-stimulus interval of 15 s. We consistently instructed participants to keep their hands separate to cut contradicting tactile and visual information, but otherwise, move freely within the space (**Figure 1**).

Questionnaire

At the experiment conclusion, participants complete a questionnaire (Gonzalez-Franco and Peck, 2018) on their subjective sense of ownership (three questions), agency (four questions), and self-location (two questions). The questionnaire is particularly for VR experiments and builds on previous questions that appear in the literature. Participants scores each statement on a 7-point Likert scale that ranges from–3 ("strongly disagree) to 3 ("strongly agree"). Participants in experiment 2 filled the questionnaire twice, once at the end of each condition. A full description of the statements and ratings appears in **Supplementary Table S1**.

Statistical Analyses

We summarized participants' responses to a single score for ownership, self-location, and agency (**Supplementary Table S2**). Following on similar studies (Ehrsson et al., 2007; Petkova and Ehrsson, 2008; Guterstam et al., 2011; Kalckert and Ehrsson, 2012, 2014; Kilteni et al., 2012), we interpreted a group result as meaningful if the median score was equal to or higher than 1. We then conducted a one-way Wilcoxon-signed rank test on the median score. In experiment 1, we used a two-way Wilcoxson rank-sum test to analyze group differences in each category. We also used a two-way ANOVA to calculate the interaction effect of a category within-factor and a group between-factor (**Supplementary Tables S3–S5**). In experiment 2, we used a paired Wilcoxson signed-rank test to analyze the differences in questionnaire ratings between the congruent and incongruent conditions. We used a two-way ANOVA with a category within-factor and a condition within-factor (**Supplementary Tables S6–S8**). We then examined the effect of condition order (congruent first or incongruent first) on each category rating with a within-factor of condition and a between-factor of order (**Supplementary Tables S9–S11**). In both experiments, we calculated the Person correlation between body-ownership ratings and the other categories. We also conducted a mediation analysis to examine if sensations of agency or self-location mediate the effects of condition on body ownership (see **Supplementary Table S12 and Supplementary Figure S1** for full details). All the statistical analyses included Bayes Factors inference calculations (Liang et al., 2008; Rouder et al., 2012; Faulkenberry, 2021). A Bayes Factor score below 3 is inconclusive, over 10 is strong, and over 100 is decisive (Lee and Wagenmakers, 2014). We conducted all the analyses using the MATLAB software (MathWorks), statistical tests were double-sided and corrected for multiple comparisons using False Discovery Rate (α = 0.05). Where the correction deemed the score insignificant, we also added a corrected p-value. Effect sizes in the Wilcoxon tests are Cliff's Delta and Theta square in the ANOVA tests.

RESULTS

Participants Report Ownership and Agency of Switched Hands

We first analyzed the questionnaire ratings on ownership and agency (**Figure 2**). Experiment 1. Participants in the congruent group (n = 20) reported a strong sense of body ownership (M = 2 ± 0.21, p < 0.001, W = 210, δ = 1, BF10 > 100) and agency (M = 2 ± 0.26, p < 0.001, W = 184.5, δ = 0.85, BF10 = 52.9). We further found high ratings in the incongruent group (n = 29) for ownership (M = 2 ± 0.21, p < 0.001, W = 362, δ = 0.79, BF10 > 100) and agency (M = 1.5 ± 0.22, p < 0.001, W = 407.5, δ = 0.86, BF10 > 100). The rank-sum test showed no significant group differences that survived correction for multiple comparisons, neither for ownership (Z = 2.14, p = 0.034, W = 604, δ = 0.36, adjusted p = 0.102) nor agency scores (Z = 1.12, p = 0.262, W = 555.5, δ = 0.19). The Bayes Factors analysis further confirmed the group null results for agency ratings (BF10 = 0.24) and was inconclusive for ownership ratings (BF10 = 1.99). We next conducted an ANOVA test on the questionnaire scores with a with-in factor of the category (agency and ownership) and a between-factor of the group to compute an interaction effect on the factors (**Supplementary Table S5**). The interaction between the factors was insignificant ($F_{(1, 94)}$ = 0.49, p = 0.488, η^2 < 0.01, BF10 = 0.13), which indicates that switching hands did not alter the difference between agency and ownership (**Figure 2A**). Experiment 2. The within-group study (n = 20) replicated the main results from experiment 1 (**Figure 2B**). In the congruent condition, participants had a strong sense of ownership (M = 2.17 ± 0.15, p < 0.001, W = 210, δ = 1, BF10 > 100) and agency (M = 1.67 ± 0.19, p < 0.001, W = 210, δ = 1, BF10 >100). The ratings in the incongruent condition were also strong for ownership (M = 1.33 ± 0.21, p < 0.001, W = 165.5, δ = 0.8, BF10 = 31.6) and agency (M = 1 ± 0.19, p < 0.001,

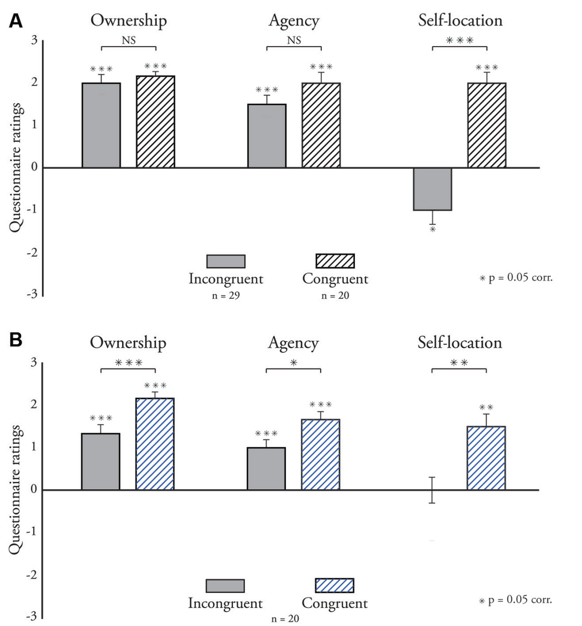

FIGURE 2 | Median questionnaire ratings. **(A)** Experiment 1. We compared questionnaire ratings between the incongruent (n = 29) and congruent (n = 20) groups on body ownership, agency, and self-location. **(B)** Experiment 2. We measured and compared participants' ratings of body ownership, agency, and self-location in the congruent and incongruent conditions (n = 20). Error bars indicate the standard error. *$p < 0.05$; **$p < 0.005$; ***$p < 0.0005$; NS, Not Significant.

W = 169, δ = 0.8, BF10 = 58.6). Unlike experiment 1, we found significant differences between the congruent and incongruent conditions on ownership ratings (Z = 3.56, $p < 0.001$, W = 167, δ = 0.56, BF10 > 100) and agency ratings (Z = 2.69, p = 0.007, W = 147, δ = 0.38, BF10 = 10.7). Like experiment 1, an ANOVA analysis with two with-in factors of category and condition (**Supplementary Table S8**) showed no significant interaction on the factors ($F_{(1, 76)}$ = 0.71, p = 0.401, $\eta^2 < 0.01$, BF10 = 0.43).

Virtual Switched Hands Are Not Perceived as Collocated With Real Hands

We analyzed participants' reports on the self-location of the avatar in comparison to their real hands (**Figure 2**). Experiment 1. Participants in the congruent group (**Figure 2A**) reported that the virtual hands' position corresponded to the location of their real hands in space ($M = 2 \pm 0.26$, $p < 0.001$, W = 186, δ = 0.75, BF10 = 63.9). In contrast, participants in the incongruent group (**Figure 2A**) perceived that the virtual hands' location did not correspond with their real hands ($M = -1 \pm 0.34$, p = 0.015, W = 73.5, δ = −0.31, BF10 = 3.2). An analysis of group differences shows that location ratings were higher in the congruent group (Z = 4.57, $p < 0.001$, W = 723, δ = 0.77, BF10 > 100). We performed an ANOVA to observe the interaction effect of condition with category ratings of self-location and ownership, or self-location and agency (**Supplementary Tables S3, S4**). There was a significant interaction effect of self-location with the agency ($F_{(1, 94)}$ = 17.11, $p < 0.001$, η^2 = 0.11, BF10 > 100) and self-location with body ownership ($F_{(1, 94)}$ = 15.06, $p < 0.001$, η^2 = 0.08, BF10 > 100). Experiment 2. Self-location ratings in the within-group experiment corroborated the results of experiment 1 (**Figure 2B**). In the congruent condition, participants had a strong sense of self-location ($M = 0 \pm 0.31$, p = 0.869, W = 49.5, δ = 0.1, BF10 = 0.43), while self-location ratings in the incongruent condition were weak ($M = 1.5 \pm 0.3$, p = 0.001, W = 158, δ = 0.5, BF10 = 19). A paired analysis showed higher self-location ratings in the congruent condition (Z = 3.26, p = 0.001, W = 160, δ = 0.5, BF10 > 100). Unlike experiment 1, the ANOVA analyses (**Supplementary Tables S6, S7**) did not show significant interaction effects on ratings of self-location with the agency ($F_{(1, 76)}$ = 2.61, p = 0.111, η^2 = 0.02, BF10 = 0.43) and self-location with ownership ($F_{(1, 76)}$ = 0.99, p = 0.324, η^2 = 0.01, BF10 = 0.16).

Condition Order Did Not Affect Ratings of Ownership, Agency, or Self-location

Experiment 2. We explored the effects of starting the experiment in the congruent (n = 10) or incongruent (n = 10) condition on questionnaire ratings. We conducted a three two-way ANOVA (**Supplementary Tables S9–S11**), one for each category rating, with a within-factor of condition (congruent/incongruent) and a between-factor of order (congruent first/incongruent first). The results were not significant for the main effect of condition order in self-location ratings ($F_{(1, 36)}$ = 0.01, p = 0.91, $\eta^2 < 0.01$, BF10 = 0.16), agency ($F_{(1, 36)}$ = 0.46, p = 0.503, η^2 = 0.01, BF10 = 0.2), and body ownership ($F_{(1, 36)}$ = 0.25, p = 0.623, $\eta^2 < 0.01$, BF10 = 0.18). We also did not find any interaction effects on the factors for self-location ($F_{(1, 36)}$ = 0.12, p = 0.735, $\eta^2 < 0.01$, BF10 = 0.17), agency ($F_{(1, 36)}$ = 1.09, p = 0.303, η^2 = 0.03, BF10 = 0.29), or ownership ($F_{(1, 36)}$ = 0.02, p = 0.902, $\eta^2 < 0.01$, BF10 = 0.16).

Switched Hands' Effect on Body Ownership Is Mediated by Agency, but Not by Self-location

Experiment 1. Self-location did not correlate with ownership in the congruent group (R = 0.17, Z = 0.7, p = 0.486, BF10 = 0.22) nor the incongruent group (R = −0.19, Z = 0.96, p = 0.335, BF10 = 0.22). Agency and ownership did not correlate in the congruent group (R = 0.21, Z = 0.9, p = 0.375, BF10 = 0.25) but correlated in the incongruent group (R = 0.6, Z = 3.44, $p < 0.001$, BF10 = 50.96). We found that the condition can affect body ownership ratings ($t(\beta_1)$ = 2.38, $p(\beta_1)$ = 0.021, R^2 = 0.11, BF10 = 1.55). But, the agency does not mediate the effect (**Supplementary Table S13**), nor is the effect mediated by self-location (**Supplementary Table S14**). *Experiment 2*. Self-location correlated with ownership in the congruent condition (R = 0.57, Z = 2.6, p = 0.009, BF10 = 4.87) but did not in the incongruent condition (R = −0.01, Z = 0.1, p = 0.921, BF10 = 0.17). Agency did not correlate with ownership in the congruent condition (R = 0.362, Z = 1.57, p = 0.117, BF10 = 0.58) nor the incongruent condition (R = 0.39, Z = 1.72, p = 0.086, BF10 = 0.74). In the mediation analysis, we found that condition affects body ownership ratings ($t(\beta_1)$ = 3.42, $p(\beta_1)$ = 0.002, R^2 = 0.24, BF10 = 18.28). Self-location does not mediate the effect (**Supplementary Table S16**), but the effect is partially mediated by the agency (**Supplementary Table S15**). When controlling for condition (β_1), agency (β_2) still showed a significant effect on body ownership ($t(\beta_1) = 2.62$, $p(\beta_1) = 0.013$, $t(\beta_2) = 2.47$, $p(\beta_1) = 0.018$, $R^2 = 0.31$, BF10 = 19.01).

DISCUSSION

The current study explored the anatomical plausibility constraints of body ownership illusions. We used virtual reality to develop two immersive environments where participants' fake hands are incongruent or congruent with their real hands. In our between-group experiment, participants reported a strong sense of body ownership in the congruent condition, confirming the immersive properties of the virtual environment (Riva et al., 2007; Petkova and Ehrsson, 2008; Slater et al., 2009, 2010; Sanchez-Vives et al., 2010; Yuan and Steed, 2010; Kilteni et al., 2012; Kuliga et al., 2015; Feuchtner and Müller, 2017). We also found that participants in the incongruent group had a strong sense of body ownership, despite the hand switch.

We replicated these results in our within-group experiment that included condition conditions. Participants reported a strong sense of body ownership in the incongruent condition despite the fact they also experienced the congruent condition. These findings contradict previous assumptions that body ownership illusions are contingent on the anatomical plausibility of the fake body part (Graziano et al., 2000; Ehrsson et al., 2004; Tsakiris and Haggard, 2005; Lloyd, 2007; Sanchez-Vives et al., 2010; Kalckert and Ehrsson, 2012; Ide, 2013; Erro et al., 2020). Our setup forms an extreme instance of anatomical implausibility that violates its three known constraints. Participants performed manual tasks with virtual avatars of the opposite and incongruent hands (Tsakiris and Haggard, 2005) whose locations are distant from (Lloyd, 2007; Sanchez-Vives et al., 2010; Erro et al., 2020) and at an angle to their real hands (Ehrsson et al., 2004; Kalckert and Ehrsson, 2012; Ide, 2013). Contrary to a prediction of failed ownership illusion under such conditions, we found that participants report significant sensations of ownership over the anatomically implausible hands. We propose that this finding links to goal-directed tasks undertaken by our participants that resulted in increased feelings of body agency.

Agency is the sense of intending and executing actions, such as the feeling of controlling one's voluntary movements and their effects on the external environment (Tsakiris et al., 2006). The sense of agency is not uniform and includes multiple, perhaps separate, processes. For instance, we can experience agency over an external object in disassociation from our body (external agency), such as controlling an avatar in a computer game. We can also have agency over our somatic actions (body agency), like the purposeful movement of our hands (Kalckert and Ehrsson, 2012). Though agency and body ownership are somewhat disassociated (Kalckert and Ehrsson, 2012; Braun et al., 2018), this type of "body agency" can promote feelings of ownership if present (Kalckert and Ehrsson, 2012). Body agency could thus boost the sensations of body ownership our participants report in the incongruent condition. Yet, it is unclear what experimental and sensorimotor circumstances can bring about body agency rather than an external agency. Participants in previous studies on anatomical implausibility had reported low levels of body ownership coupled with high levels of agency (Tsakiris and Haggard, 2005; Lloyd, 2007; Guterstam et al., 2011; Ide, 2013; Kalckert and Ehrsson, 2014; Erro et al., 2020). The discrepancy in sensations may be due to the limited and inconsequential tasks that participants execute (Kalckert and Ehrsson, 2012). We propose that agency and ownership sensations reported in our study rest on goal-directed and meaningful actions in the form of affordances (Gibson, 1977). According to this theory, tasks of increasing complexity and unpredictability promote sensations of body ownership (Van Den Bos and Jeannerod, 2002; Kilteni et al., 2015). The complex interplay between body ownership and agency could be the subject of a future study where the manual task and its purposefulness are independent variables.

In experiment 1, we did not find any interaction between agency and body ownership ratings in the group analysis, which fits the non-significant differences in individual category ratings. On the other hand, we found that participants in experiment 2 reported weaker sensations of ownership and agency over the switched hands. Surprisingly, we again did not find any interaction on the categories when comparing between conditions. Further analysis revealed that agency mediates the effect of hand congruency on body ownership ratings. Although the virtual scenario is similar in both experiments, the context of the experience changes the relationship between agency and ownership. When participants can compare the experiences of both conditions, they report weaker sensations of agency and body ownership. A possible explanatory factor is the shortened time duration participants spent in each virtual scenario compared to experiment 1. Sensations of agency take time to emerge and follow a temporal learning curve shared by infants and adults alike (Haggard, 2017). In our case, participants might take longer to gain control over the incongruent hands that, in turn, leads to weaker sensations of ownership.

Like previous studies, we find that participants report sensations of ownership even when the fake hands are not collocated with their hands (Kilteni et al., 2015; Gonzalez-Franco and Peck, 2018). Yet, this finding contradicts the assumption that body ownership illusions are contingent on the proximity of the fake hand, which must be in reach of the physical hand (Lloyd, 2007; Sanchez-Vives et al., 2010; Erro et al., 2020). We observe that, under certain conditions, a greater distance between the real and fake hands does not cancel the perception of body ownership.

Our findings also show the capabilities of virtual reality as an effective platform to create subjective experiences that would not otherwise be possible. Virtual reality allows for detailed observations, accurate behavioral measurements, and systematic environmental manipulations under controlled laboratory conditions (Blascovich et al., 2002; Kuliga et al., 2015). More immersive systems can produce higher levels of behavioral realism (Slater et al., 2006), where the user experiences the environment as if it was part of the real world. In conclusion, the present study challenges previous assumptions and shows that body ownership illusions can extend to fake body parts that are anatomically implausible.

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 Interdisciplinary Center Herzliya (IDC), School of Psychology ethics committee. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

OY drafted the manuscript. JG, MW, DC, DF, and AA provided revisions and approved the draft for submission. The virtual environment was developed by JG, MW, and GO with help from DF. OY, MW, and DC collected the data. OY analyzed the data, interpreted the results, and produced all the figures. AA provided the funding for the study. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIALS

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BRIEF RESEARCH REPORT
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When Right Goes Left: Phantom Touch Induced by Mirror Box Procedure in Healthy Individuals

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In the present article, we investigated the possibility of inducing phantom tactile sensations in healthy individuals similar to those that we observed in patients after stroke. On the basis of previous research, we assumed that manipulating visual feedbacks may guide and influence, under certain conditions, the phenomenal experience of touch. To this aim, we used the Tactile Quadrant Stimulation (TQS) test in which subjects, in the crucial condition, must indicate whether and where they perceive a double tactile stimulation applied simultaneously in different quadrants of the two hands (asymmetrical Double Simultaneous Stimulation trial, Asym-DSS). The task was performed with the left-hand out of sight and the right-hand reflected in a mirror so that the right-hand reflected in the mirror looks like the own left-hand. We found that in the Asym-DSS trial, the vision of the right-hand reflected in the mirror and stimulated by a tactile stimulus elicited on the left-hand the sensation of having been touched in the same quadrant as the right-hand. In other words, we found in healthy subjects the same phantom touch effect that we previously found in patients. We interpreted these results as modulation of tactile representation by bottom-up (multisensory integration of stimuli coming from the right real and the right reflected hand) and possibly top-down (body ownership distortion) processing triggered by our experimental setup, unveiling bilateral representation of touch.

Keywords: tactile awareness, multisensory integration, mirror image, bilateral touch representation, body ownership and disownership

INTRODUCTION

Tactile processing is a fundamental aspect of body ownership construction. It is characterized by both operations whose product remains implicit (i.e., linked to processes that do not reach the subject's consciousness, e.g., Berti et al., 1999) and operations whose product becomes explicit and reported by the subject as conscious experience. In different domains, both in healthy participants and in brain damaged patients it has been shown that explicit (phenomenal) experience, although based on specific neural signal (Blakemore et al., 2000), can be nonetheless non-veridical. In other words, people can report experiences that are not related to actual events. For instance, in the motor domain, it has been shown that subjects can become aware of the movements they programmed and not of the action they actually performed, with vision deceiving proprioception (e.g., Fourneret and Jeannerod, 1998). Consistently with this observation, motor awareness can be reported *before* the actual execution of an action (e.g., Libet et al., 1983) and even in *absence* of any action (as in anosognosia for hemiplegia, see Pia et al., 2004; Berti et al., 2005; Berti and Pia, 2006; Garbarini et al., 2012). Also in the sensory domain, the non-veridical tactile experience can be observed and is particularly striking in brain-injured patients. Halligan and colleagues (Halligan et al., 1996, 1997) described a stroke patient who reported feeling touch when he watched a stimulus being applied to his affected limb. Abnormal sensation has also been observed in patients with pathological embodiment (a disturbance of the feeling of body ownership, Garbarini et al., 2020) who report to perceiving the tactile stimuli applied to someone else's hand (positioned in egocentric perspective) they believe to be their own (Garbarini et al., 2014; Pia et al., 2020). Moreover, in the neurological literature, a phenomenon is described, called "synchiria", where patients report to be touched on both hands when they are actually touched only on the ipsilesional hand (Medina and Rapp, 2008; Medina and Coslett, 2016). Another instance of unusual tactile experience is "allochiria", whereby patients report a stimulus delivered on the contralesional hand to be experienced on the ipsilesional hand (Oberstainer, 1881; Kawamura et al., 1987; Young and Benson, 1992). More recently, we reported a new phenomenon we called "synchiric extinction" (Ricci et al., 2019). We used the Tactile Quadrant Stimulation test (TQS), where stimuli could be delivered to one of four quadrants previously identified on the participants' hands, either to one (Single Stimulation trial, SS) or to both hands (Double Simultaneous Stimulation trial, DSS). Most importantly, during DSS, stimuli were delivered to asymmetrical positions. Patients had to verbally report their tactile experience and also had to point to the stimulated quadrants. Results showed that in DSS trials, at least 50% of the patients, although "correctly" reporting a bilateral tactile experience, erroneously pointed, on the contralesional hand, to the quadrant corresponding to the one stimulated on the intact hand. We interpreted these findings as a manifestation of pathological neuroplastic mechanisms, triggered by the brain lesion, unmasking bilateral touch representation following unilateral stimulation (Noachtar et al., 1997; Hansson and Brismar, 1999; Tamè et al., 2012, 2016) that would be inhibited in the healthy brain (Medina and Coslett, 2016). In stroke patients, hyperactivation of the healthy hemisphere (Kinsbourne, 1977; Johansen-Berg et al., 2002; Corbetta et al., 2005; Grefkes et al., 2008; Salatino et al., 2014; Gammeri et al., 2020) would abnormally activate, via inter-hemispheric transfer (Iwamura et al., 1994; Iwamura, 2000; Fabri et al., 2001; Eickhoff et al., 2008; van der Knaap and van der Ham, 2011; Ricci et al., 2012; Bagattini et al., 2015) homologous representations of the healthy side in the damaged hemisphere after ipsilesional tactile stimulation, thus producing contralesional phantom sensations. We also proposed that the relative weight of homotopic representations, in the damaged hemisphere, might be enhanced by stimulation of the affected hand, as it occurs in the phenomenon of stochastic resonance (SR), whereby adding noise to sub-threshold stimuli improves their detection (Collins et al., 1996; Perez et al., 2007, 2010). The above mechanisms would be responsible for synchiria, when abnormal activation of homotopic representations are supra-threshold, or synchiric extinction, with sub-threshold homotopic representations requiring to be enhanced by stimulation of the affected hand.

Thus synchiric extinction and synchiria support the evidence of bilateral touch representations (Tamè et al., 2012, 2016) and the idea that ipsilateral tactile representation would be sub-threshold (Ricci et al., 2019) and/or inhibited (Medina and Coslett, 2016) in the healthy brain.

A question we ask in the present article is whether it is possible to induce "phantom" sensation in normal subjects, similar to the one we described in patients, taking advantage of the well-known modulatory effect that vision can have over touch. We already know from previous experiments that vision not only improves many aspects of somatosensory processing when tactile stimulus is actually applied to participants' body (e.g., Tipper et al., 1998, 2001; Pavani et al., 2000; Longo et al., 2011; Longo and Sadibolova, 2013; Tamè et al., 2013), but it can also induce the illusion of feeling touch on a fake hand, as in the Rubber Hand Illusion (Pyasik et al., 2019). Therefore the presence/absence of veridical/non-veridical tactile experience on the participants' hands was assessed using an adapted version of TQS where we manipulated through the mirror box procedure the visuotactile stimulation applied on the participants' hands. Subjects had to report tactile stimuli delivered to both hands in different quadrants while looking at the reflection of the right-hand into the mirror and having the left-hand out of sight.

We hypothesized that the feeling of touch on the right-hand together with the vision of touch on the same (right) hand into the mirror (where the right-hand looks like the left-hand) would bias the perception of the left-hand touch localization. Crucially, the expected left-hand errors would be of synchiric type (that is, the reported feeling of touch on the left-hand would be on the same quadrant of the one actually touched on the right-hand) and not simple mislocalization errors. We do not expect to find synchiric errors on the right-hand. Moreover, the comparison between putative synchiria during right-hand SS and synchiric extinction during asymmetrical DSS would inform us on whether the perception of phantom touch on the left-hand is exclusively driven by the vision of the right-hand in the mirror accompanied by tactile sensation of the same (right) hand, or whether touch of the left-hand is necessary to induce synchiric sensations. We expect to observe no differences between SS and DSS in the former case. On the other hand, we expect to observe phantom touch during DSS but not during right-hand SS if left-hand tactile stimulation is necessary to produce a phantom sensation in the same location stimulated on the right-hand. The influence of response modality on phantom sensations was also investigated.

METHODS

Participants

Thirty healthy volunteers (mean ± SD, 29 ± 7; 19 women) participated in the study (**Table 1**). They had a normal or corrected-to-normal vision, and no history of neurological or psychiatric illness. Handedness was estimated using the Edinburgh Handedness Inventory (Oldfield, 1971) test, which ranges from −100% (completely left-handed) to + 100% (completely right-handed, see **Table 1**). Participants gave written informed consent to participate in the study, which was approved by the Ethical Committee of the University of Turin.

Stimuli

The tactile stimuli were administered by the experimenter using calibrated nylon filament (Von Fray hair, size 15) to one of four quadrants, identified on the dorsum of each hand by a cross (5 × 5 cm) drawn on the center of the participant's hand (**Figure 1**).

Procedure

Participants sat with their hands on the table. Tape squares (1 × 1 cm) were placed on the table to mark the position where participants had to place the tip of the index finger for the right and the left-hand, 30 cm on either side of their sagittal midline.

Tactile stimuli were administered to one of the four quadrants on the left-hand (Single Stimulation Left-hand, SS-L), the right-hand (Single Stimulation Right-hand, SS-R) or both hands (Double Simultaneous Stimulation, DSS) to asymmetrical (Asym-DSS) or symmetrical (Sym-DSS) quadrants (**Figure 1**).

Stimuli were administered during three experimental conditions. In the *Baseline Condition* (BC) participants, blindfolded were asked to *verbally* report the side(s) of stimulation (left, right, or both) and then to *point* to the location(s) where they felt the tactile sensation(s), using the opposite hand (Ricci et al., 2019). During DSS trials participants used the right-hand first. After administration of

TABLE 1 | Participants' demographic and experimental data.

Participant	Sex	Age	Education (Years)	Edimburgh Test score	Order 1 = MC-P first 2 = MC-S first
1	F	38	21	60%	1
2	M	22	17	71%	1
3	M	25	19	52%	1
4	F	20	16	100%	1
5	F	30	23	100%	1
6	M	24	18	100%	1
7	F	53	13	100%	1
8	M	33	16	100%	1
9	F	21	16	100%	1
10	F	23	16	83%	1
11	F	30	23	100%	1
12	F	30	23	100%	1
13	F	42	18	100%	1
14	F	21	16	100%	1
15	F	31	16	100%	1
16	M	27	16	75%	2
17	M	32	13	86%	2
18	M	24	18	100%	2
19	F	32	13	100%	2
20	F	20	16	75%	2
21	F	32	18	100%	2
22	F	35	26	100%	2
23	F	35	21	100%	2
24	F	34	19	100%	2
25	M	22	16	100%	2
26	F	31	24	100%	2
27	M	31	13	100%	2
28	M	32	13	100%	2
29	M	21	16	71%	2
30	M	34	15	100%	2

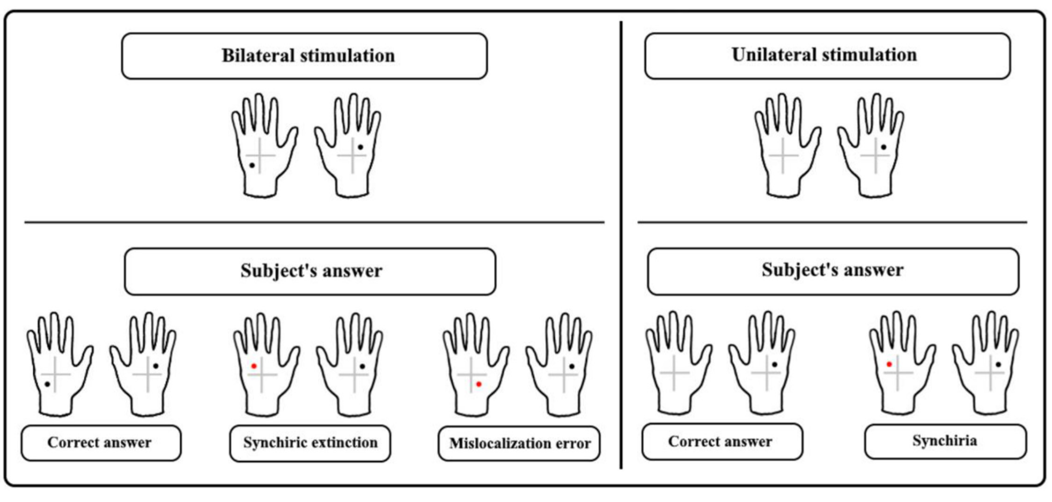

FIGURE 1 | The upper panel shows examples of bilateral asymmetrical tactile stimulation and unilateral stimulation. In the lower panel response, examples are given showing the correct answer and three types of errors: synchiric extinction and mislocalization error regarding bilateral stimulation, and synchiria regarding unilateral stimulation.

the BC, participants underwent two *Mirror Conditions* (MC, see below), where a mirror (45 × 60 cm) was positioned perpendicularly to the subjects' body, centered on their sagittal midline (Medina et al., 2018). In both MC, the subject's hands were positioned at 30 cm of distance from the mirror, one to the right and one to the left of it (**Figure 2**). Participants were asked to look at the reflection of their right-hand in the mirror so that the mirror covered the left non-dominant hand. This experimental setting induced the perception that the right-hand mirror imagine fell exactly where the left-hand was positioned (Medina et al., 2018). In the *Mirror Condition-Pointing (MC-P*), after tactile stimulation, the subjects closed their eyes and *verbally* reported the side(s) (left, right, or both) of stimulation. Then they *pointed* to the location(s) where they felt the *tactile sensation(s)*, using the opposite hand. The *Mirror Condition-Silhouette (MC-S*) was identical to MC-P with the difference that participants reported the location(s) where they felt the sensation(s) using silhouettes of the right and the left-hand (14 × 8 cm) which were located on the table, 5 cm to the right and the left of the real hands (**Figure 2C**). Silhouettes were divided into four quadrants by a central cross (5 × 5 cm). For both MC, during DSS trials participants were not instructed on which hand to use first to report tactile stimuli. However, they tended to use the dominant hand first. **Figure 2** depicts the three experimental conditions BC, MC-P, and MC-S.

The order of administration of MC-P and MC-S was counterbalanced across participants (**Table 1**). For each experimental condition stimuli were delivered according to two lists of 32 trials—i.e., eight trials (each quadrant was stimulated twice) for each stimulation condition—which follow a pseudo-random order. Participants underwent a total of 192 trials. The experiment lasted 60 min.

Bodily Sensations Evaluation

To investigate participants' subjective experience during mirror conditions, we audio-recorded spontaneous comments and observed the behavior of a subgroup of ten participants. In subjects not spontaneously verbalizing the experience, the experimenter asked one of the following questions: "what do you think?" or "how do you feel?" This session occurred before the first MC, and soon after participants started looking at the mirror right-hand reflection.

Data Analyses

To assess the presence of synchiric extinction (i.e., errors due to localization of contralateral stimuli at homologous locations of ipsilateral stimuli) and synchiria (i.e., bilateral sensations during single stimulation) induced by the mirror, we analyzed separately stimulation conditions that could give rise to synchiric extinction and synchiria, i.e., Asym-DSS and SS trials, respectively. The analyses of Sym-DSS trials, which were not crucial for the aims of the study, are reported in the **Supplementary Material**. In the Asym-DSS, synchiric extinction was compared to mislocalization (i.e., stimulus localization in a location that was not touched in either hand) and classical extinction (i.e., failure to detect the left or the right stimulus), while in SS trials, synchiria was compared to mislocalization (i.e., stimulus localization in one of the quadrants not touched in the stimulated hand) and omissions. The number of errors constitutes the dependent variable (Ricci et al., 2019). See **Figure 1** for a description of the types of errors.

Since data were non-normally distributed as assessed by the Shapiro-Wilk test, we used non-parametric Friedman and Wilcoxon tests (with Bonferroni correction when necessary) to compare within each *condition* (BC, MC-P, MC-S) the *type of errors* (Synchiric extinction, mislocalization, extinction/omissions) for each *hand* (left/covered hand vs.

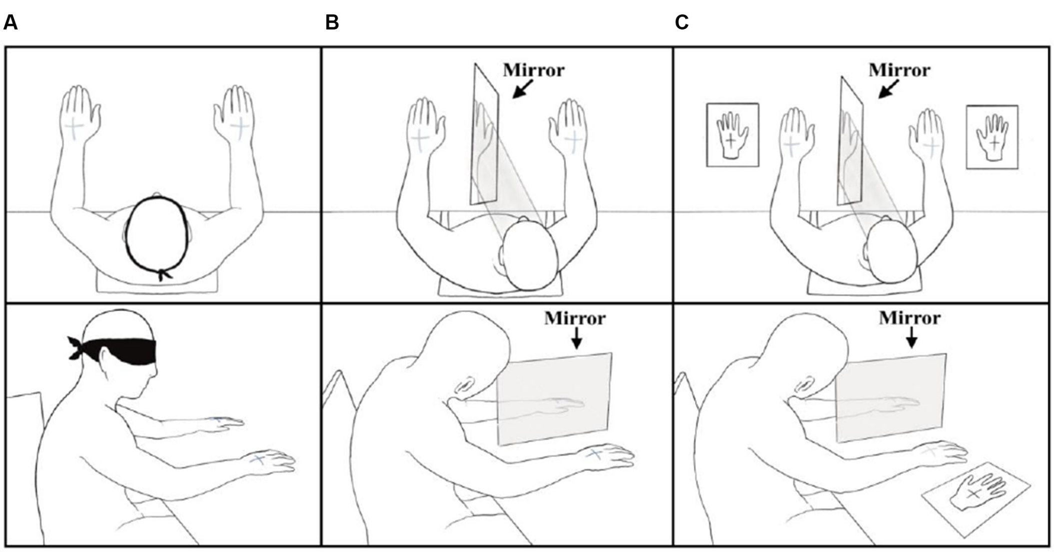

FIGURE 2 | Top view and side view of the Baseline Condition **(A)**, Mirror Condition-Pointing **(B)**, and Mirror Condition-Silhouette **(C)**.

right/uncovered hand), and the two *hands* for each *type of error*. The analyses concerning the three main within-subjects factors (condition, error, and hand) and Spearman's rho correlational analysis to assess the putative relationship between synchiric extinction for the left-hand and handedness are reported in the **Supplementary Results**.

RESULTS

Asymmetrical DSS

Comparisons within each *condition* between *types of error* for each *hand* showed that, for the *left-hand*, in the *MC-S*, synchiric extinction was significantly greater than mislocalization [$z = -4.630$; $p < 0.0001$; $r = 0.59$] and extinction [$z = -4.606$; $p < 0.0001$; $r = 0.59$], and mislocalization was greater than extinction [$z = -2.803$; $p < 0.01$; $r = 0.36$]. Also, in the MC-P, synchiric extinction was greater than mislocalization [$z = -4.417$; $p < 0.0001$; $r = 0.57$] and extinction [$z = -4.679$; $p < 0.0001$; $r = 0.60$], without differences between these two last conditions after Bonferroni correction [$p = 0.036 > 0.0167$]. In the BC there were no differences between synchiric extinction and mislocalization and there was no extinction (**Figure 3A**).

For the *right-hand*, in MC-S, synchiric extinction did not differ from mislocalization [$z = -1.784$; $p = 0.074$; $r = 0.23$], while both synchiric extinction [$z = -3.353$; $p < 0.01$; $r = 0.43$] and mislocalization [$z = -2.754$; $p < 0.01$; $r = 0.35$] were greater than extinction. For MC-P, synchiric extinction was greater than mislocalization [$z = -3.072$; $p < 0.01$; $r = 0.39$] and extinction [$z = -4.146$; $p < 0.0001$; $r = 0.53$], without differences between these two last conditions after Bonferroni correction [$p = 0.027 > 0.0167$]. Finally, for BC, synchiric extinction and mislocalization did not differ between them, but both of them were greater than extinction (synchiric extinction: $z = -4.218$; $p < 0.0001$; $r = 0.54$; mislocalization: $z = -3.398$; $p < 0.01$; $r = 0.43$; **Figure 3B**).

Comparisons of each *type of error* between *hands* for each *condition*, revealed more synchiric extinction for the left-hand (behind the mirror) than for the right-hand in the two mirror conditions [MC-S: $z = -4.685$; $p < 0.0001$; $r = 0.60$; MC-P: $z = -3.884$; $p < 0.0001$; $r = 0.50$]. The two mirror conditions also showed more mislocalizations [MC-S: $z = -2.840$; $p < 0.01$; $r = 0.37$; MC-P: $z = -2.130$; $p < 0.05$; $r = 0.27$] and more extinction [MC-S: $z = -2.588$; $p < 0.05$; $r = 0.33$; $r = 0.37$; MC-P: $z = -2.032$; $p < 0.05$ $r = 0.26$] in the left than in the right-hand. Interestingly, an opposite result was found for synchiric extinction in BC, i.e., more bias in the right than in the left-hand [$z = -2.238$; $p < 0.05$; $r = 0.28$], and no differences for the other two types of bias.

To summarize, data showed induction of synchiric extinction by the mirror conditions in the left covered hand, and that within this hand, synchiric extinction was significantly greater than mislocalization. In addition, the type of mirror condition affected synchiric bias, with the silhouette condition producing a greater bias than the closed-eye pointing condition.

Single Stimulation (SS)

In SS trials, in BC participants did not show any synchiria on the left-hand and a very small error ($M = 0.03$ $SD = 0.18$) on the right-hand. Also in the mirror conditions, synchiria was <0.3. Participants did not show any omission in BC and very small omission rate (<0.03) in the mirror conditions. They instead showed mislocalizations, with MC-S producing a greater bias than MC-P and BC. See **Supplementary Results** for details on this analysis.

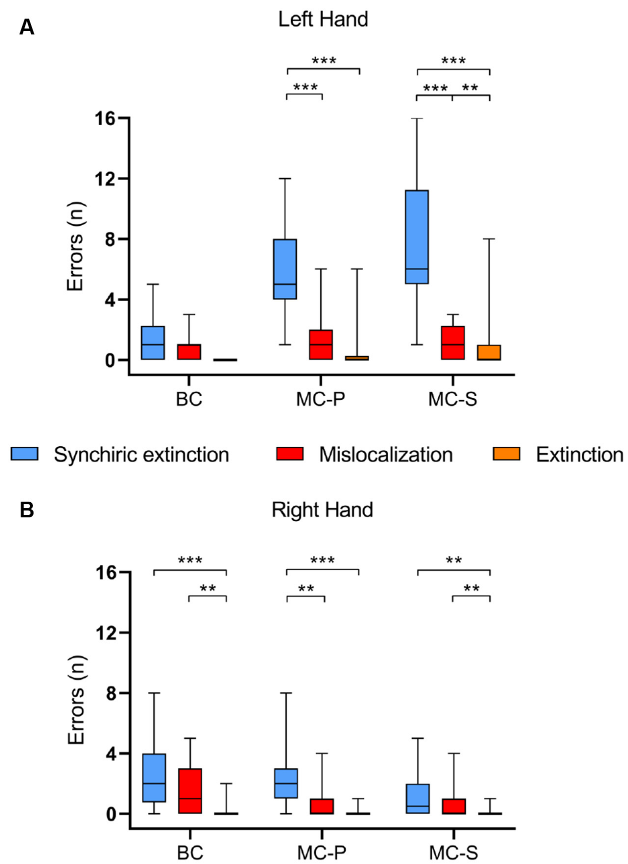

FIGURE 3 | Group performances on the Baseline condition (BC), Mirror Condition-Pointing (MC-P), and Mirror Condition-Silhouette (MC-S). The graph depicts the median value of synchiric extinction, mislocalization errors, and extinction for each condition regarding **(A)** the left-hand and **(B)** the right-hand. Boxes represent the first to the third quartile, whiskers represent the data range. $^{**}p < 0.01$; $^{***}p < 0.0001$.

Bodily Sensations

As it emerged by a qualitative analysis of participants' behavioral and verbal reactions (see **Supplementary Results**), participants expressed disorientation, astonishment, negative emotions, and, sometimes, some degree of amusement. They felt as if the mirrored image of the right-hand were the left-hand and that this feeling was quite uncomfortable. Thus these data revealed some sort of embodiment of the participants' left-hand into the mirrored image of their right-hand. The participants' verbalizations also convey a feeling of discomfort caused by the mirror experience.

DISCUSSION

In the present study, we evaluated if it was possible to induce phantom tactile sensations in healthy subjects similar to those observed in patients after stroke, based on the assumption that vision can, under certain circumstances, guide and influence tactile perception. To this aim, we used the TQS protocol in which subjects, in the crucial condition, must indicate whether and where they detected a double tactile stimulation applied simultaneously in different quadrants of the two hands. The task was performed with the left-hand out of sight (covered hand) and the right-hand (uncovered hand) reflected in a mirror placed so that the two hands were equidistant from the mirror. This situation induces the so-called mirror box illusion, whereby the right-hand reflected in the mirror looks like the own left-hand (Ramachandran et al., 1995).

Interestingly, we found that the vision of the right-hand reflected in the mirror and stimulated by a tactile stimulus, elicited on the left-hand, that received the stimulation in a different quadrant, the sensation of having been touched in the same position as the right-hand. In other words, we found in healthy subjects the same phantom touch effect that we previously observed in patients (Ricci et al., 2019). Here, we also observed enhanced effect in the silhouette condition, when the response mainly relied on vision.

The fact that vision can guide and even deceive tactile perception has been observed in the Rubber Hand Illusion (RHI, Botvinick and Cohen, 1998; Tsakiris and Haggard, 2005), where simultaneous stimulation of one's own hand and of a corresponding rubber hand elicits the sensation that tactile stimuli are given on the rubber hand, with a consequent feeling of ownership over the rubber hand. In the RHI, the initial incongruence between touch, proprioception, and vision is resolved by reallocating the own hand on the position occupied by the rubber hand. Although some incongruence between touch, vision, and proprioception may also occur in our setup, the first important difference with respect to the RHI paradigm is that we do not apply continuous stimulation to induce an illusion. Our subjects are presented with one stimulus per trial. Although multisensory integration of conflicting stimuli, resulting in perceptual biases, does not necessarily require continuous stimulation (Ernst and Banks, 2002; Papeo et al., 2010; Takasugi et al., 2011; Liu and Medina, 2021), our paradigm also differs from the RHI because in the RHI, beyond the presence of a fake hand, completely unrelated to the body, the fake hand is of the same identity as the stimulated real hand (e.g., left rubber hand/left real hand). In addition, in the RHI only one real hand (hidden from vision) is stimulated.

More similar to our experimental situation is the protocol used by Petkova and Ehrsson (2009) where participants reported feeling touches on a right rubber hand when they saw it simultaneously stimulated with their left-hand. The authors explained their observation suggesting an automatic integration between visual, tactile, and proprioceptive information coming from the two hands which caused the transfer of sensation from the left-hand to the right rubber hand. This transfer would be mediated by neurons with bilateral tactile receptive fields in the parietal cortex (Iwamura et al., 1994, 2002; Iwamura, 2000). According to the authors, the tactile stimulation of the participant's real hand may have activated ipsilateral somatosensory areas. When this *prolonged* activation was combined with the visual stimulation coming from the fake hand, the activation reached the threshold for conscious awareness for the stimuli applied to the fake hand. Likewise, in our experiment, stimulation and viewing of the right-hand in the mirror may have triggered a mechanism similar to that hypothesized by Petkova and Ehrsson. In our protocol, during asymmetric bilateral stimulation, a tactile localization bias might have arisen from automatic integration between contrasting information (felt touch on the left-hand and seen touch on the right-hand reflected in the mirror). This bias would be mediated by bilateral touch representations (Tamè et al., 2012, 2016; Schaefer et al., 2013). Specifically, right-hand stimulation would activate a sub-threshold ipsilateral somatosensory representation, that would reach the threshold for awareness (with transfer or duplication of sensation to the left-hand) when subjects see the right reflected hand. However, our experiment has fundamental differences from that of Petkova and Ehrsson. The first is that, in our paradigm, in the critical condition, both hands were stimulated and subjects indicated the position of the tactile perception on the *real* left covered hand even though the location was not the real one, but the one corresponding to the location stimulated on the real right-hand. So what happens in our case is the transposition/duplication of a tactile experience from a real hand to another real hand and not from a real hand to a fake hand. This, however, could have happened with the mediation of the mirror image of the right-hand that looks like the left own hand. We do not have a direct assessment of how much the reflected hand is felt as the own left-hand. However, although preliminary, the participant's comments suggest a sort of incorporation of the mirror image of the right-hand, as a left-hand, into their body representation. We will specifically investigate this aspect in future studies.

We may speculate that the conflicting multisensory integration induced by our setup together with a possible "incorporation" of the reflected right-hand as the own left-hand might have induced the "phantom touch" on the left real hand. It must be noted that we found phantom touch only in double stimulation trial. That is, when the participants looked at the reflected image of the right-hand being touched, without receiving any stimulation on the real left-hand, they did not report any phantom sensation. This indicates that a single stimulation of the right-hand is not sufficient to induce a non-veridical tactile experience on the left-hand. Similarly to what we observed in patients after stroke (Ricci et al., 2019), stimulation of the left-hand is needed to feel a tactile stimulus on the left-hand on the same quadrant of the right-hand. It is possible that in healthy subjects, sub-threshold ipsilateral somatosensory representations of the right-hand, reinforced by the reflected vision of the same hand, may need the stimulation of the left-hand to reach awareness, as it occurs in the phenomenon of stochastic resonance (SR), whereby adding noise to subthreshold stimuli allows their detection

(Perez et al., 2010). The processing of this stimulation would be therefore modulated by the bottom-up (multisensory integration of stimuli coming from the right real and the right reflected hand) and possibly top-down (body ownership distortion) influences giving rise to the phantom sensation reported in bilateral trials.

We also found a modulation of the phenomenon by response factors. The use of vision (silhouettes) to localize sensations boosted the phenomenon. Moreover, strong right-handedness was associated with decreased synchiric extinction, likely arising from decreased interhemispheric interaction (Christman et al., 2009). Finally, in the baseline condition, a greater bias occurred in the right-hand, implying the possibility of inducing an even greater effect in correspondence of the inverse set-up. These findings, in line with previous evidence (Ricci and Chatterjee, 2004; Ricci et al., 2005), suggest the contribution of output stages of spatial processing to stimulus awareness and warrant further in-depth investigation to comprehend the role played by the response and decision-making aspects to non-veridical tactile sensations (Takasugi et al., 2011; Badde et al., 2019).

In conclusion, this is the first evidence of transposition/duplication of tactile sensation from one real own hand to the other real own hand in normal subjects, demonstrating that it is possible to induce "phantom" experience outside a paradigm where alien and/or fake hands are used. The behavioral protocol we have proposed, if coupled with psychophysiological and neuroimaging techniques can represent an effective tool to deepen our knowledge on the physiological and anatomical aspects of multisensory integration and on the mechanisms underlying uni- and bilateral representations of touch.

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 Ethics committee of the University of Turin. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

RR, MC, and AB coordinated the study. RR, MC, AB, and AS designed the study. IS, EC, and EzC performed the experiments. MC and RR supervised data analyses. IS, RR, MC, and AS analyzed the data. AB and RR wrote the manuscript. MC, EC, IS, EzC, and AS critically reviewed the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIALS

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fnhum.2021.734235/full#supplementary-material.

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