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PLASTIC MODULATIONS OF THE BODY METRIC REPRESENTATION:

NEUROPHYSIOLOGICAL AND BEHAVIORAL EVIDENCE

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Declaration

I declare that the work presented in this thesis is my own.

Where information has been derived from other sources, I confirm that this has been reported in the thesis.

Serena Giurgola

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Abstract

The knowledge of the size of the own body-parts is essential for efficiently moving in the external environment and accurately interacting both with objects and with other people. In an interdisciplinary approach which combines neurophysiological (i.e., non-invasive brain stimulation) and behavioral paradigms, the present dissertation investigates the cognitive and neural signatures underlying the representation of body-parts size. Study #1 demonstrates the casual role of the primary somatosensory cortex in one's own body-parts size processing. In healthy adults, 1-Hz repetitive Transcranial Magnetic Stimulation over the hand representation in the somatosensory map of both hemispheres leads to perceptual distortions (i.e., overestimation) of the own hand size – as assessed with a visual perceptual task – which do not extend to other body districts (namely, the foot). Instead, cortical excitability shifts induced by repetitive Transcranial Magnetic Stimulation over the right or left inferior parietal lobule do not affect the perceptual estimation of the own hand size. This evidence highlights the causal involvement of the primary somatosensory cortex in the construction and updating of one's own body metric representation. Study #2 focuses on the plastic changes which occur by manipulating the sense of body ownership, showing that, in healthy adults, the embodiment of external hands bigger (but not smaller) than the own affects the perceptual conscious representation of the own hand dimension. Finally, by comparing body metric representation in typically developing children and healthy adults, Study #3 shows how perceptual distortions of body-parts representation arise during the developmental course. Overall, findings from this dissertation support the extremely flexible nature of one's own body metric representation, showing how plastic distortions of the own body-parts size develop gradually during the lifespan and can be modulated by neurophysiological changes as well as by illusory manipulations of self-attribution.

La conoscenza della grandezza delle proprie parti corporee è essenziale per muoversi in maniera efficiente nell'ambiente esterno e per interagire accuratamente sia con gli oggetti sia con le altre persone. Attraverso un approccio interdisciplinare che combina paradigmi neurofisiologici (stimolazione cerebrale non invasiva) e comportamentali, la presente tesi indaga i meccanismi cognitivi e neurali sottostanti la rappresentazione della grandezza delle parti corporee. Lo Studio #1 dimostra il ruolo causale della corteccia somatosensoriale primaria nell'elaborazione della grandezza delle proprie parti del corpo. Nei soggetti adulti neurologicamente sani, la Stimolazione Magnetica Transcranica ripetitiva a 1-Hz della rappresentazione della mano nella mappa somatosensoriale di entrambi gli emisferi, induce delle distorsioni percettive (sovrastima) della grandezza della propria mano – come valutato con un compito visuo-percettivo – che non si estendono ad altri distretti corporei (il piede). Invece, cambiamenti nell'eccitabilità corticale indotti da Stimolazione Magnetica Transcranica ripetitiva del lobulo parietale inferiore destro o sinistro non influenzano la stima percettiva della grandezza della propria mano. Tale evidenza sottolinea il coinvolgimento causale della corteccia somatosensoriale primaria nella costruzione e nell'aggiornamento della rappresentazione metrica del proprio corpo.

Lo Studio #2 si focalizza sui cambiamenti plastici che avvengono manipolando il senso di appartenenza corporea mostrando che, negli adulti neurologicamente sani, l'*embodiment* di mani più grandi (ma non più piccole) della propria influenza la rappresentazione percettiva cosciente della dimensione della propria mano. Infine, comparando la rappresentazione metrica del corpo in bambini a sviluppo tipico con quella degli adulti neurologicamente sani, lo Studio #3 mostra come le distorsioni percettive della rappresentazione corporea emergono durante il corso dello sviluppo. Complessivamente, i risultati della presente tesi supportano la natura estremamente flessibile della rappresentazione metrica del proprio corpo, mostrando come le distorsioni plastiche della grandezza delle proprie parti corporee si sviluppano gradualmente nell'arco della vita e possono essere modulate sia da cambiamenti neurofisiologici, sia da manipolazioni illusorie del senso di *embodiment*.

Summary

The question of the Self has intrigued philosophers and psychologists for a long time. In the last decades, this issue has been faced by neuroscientists focusing, in particular, on the contribution of the *sense of body* to the *sense of Self.* Indeed, the representation of the body is a nuclear aspect of self-image and personal identity, since it affects how we represent ourselves and allows us to correctly distinguish our body from other bodies and from the external world.

The so-called bodily-Self is a multisensory construct where visual, auditory, tactile, interoceptive and proprioceptive information are merged in order to create the sense of body ownership (i.e., the feeling that our body-parts belong to ourselves) and a coherent sense of our body location in the space. Thus, the representation of the body in the human brain has become an intriguing topic in neuroscience research, suggesting the existence of several cognitive and neural representations of the body and its parts, including the knowledge of body-parts size (i.e., *body metric representation*).

The present dissertation will focus on the cognitive and neural mechanisms underlying the metric properties of body-parts representation. In an interdisciplinary effort which integrates neurophysiological methods, such as non-invasive brain stimulation techniques, and behavioral paradigms, like bodily illusion manipulations, my work collects a set of experiments, aimed at uncovering mechanisms of cross-modal plasticity underlying the representation of body-parts size. In these series of experiments, I explored the plastic changes that can occur on the one hand at the cortical level by driving (or inhibiting) short-term local plastic processes in selected neuronal populations, on the other hand at the behavioral level, for example by manipulating the sense of body ownership. Finally, I investigated developmental changes in perceived body size, by studying body metric properties in healthy children. Taken together, results converge in showing the extremely

malleable nature of one's own body size representation: body size is flexible, it can be distorted either by modifying the cortical excitability (Study #1) and by illusory cross-modal experiences (Study #2), and it develops gradually during the lifespan (Study #3).

Specifically, in the first series of studies repetitive Transcranial Magnetic Stimulation (rTMS) was used in order to investigate the causal role of the primary somatosensory cortex (S1) in the perceptual representation of one's own hand size. Results show that, in healthy participants, rTMS-induced changes of the central somatosensory maps in S1 lead to an overestimation of one's perceived hand size. These findings highlight the importance of S1 in the construction and maintenance of body size representation, supporting its role in high-order cognitive processes related to body perception. Thus, a more complex role for S1 is proposed, challenging the classical view of S1 as cortical low-level primary-sensory area just involved in tactile information processing.

Capitalizing on these findings, I tested whether a reverse inference could corroborate the link between top-down high-level processes (*embodiment*) and the body metric. Thus, a subsequent set of behavioral experiments was designed in order to explore whether and how the sense of body ownership could shape how we perceive our body size. To this aim, a modify version of the rubber hand illusion (RHI) paradigm was developed, to probe whether the embodiment of fake hands of different sizes would affect the perceptual representation of the own hand. By testing healthy adult participants, results revealed that the embodiment of a fake hand bigger (but not smaller) than the own hand causes an overestimation of the size of the own hand. This evidence shows the tight link between the sense of ownership and body metric.

In a final set of behavioral experiments, the cognitive mechanisms underlying body size perception during development have been investigated in children.

Overall, these findings shed new light on the dynamic aspects of body representation, showing how body size perception is plastic: perceptual distortions of the own body-parts size can be induced by neurophysiological manipulation (Study #1) as well as by illusory manipulations of self-attribution and embodiment (Study #2); moreover, the subjective distortions of the own body size representation reported in healthy adult cognition appear earlier during childhood (Study #3). Crucially, the studies discussed in the present dissertation provide new insights about the functional role of S1, showing how this brain region may contribute to our understanding of body metric perception.

1. INTRODUCTION

1.1. Body representations: from *Body Image & Body Schema* to *Body Model*

A growing body of research in neuroscience has shed light on bodily awareness, providing rich insight into the cognitive mechanisms and the neural correlates underpinning body perception. In this regard, neuropsychological evidence supports the existence of a plethora of body representations in the human brain, functionally sustained by several brain regions (Berlucchi & Aglioti, 1997, 2010; De Vignemont, 2010; Gallagher, 2005; Haggard & Wolpert, 2005; Pitron & De Vignemont, 2017). These brain areas contribute to the construction of different Mental Body Representations (MBRs), defined as various abstract representations of one's own body, derived from sensory inputs but different from them, and characterized by functional roles in perception and action (Serino & Haggard, 2010). Nowadays, a shared view is that the knowledge of our own body is multidimensional, and comprises of various types of conscious and unconscious body representations (Vallar & Rode, 2009), including the knowledge of body-parts size, their integration into a whole body and their location in the space (Serino et al., 2010). Despite the little consensus on the precise types of body representations in the human brain (Gallagher, 2005; Head & Holmes, 1911; Paillard, 1999; Schwoebel & Coslett, 2005; Sirigu, Grafman, Bressler & Sunderland, 1991), a classical and well accepted distinction between two forms has been proposed to exist, discerning the so-called *body image* from the *body schema,* respectively (Gallagher, 2005). In its primarily proprioceptive origin, the body schema includes the knowledge of one's own body-parts position in the space in a given moment, based on which we can guide our actions in the world and our interactions with the environment. Indeed, body schema is continuously updated during movements, supporting the spatial organization of our actions (Head et al., 1911). Thus, the predominantly somatosensory

nature of the body schema reflects a multisensory-based, largely unconscious, tracking and updating of the body-parts position in the space. Instead, the body image represents the perceived form of our body in third person perspective, in terms of its size and shape (Head et al., 1911). Hence, the visual nature of the body image gives rise to the conscious personal identity, structuring the own body as unique and distinct from the other bodies and the external environment. Interestingly, since the classical conceptualization by Head et al. (1911), both the body schema and the body image appear to rely on the processing of sensory, proprioceptive and somatic information, even if in a different way: while the body schema redirects to the central somatotopic mapping of tactile inputs before they reach consciousness, the body image combines visual and somatosensory inputs into a coherent conscious bodily experience (Head et al., 1911). Thus, somatosensation reveals a tight link between tactile processing and body perception. As argued by Longo (2015a, 2015b), somatosensation is a core aspect for the representation of the entire body and its parts, since the skin (i.e., the primary receptor surface) is physically coextensive with the body. In this regard, Longo, Azañón and Haggard (2010) proposed a recent cognitive model to explain the processing of *somato-perceptual* information, called *"body model"*, by which high-level somatosensory percepts result from the combination of afferences derived from peripheral nerves with stored body representations. As explained by the authors, *somatoperception* refers to the processing of the body itself, ensuring somatic perceptual constancy (Longo et al., 2010). Specifically, according to Longo and co-workers (2010), somatoperception relies on three key cognitive mechanisms: i) the processing of remapping of somatic inputs from the physical body surface into egocentric reference frames; ii) the interoceptive perception of the state of the own body; iii) the exteroceptive perception of the external objects through the contact with the own body. In addition to the classical superficial and postural schemas proposed by Head et al. (1911), the body model

would support also the representation of the metric properties of the body, namely the body size and shape, which in turn affects – in a top-down fashion – somatosensory functions such as tactile size perception and position sense. It is worthy to note that the sense of touch and its first processing in S1 is crucial for building up a first representation of the body. Indeed, tactile processing carries information at the same time about external objects touching the skin, and also about the own body itself (Serino et al., 2010). Thus, somatosensation is always twofold and, based on its dual nature, different kinds of interactions have been described (Serino et al., 2010): the relationship between the physical body surface and the somatosensory maps in S1 (in particular, how the physical body shapes tactile perception; see Figure 1, pathway 1), the modulation of the own body representation by somatosensory inputs (Figure 1, pathway 2), the contribution of high-order body representation to low-level tactile processing through feedback pathway in S1 (Figure 1, pathway 3), and the influence of body representation on tactile object perception (Figure 1, pathway 4). Serino et al. (2010) proposed an analytical model consisting of these four different pathways, in order to clarify the relationship between the physical body, mental body representations, the sense of touch and the role of the somatosensory cortices in these interactions. These pathways will be deeply examined in the present dissertation.
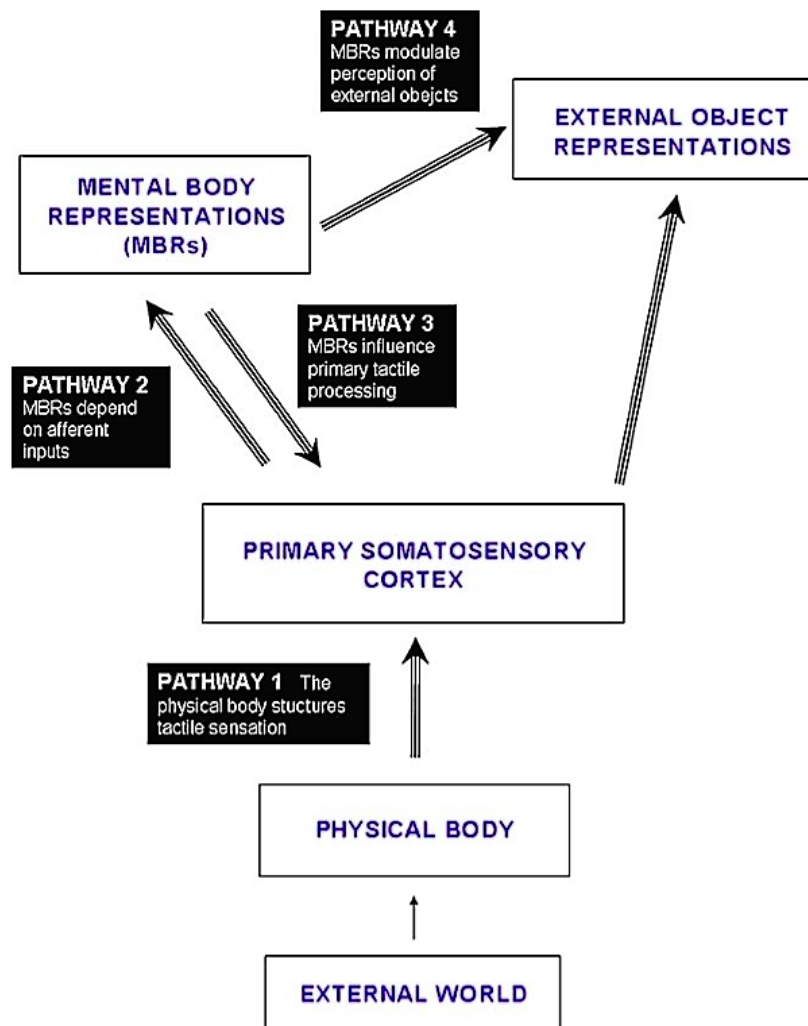
Figure 1. Schematic representation of the analytic model about the link between body representations and tactile processing. Four different pathways have been proposed in order to explain the relationship between the physical body surface and S1 (pathway 1), the bidirectional influence between S1 and the mental representations of one's own body (pathway 2-3) and the modulation of such body representations on the perception of external objects (pathway 4). Adapted from Serino et al. (2010).

1.2. Somatosensory cortex and body representation: a mutual relationship

The somatosensory *homunculus* is a classically used description of the way in which body-parts are processed in the brain (Harding-Forrester & Feldman, 2018). The contribution of S1 to the representation of body-parts has been well established since the pioneering studies of Penfield and colleagues in humans (Penfield & Rasmussen, 1950). Among the

different sensory systems, the cortical somatosensory system appears as a main neural node involved in body perception. Indeed, tactile afferent projections to the contralateral S1 reflect the spatial maps of the peripheral receptors in the skin (i.e., mechanoceptors, thermoreceptors and nociceptors), thus preserving the spatial organization of the body surface: neurophysiological studies demonstrated that adjacent cortical neurons in S1 receive afferent projections from adjoining receptive fields on the physical body surface (Blakenburg, Ruben, Meyer, Schwiemann, & Villringer, 2003; Kaas, Nelson, Sur, Lin & Merzenich, 1979; Mountcastle, 1997; Penfield et al., 1950). This somatotopic cortical organization in S1 provides a point-to-point mapping of the different body districts, according to which the surface of our physical body is coded in a topographical way. Thus, in each hemisphere, S1 neurons encode the somatotopic representation of the contralateral side of the body (Penfield & Boldrey, 1937). However, body map representations in S1 are not fixed, and they dynamically adapt to experimental manipulations as well as to central/peripheral nervous system injury. For example, in case of deafferentation following nerve block, afferent inputs from the skin do not reach the corresponding regions of S1 any more. The lack of afferent information from the deafferented body-part to the matching sector of the S1 map induces a reorganization of the bordering regions, that extend their cortical boundaries in the portions of S1 previously responding to the deafferented body-part. This is well documented by studies in monkeys, showing that the portions of S1 previously responding to the resected projections, plastically reorganize, processing stimuli delivered to adjacent sectors of the body surface thus, in turn, mapping new body-parts (Jenkins, Merzenich & Recanzone, 1990; Merzenich & Jenkins, 1993). This form of short-term cortical plasticity could rely on the unmasking of connections between adjoining portions of S1 (Buonamano & Merzenich, 1998; Kew et al., 1997). These connections could be normally masked by stronger inputs, resulting functionally silent or below

threshold; they may become effective whether a region of S1 no longer receives the proper range of somatosensory inputs, leading to the unmasking of lateral pre-existing synaptic connections from neighbouring representations.

Short-term plastic reorganization processing has been reported also in case of deafferentation due to anaesthesia. For example, Rossini and colleagues (1994) reported in humans an increase of the cortical activity related to the unanesthetized fingers, following the anaesthesia of the adjoining 4th finger. Interestingly, it has been acknowledged that cutaneous anaesthesia modulates also tactile perception, in a somatotopic fashion. This effect was supported by recording changes in evoked cortical potentials from the somatosensory cortex: peripheral anaesthesia of the right hand improves left hand tactile sensitivity, while anaesthesia of the foot does not influence tactile hand acuity (Bjorkman, Rosen & Lundborg, 2004; Werhahn, Mortensen, Van Boven, Zeuner, & Cohen, 2002). A possible explanation of this phenomenon is the unmasking of inter-hemispheric interactions between homologous portions of S1, via corpus callosum. According to Pluto, Chiaia, Rhoades and Lane (2005), cutaneous anaesthesia should inhibit the cortical activity of the contralateral S1, in turn reducing the contralateral inhibition and providing the unmasking of silent synaptic connections. These findings support short-term plastic reorganization processes that can occur in local neural populations of S1 following alterations of its peripheral inputs from the physical body surface.

Similar forms of plasticity occur in the human somatosensory cortex of amputee patients (Ramachandran & Hirstein, 1998). In case of amputation, the link between the activity in the somatosensory cortex, somatosensation and patient's body perception is strengthened by the so-called "phantom limb" syndrome, following long-term plastic changes in S1 (Ramachandran, 1993; Ramachandran, 1998; Ramachandran et al., 1998; Ramachandran, Rogers-Ramachandran, & Stewart, 1992): patients with phantom limb syndrome claim to

perceive the missing limb as still present, reporting tactile sensations as if they were arisen from the amputated limb *('referred sensation'*; Aglioti, Smania, Atzei & Berlucchi, 1997; Halligan, Marshall & Wade, 1994; Ramachandran, 1998; Ramachandran et al., 1992).

Several accounts suggest that plastic reorganizations of S1 maps also occur following tactile stimulation. In this regard, Pascual-Leone & Torres (1993) showed that Braille readers are endowed with enhanced tactile discrimination capabilities as compared to non-Braille readers. Interestingly, the representation of their right index finger in S1 maps (that they usually use during Braille reading) results expanded, as compared to the homologous left index finger, that is typically not used during this kind of reading (Pascual-Leone et al., 1993).

Overall, this evidence clearly shows the mutual relationship between body representation and tactile processing. On the one hand, tactile inputs shape the S1 somatosensory maps, since S1 neurons code tactile stimuli delivered on a specific body district, in topographic way. Moreover, tactile processing directly influences body representation, as well exemplified for instance by the Rubber Hand Illusion (RHI) paradigm (Botvinick & Cohen, 1998), during which subjects perceive a fake hand as part of their own body following visuo-tactile interaction. On the other hand, S1 cortical maps define how somatosensory information are experienced on the physical body surface (Serino et al., 2010). Thus, tactile processing influences sensory body representations.

At the same time, the representation of the body and its parts crossmodally modulates tactile sensation. For example, visual information related to the body enhances tactile acuity, as demonstrated by the effect known as *visual enhancement of touch* (*VET*) either in healthy individuals (Kennett, Taylor-Clarke, & Haggard, 2001; Press, Taylor-Clarke, Kennett & Haggard, 2004; Taylor-Clarke, Kennett & Haggard, 2002) and in neurological population (Serino, Farnè, Rinaldesi, Haggard & Làdavas, 2007). Specifically, Kennet and

co-workers (2001) tested a group of healthy participants assessing the two-point discrimination threshold (2pdt) on their forearm in different conditions: while viewing the own forearm (experimental condition), or while viewing a neutral object/while being blindfolded (control conditions). Tactile sensitivity was significantly improved while viewing the own forearm being stimulated, as compared to the control conditions. Crucially, several neurophysiological accounts indicate that VET occurs in S1, thus suggesting that S1 represents a core neural node in boosting touch processing from the vision of the body (Fiorio & Haggard, 2005; Schaefer, Heinze & Rotte, 2005a, 2005b, 2005c; Taylor-Clarke et al., 2002). In this regard, Serino et al. (2010) speculate that the visual perception of the body modulates S1 cortical activity, probably providing a better definition of the bodily space to which tactile inputs are referenced. Moreover, tactile and visual events occurring on our body are integrated in a multisensory body-centered representation: touch is body-referenced since the skin (i.e., the primary receptor surface) is physically coextensive with the body (Longo, 2015a, 2015b); as a consequence, representations of the body are central in somatosensation as well as in tactile object processing. Thus, tactile perception related to objects touching the skin relies on one's own body awareness. As argued by Martin (1992), in order to create the spatial and volumetric representation of the objects, tactile object information is combined with multisensory proprioceptive body signals.

Taken together, this set of evidence supports the bidirectional interaction between exteroceptive touch and high-level body representations, including the knowledge of the own body metric, sustained by cerebral neuroplasticity at either an unimodal and a multisensory level.

1.3. Distorted representation of the metric properties of the body

The first depiction of the body and its parts at the cortical level comes from the electrophysiological studies by Penfield et al. (1937), illustrating the well-known somatosensory homunculus in S1 maps. By using electrical invasive cortical stimulation of S1 neurons in a surgical patient, they elicited sensations from the corresponding body districts, thus showing somatic sensory body representation in specific portions of the human postcentral gyrus (Penfield et al., 1937). This evidence demonstrates that each side of the body surface is represented in a topographical way in the contralateral S1. This somatotopic depiction includes the description of the different body-parts dimension (Penfield et al., 1937, 1950). However, the true morphology of one's own body is not accurately reflected in the somatosensory cortical maps. Indeed, the representation of the body surface in S1 results distorted: each sensory receptor is mapped onto the cortex; thus, the more sensory receptive fields are contained in a specific portion of the skin, the more that skin region is cortical magnified in S1 maps: the size of each body district in the somatosensory homunculus directly depends on the sensory receptors density, that varies among body-parts, and hence varies among the portions of S1 too (Brown, Koerber & Millecchia, 2004). As a consequence, the face and the hands appear extremely magnified, while the arms, the legs and the torso are not characterized by a such large representation in S1. Moreover, the somatosensory homunculus is inverted with respect to the physical disposition of the body-parts, since the face and the hands are mapped laterally onto the cortex, while the legs are represented more medially (Penfield et al., 1937).

From a cognitive point of view, the body model proposed by Longo and co-workers (2010) provides a theoretical model to clarify the cognitive mechanisms underlying the processing of the metric properties of the body, such as body size and shape, which are critically involved in somatosensory functions like tactile perception and position sense. The notion

of *position sense* refers to the ability of perceiving the location of the own limbs in the space, even without seeing them (Longo, 2017). The knowledge of the own body-parts position in the space is essential for efficiently moving in the world and interacting with external objects. In order to correctly perceive the own body-parts position in the space, body posture inputs need to be combined with information about the own body size and shape. Different kinds of afferents inputs from the body convey information about body posture, including receptors in the skin, receptors in muscle spindles and receptors in the joints (Proske & Gandevia, 2012). However, this information is not enough to specify the location of body-parts in space. Furthermore, the knowledge of the length of the body segments can not be inferred by signals converging from peripheral afferences, so it must be retrieved from stored body size and shape representations (Longo et al., 2010). Given the lack of specific receptors processing such body size and shape, the existence of an implicit knowledge about the metric properties of the own body, deeply linked to somatosensory inputs, has been proposed to exist (Longo et al., 2010). In this regard, Longo et al. (2010) developed a "psychomorphometric" task to examine the body representation underlying hand position sense in healthy adult individuals. In their study, the participant's hand was placed on a table with the palm facing down, under an occluding board keeping it hidden from the view. For each of their fingers, participants were invited to use a long baton to indicate, on the board, the position that was considered exactly above their tips and knuckles. Thus, they were required to judge the felt location of ten hand landmarks (i.e., five on the tips and five on the knuckles, respectively), localizing them on the external space. By comparing the relative location of the judgements for each landmark, the authors extracted the configuration of the judgments for each hand, hence reproducing an implicit map of the perceived hand shape and dimension (see Figure 2). The comparison between this map with the actual shape of participants' hands showed that

the implicit perceptual representation of the own hand structure results remarkably distorted, in a strong consistent and massive way across subjects, regardless of the hand laterality. In particular, participants' hand maps result overestimated in width, while subjects clearly underestimate the length of their fingers, that gradually increases from the thumb to the little finger (Figure 2). Intriguingly, Longo and Haggard (2012a) noticed how these distortions seem to mirror the distortions that characterize the somatosensory homunculus in S1. As argued by the authors, the representation of the metric properties of the body underlying position sense (i.e., the so-called *body model*) maintains the typical somatotopic distortions of S1 maps, even if in attenuated way.
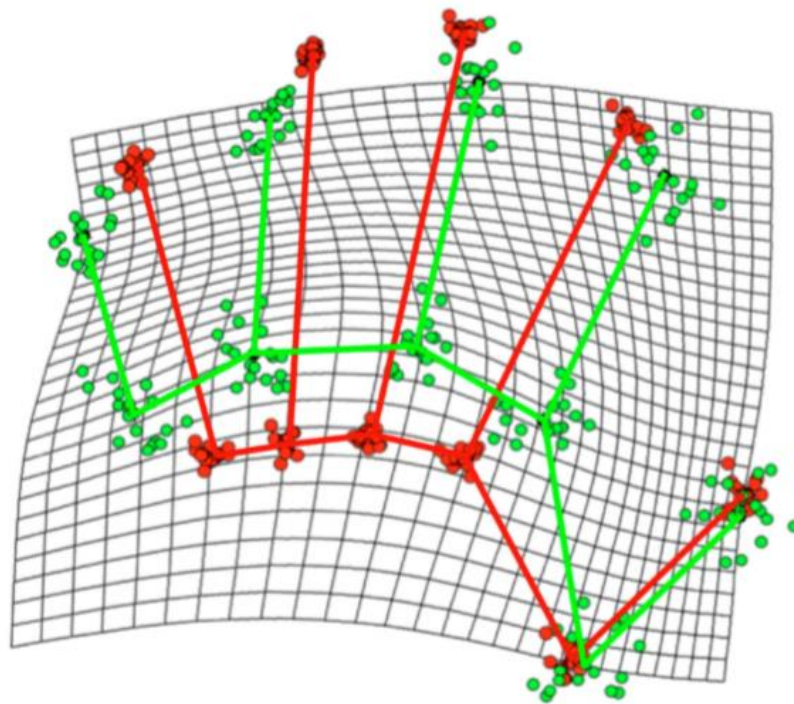
Figure 2. Implicit perceptual map underlying hand position sense, showing distortions of the own hand representation. Comparison between participants' hand actual structure (red lines) and the implicit perceptual map of the own hand size and shape extracted by localization judgments (green lines). The green lines represent the implicit perceived hand map, created by linking the tips of each finger with the knuckles and, in turn, by connecting the adjacent knuckles. The warped grid under the maps clearly shows how a rectangular grip placed over the actual hand shape would be stretched, in order to commute the actual hand shape into the implicit hand maps shape. Adapted from Longo et al. (2010).

Interestingly, Longo and Haggard (2010) show a dissociation between this implicit, largely unconscious distorted hand representation underlying position sense, and a more explicit knowledge of the own body. In the same study, participants were presented with a series of hand images that were stretched in size and shape with respect to the own hand, and they were required to select the hand image much more similar to their own. Surprisingly, subjects' performance was highly accurate in this explicit task. Accurate judgements of the own hand shape in explicit task were also confirmed in subsequent experimental studies (Longo, 2015b; Longo & Haggard, 2012b). This confirms the existence of a deep difference between the veridical representation of the own hand, that is conscious to the own body awareness, and the distorted implicit hand representation mediating position sense, that is inaccessible to the own body consciousness. Moreover, this evidence seems to suggest that different kinds of body representation could arise from different information: on the one hand from somatosensory, largely distorted, signals; on the other hand from visual, more veridical, inputs (Longo et al., 2010).

Subsequent studies confirmed the existence of distortions similar to those found by Longo et al. (2010). For example, Longo et al. (2012b) examined participant's perceived hand size by adopting a *line length task*. In this task, lines of different lengths were presented on a PC screen and participants had to indicate whether each line was shorter or longer as compared to the own finger length / hand width. In line with previous findings (Longo et al., 2010), in the line length task subjects underestimated their finger length which, again, progressively increased from the thumb to the little finger. Thus, the same pattern of distortion that was found during the localization judgments (see Longo et al., 2010) emerged.

Overall, several reports have confirmed that highly distortions of body representation constitute a core feature even in healthy adults cognition (Fuentes, Longo, & Haggard,

2013; Hach & Schütz-Bosbach, 2010; Linkenauger, Witt, Bakdash, Stefanucci, & Proffitt, 2009; Linkenauger et al., 2015; Longo & Haggard, 2011; Longo et al., 2010, 2012b; Saulton, Dodds, Bülthoff, & de la Rosa, 2015). As highlighted by recent accounts, the inherent representation of the own body size and shape appears remarkably distorted regardless of experimental manipulations or psychiatric/neurological conditions (Tamè, Bumpus, Linkenauger & Longo, 2017). Far from being related to pathological conditions, such distorted body representations are considered an intrinsic feature of the healthy adult psychological cognition (Longo, 2017).

1.4. Plastic modulation of body metric representation

As observed in the previous sections, body representation includes the metric properties of body-parts, such as their size (Longo, 2015a). Tactile signals contribute to the construction and updating of the mental representations of the own body, including the appreciation of its size (Serino et al., 2010; Tamé, Braun, Holmes, Farnè & Pavani, 2016; Vallar et al., 2009). Indeed, body size representation is flexible - given the highly dynamic properties of the sensorimotor maps in the brain (Bolognini, Convento, Rossetti & Merabet, 2013; Mogilner et al., 1993) - and can be distorted by incoming tactile inputs. As shown by several evidence, altering somatosensory afferent inputs through anaesthesia modifies the conscious body image (Gandevia & Phegan, 1999; Türker, Yeo, & Gandevia, 2005). In this regard, Gandevia et al. (1999) demonstrated that sudden distortions of the perceived body size can be occasionally induced by altering incoming tactile afference. In particular, by testing a group of healthy participants, Gandevia et al. (1999) showed that reducing peripheral afferent inputs by means of peripheral nerve block or anaesthesia can lead to an overestimation of the perceived size of the deafferented/anaesthetized body district;

repetitive cutaneous stimulation induces a complementary, although less reliable, effect. Specifically, the authors adopted two psychophysical methods to investigate if the perceived size of a body-part can change when its sensory input is changed too: a template matching task and a drawing task. In both tasks, the participant's thumb was completely anaesthetized. In the template matching task, subjects were required to select the perceived size of their anaesthetized thumb in a series of scaled drawings representing the thumb, which could match or not its apparent size. Instead, the drawing task was a motor task in which subjects had to draw their thumb in order to depict its perceived size. Results documented a change in perceived body size induced by thumb anaesthesia following nerve block; indeed, an increase of the perceived size of the thumb due to reduced afferent transmission was found. Interestingly, the perceived size of the lips, which neighbor the thumb representation in S1 map, showed a similar increase, while the perceived size of both index fingers was not affected. The nature of this effect suggests that the amount of tactile inputs conveyed from the body to the cerebral cortex directly affects MBRs (Serino et al., 2010). Crucially, the authors speculated that the topography of the effect seems to support the fact that this input comes from S1 (Gandevia et al., 1999). Thus, even if not demonstrated in the study by Gandevia et al. (1999), this evidence suggests that the perceived size of our own body involves plastic changes that can occur at the cortical level. Subsequent studies demonstrated that the metric properties of the body representation can be distorted in a top-down fashion by manipulating the sense of body ownership (i.e., the sensation that our different body-parts belong to ourselves; Blanke, 2012; Blanke, Slater & Serino, 2015; Collins, Guterstam, Cronin, Olson, Ehrsson & Ojemann, 2017; Ehrsson, Wiech, Weiskopf, Dolan & Passingham, 2007; Kilteni & Ehrsson, 2017; Makin, Holmes & Ehrsson, 2008). Multisensory-based cerebral mechanisms in the brain are responsible of this feeling and neuropsychological evidence suggest that the sense of body ownership can

be altered in healthy individuals as well as in neurological patients, for example following acquired-brain injuries (Bolognini, Ronchi, Casati, Fortis & Vallar, 2014; Fossataro, Bruno, Gindri, Pia, Berti & Garbarini, 2017; Fossataro, Gindri, Mezzanato, Pia & Garbarini, 2016; Garbarini, Fornia, Fossataro, Pia, Gindri & Berti, 2014; Garbarini et al., 2015; Garbarini, Pia, Fossataro, & Berti, 2017; Pia, Garbarini, Fossataro, Fornia & Berti, 2013; Vallar & Ronchi, 2009). A great amount of evidence shows that body ownership is plastic and can be altered in healthy subjects by neurophysiological manipulations, such as the *rubber hand illusion* (*RHI*, Botvinick et al., 1998). During this experimental procedure, a human-like fake hand is placed aligned with the participant's body midsagittal plane, horizontally aligned with the own hand; subjects are touched on the own hand, receiving a synchronous stroking of both their real hand - hidden from the view - and the rubber hand, that is visible (i.e., strokes are delivered spatially and temporally in phase). This visuo-tactile manipulation induces the strong phenomenal feeling that the fake hand becomes incorporated into the own body (i.e., experience of *"embodiment"*) while the own hand is experienced as left in a sort of "abandoned" state (the phenomenon of *"disembodiment"*). From a phenomenological point of view, the rubber hand illusion is modulated by top-down influences deriving from the mental representations of one's own body (Farnè Pavani, Meneghello & Ladavas, 2000; Pavani, Spence & Driver, 2000; Tsakiris & Haggard, 2005). Neuropsychological evidence suggests that the sense of body ownership can be altered regardless of the incongruence between the metric properties of the external fake hand and the perceptual representation of the own body size. In this regard, Pavani and Zampini (2007) tested the role of the rubber hand dimension on the embodiment of the fake hand, in order to investigate the possible influence of the metric properties of the body on the sense of body ownership. In the study by Pavani et al. (2007), a group of healthy participants was exposed to a modified version of the RHI paradigm. Subjects watched a

real-time video image of the own hand, whose bidimensional extensions (horizontal and vertical) were changed, in order to appear enlarged or reduced with respect to the own hand dimension. Thus, during the RHI procedure, the size of the hand exposed to the illusion was modified in the video image, so that the seen hand could be reduced, veridical, or magnified in comparison to the own hand. Both the proprioceptive illusion (by means of an inter-manual pointing task) as well as the phenomenological illusory experience (through a questionnaire) were measured. During the inter-manual pointing procedure, in the baseline condition (pre-adaptation phase) participants were required to slide their right index finger on a graduate scale placed under the table and hidden from the view, and to indicate the perceived position of their left middle finger. After this pre-adaptation phase, they were touched on the own left middle finger while viewing the tactile inputs delivered to their hand through the video image, thus being exposed to a conflict between the seen location of the touch and the felt position of the stroking (adaptation phase). Afterwards, subjects were invited to repeat the inter-manual pointing task (post-adaptation phase). A significant shift towards the position of the video image of the hand in the post inter-manual pointing measures as compared to the baseline was found, both for the veridical and for the bigger (not for the reduced) hand video images. However, the illusory experience occurred for all the veridical, reduced and enlarged hand sizes, as documented by the questionnaire measures. These results show that the seen hand dimension directly influences the illusory embodiment of the external hand, since the proprioceptive illusion occurred both for the veridical and the magnified hand images, but was not found for the reduced ones. Capitalizing on these findings, the authors suggest the existence of a specific asymmetry concerning the embodiment of bigger, but not smaller, images of the own body districts within the internal representation of the own body. Importantly, specific aspects of

the body, such as the representation of the metric properties, directly influence the multisensory modulation of the own body representation (Pavani et al., 2007)

1.5. Modulation of tactile processing and motor control by body metric representation

As above-mentioned, the body model proposed by Longo and co-workers (2010) provides the theoretical basis to understand the cognitive mechanisms underlying the metric processing of body representation, that in turn support somatosensory functions such as tactile size perception and position sense. In line with this hypothesis, recent accounts documented that altering the conscious representation of the own body image by means of multisensory illusions, in turn induces corresponding distortions in tactile perception (Banakou, Groten & Slater, 2013; Bruno & Bertamini, 2010; De Vignemont, Ehrsson, Haggard, 2005; Haggard & Jundi, 2009; Taylor-Clarke, Jacobsen & Haggard, 2004). Moreover, distortions during object reaching and grasping following bodily illusions has been reported (Bernardi, Marino, Maravita, Castelnuovo, Tebano & Bricolo, 2013; Bruno et al., 2010; Haggard et al., 2009).

Tactile perception is body-referenced: the tactile processing of external objects touching the physical body includes not only the processing of afferent inputs, since it is also related to the internal multisensory model of one's own body (Serino et al., 2010). An evidence that tactile object perception is building up by linking tactile inputs to multisensory representations of the own body, comes from Taylor-Clarke et al. (2004). In their study, a group of healthy participants was required to report the distance between two tactile stimuli delivered at the same time to the finger and to the arm. Subjects' performance was in line with Weber's pioneering findings (Weber, 1834, 1978): the perceived size or length

of an object depends on the body area to which tactile stimuli are presented. Thus, a given object of a constant size is perceived larger when presented to a dense tactile innervation skin region (for example, the fingers) with respect to less innervated skin areas (such as the arm). Crucially, in the experiment by Taylor-Clarke et al. (2004) when participants were blindfolded and had to judge the distance between the two tactile stimuli after visually experiencing the own arm enlarged and the own finger reduced, the tendency to underestimate the tactile distance on the arm, with respect to the finger, was reduced. Indeed, subjects tended to overestimate the tactile distance perceived on the arm, as compared to the distance perceived on the finger. Since there are no peripheral receptors providing information about the metric properties of one's own body-parts, Taylor-Clarke et al. (2004) speculated that body-parts size representations are processed by synthesizing multiple visual and proprioceptive signals, that are stored in long-term memory and then retrieved and updated in order to elaborate tactile objects touching the physical body surface. Thus, tactile distance and estimation of object size would rely on an implicit cognitive representation of one's own body-parts dimension. A study by De Vignemont et al. (2005) extended this evidence showing not only that touch is body-referenced but also that the own body-representation is online updating in order to integrate sensory inputs. Healthy volunteers were asked to judge the tactile distance between two points on the own left index finger, while holding the tip of the left finger with the right hand. Afterward, they were exposed to a somatic illusion by applying tendon vibration to the biceps or triceps tendon of the right arm, thus inducing a perceived stretching or shortening of the left index finger, respectively. This induced an asymmetric distortion of the tactile distance estimation: biceps vibration elicited subjective finger stretching, in turn leading to overestimation of the two points tactile distance; instead, the finger shortening following triceps vibration did not induce participants to underestimate the tactile distance between

the two points. This evidence confirms that the perceived object size may rely on the representation of the metric properties of the own body.

In the same vein, Bruno et al. (2010) showed a distorted perception of external objects dimension following the embodiment of fake hands different in size with respect to the own hand dimension. Specifically, a group of healthy volunteers underwent a modified version of the classical RHI paradigm (Botvinick et al., 1998) in which either a magnified and a reduced model of the rubber hand were adopted. Subjects were required to judge the estimated dimension of the grasped objects, after multisensory RHI stimulation with the bigger hand and after the stimulation with the smaller hand, respectively. Results showed a distortion in haptically perceived object size: immediately after the multisensory illusory experience, participants judged objects to be bigger (after the embodiment of the bigger fake hand), or smaller (after the embodiment of the smaller rubber hand) with respect to a standard object of identical size felt by the other hand. In line with this evidence, experimental studies using virtual reality paradigms reported sudden distortions of object dimension judgements following the phenomenal illusory experience of the sense of body ownership towards a surrogate whole body different in size from the own. In this regard, Banakou et al. (2013) showed that in healthy adults, the illusory ownership of a virtual 4-years old child body induces an overestimation of objects size. In addition, Haggard and co-workers (2009) corroborated these findings showing how the representation of the own body size influences the dimensional perception of external objects, and how it extends its modulation from objects size to object weight perception. In their study, Haggard et al. (2009) adopted the RHI paradigm in order to induce a size-weight illusion, according to which a small object is felt heavier with respect to a larger object of the same dimension. Healthy participants were exposed to the RHI watching an enlarged or a reduced fake hand covered by a glove being stroked, while feeling the synchronous stroking on the own

unseen hand. After the illusory experience, they were asked to grasp and estimate the weight of a series of cylinders hidden from the view, identical in size but differing in weight. Due to the size-weight illusion, subjects experienced a change in object weight estimation, judging the grasped cylinders heavier after the embodiment of the bigger glove than when they had experienced the RHI with the small glove. Finally, recent evidence demonstrates the modulation of the own body size representation on motor control, reshaping the bodily representations involved in our interactions with the external environment. In the study by Bernardi et al. (2013), a group of healthy subjects performed a reach-to-grasp movement task while viewing the own hand through a monitor display, being veridical in size, or enlarged/shrunken. Participants were invited to reach and grasp a cylinder of constant dimension with their hand by using a precision grip (i.e., by using only their thumb and right index finger) while online viewing their own grasping movements. Results showed that viewing the own hand enlarged, but not shrunken, altered the movement kinematics reducing the maximum grip aperture. Instead, any modulation by the reduced images of the own hand on the grasping kinematics was found. Thus, altering the visual size of the own body in turn induces a recalibration of the kinematics of the own grasping movements. Interestingly, the altered kinematics of the grasping movements perdured even when the enlarged version of the own hand was hidden from the view, suggesting a relatively stable and persistent change of the body schema involved in action control. Overall, this set of evidence converges in showing on the one hand the plastic properties supporting the knowledge of the own body size, on the other hand the tight link between somatosensory processing and the metric properties of one's own body representation.

Conclusion of this chapter and overall aims of the studies

The link between the somatosensory system and the knowledge of the metric properties of the body is supported by several neuropsychological evidence (De Vignemont, 2010; Vallar et al., 2009). Body size representation was shown to depend on somatosensory afference (Gandevia et al., 1999); in addition, body metric representation is plastic, and can be altered by neuropsychological manipulations (Bruno et al., 2010; Haggard et al., 2009; Pavani et al., 2007). However, the cognitive and neural mechanisms underlying the perception of the metric properties of the body remain unclear. The next chapters will give a characterization of these issues.

In Chapter 2, I will investigate whether short-term plastic changes of internal body representation may occur as early in somatosensory processing as S1, in turn modulating the metric properties of the body. Indeed, although the relationship between somatosensory processing and body representation - including size and shape - has been acknowledged, the role of S1 in such higher-order body representation, remains poorly understood. To verify this putative neurofunctional locus, four different rTMS experiments will be presented, aimed at modulating the hand cortical representation in S1, seeking for any distortions of its perceived size. The causal involvement of S1 in the perceptual processing of the body size will be discussed.

Chapter 3 will explore whether and how the sense of body ownership could shape the perceptual representation of the own hand size. To this aim, four behavioral experiments using the RHI will be discussed, assessing whether the embodiment of fake hands of different sizes would affect the metric properties of one's own body perception.

Finally, Chapter 4 will provide evidence of the perception of the own body size in healthy children, considering its development.

2. PERCEPTUAL DISTORTION OF THE OWN BODY SIZE BY CHANGES OF ITS CORTICAL SOMATOSENSOTY MAP. A rTMS STUDY

2.1. Aim of the study

As discussed in the previous chapters, S1 is a main neural node of the cortical network representing the body, as acknowledged since the pioneering studies of Penfield et al. (1950). The somatosensory homunculus appears as a straightforward depiction of the way in which body-parts are represented at the cortical level (Harding-Forrester et al., 2018). As argued by Longo (2015a), body representations underlying somatosensory cortical processing are intrinsically related to the representation of body size and shape, sometimes mirroring the distortions that feature the somatosensory homunculus. Interestingly, as demonstrated by Gandevia et al. (1999), the link between somatosensation and body image is well-exemplified by the occurrence of perceptual distortions of the human body size that can be produced by local anesthesia or cutaneous stimulation: in healthy individuals, the reduction of afferent inputs, induced by peripheral nerve block or local

anesthesia, changes the perceived size of the anesthetized body-part. In line with the somatotopic organization of the contralateral body surface in S1, the effect of the deafferentation is body-part specific: following the anesthesia of the right thumb, the visual representation of its size is perceived as enlarged, as well as that of the lips, neighboring the representation of the thumb in the somatosensory homunculus. This evidence suggests that tactile inputs contribute to the building up and updating of the internal representations of one's own body, including the visual appreciation of its size (Serino et al., 2010; Tamé, et al., 2016; Vallar et al., 2009); this occurs notwithstanding the absence of peripheral receptors directly coding the size and shape of body-parts (Harding-Forrester et al., 2018; Kaas, Qi, & Stepniewska, 2018). Hence, the amount of tactile information transmitted from the body to the cortex can directly affect MBRs (Serino et al., 2010). If this is the case, the opposite might also occur: alterations or dysfunctions of the somatosensory cortical maps should influence the metric representation of body-parts. However, this hypothesis still needs empirical demonstration.

To address this issue, I performed a series of experiments, aimed at modulating the representation of a body-part in S1, namely the hand, by using rTMS (Bolognini & Miniussi, 2018), to assess whether and how short-term, reversible, changes at the level of the central somatosensory maps could alter the perceptual representation of the size of the own hand. I also assessed the selectivity of the effect with respect to the somatotopy of the cortical representation of body-parts (Experiments 1 and 2), and the existence of a hemispheric specialization (Experiment 3). Finally, in the last experiment (Experiment 4) the selectivity of the contribution of S1 to the representation of body size was assessed by interfering with the activity of the inferior parietal lobules (IPL) (Caspers & Zilles, 2018).

I choose to compare the effects of interfering with the activity of S1 and of IPL since the IPL, of both the left and the right hemispheres, is involved in the multisensory

representation of the body (Bolognini & Maravita, 2011; Maravita, Spence, & Driver, 2003), as well as in the so-called "superficial schema," which mediates the localization of somatic sensations on the body surface (Felician, Anton, Nazarian, Roth, Roll & Romaiguere, 2009; Head et al., 1911; Longo et al., 2010; Serino et al., 2010; Vallar & Papagno, 2003). Therefore, the stimulation of the IPL would allow verifying whether the perceptual representation of the size of the own body-parts also relies on non-primary somatosensory higher-order posterior parietal cortices, which may work in concert with the lower-level processing of S1.

2.2. EXPERIMENT 1 – Modulation of metric representation of the body by right S1 rTMS

In this experiment, rTMS was applied over the hand representation of S1 of the right hemisphere; perceptual distortions of the size of the contralateral (left) and of the ipsilateral (right) hands were assessed with a 2-forced choice visual task. The participants's task was to report whether a picture showing their own hand, whose dimension varied, being bigger or smaller than the real one, matched the size of their own hand, as actually felt.

2.2.1. Materials and Methods

Participants

Twenty neurologically healthy participants (12 females; 18 right-handed; mean age ± Standard Deviation = 24.3 ± 2.9 years; range = 20-33 years) participated in Experiment 1. All participants had normal or corrected-to-normal vision. Handedness was assessed by a standard questionnaire (Oldfield, 1971). Participants were naïve both to the experimental procedure and to the purpose of the study. They gave their written informed consent to take part in the study, which was approved by the local Ethical Committee of the University of

Milano-Bicocca, and conducted in line with the Declaration of Helsinki. Exclusion criteria included history of neurological and psychiatric disorders, and contraindications to TMS (Rossi, Hallett, Rossini, & Pascual-Leone, 2009) and were assessed with a questionnaire before the first experimental session.

Hand Size Task

The Hand Size task (HST) was a 2-forced-choice task developed to assess the perceptual estimation of participants' own hand size. In a dimly-illuminated room, participants comfortably sat in an armchair in front of the PC screen at a distance equal to their forearm. Stimuli were colored pictures of the participants' left and right hands, seen from the egocentric perspective, taken with a digital camera (ASUS Go 5" HD) before administering the task. In order to prevent shape distortions, each hand's picture was acquired by using a wooden box (length= 60 cm, height= 20 cm, width= 30 cm), placing the digital camera above the upper side of the box (open to the view), in the same position for each participant. Thus, pictures were taken at the same distance (i.e., 20 cm) for all participants, with the same zoom settings. Then, each photograph was scaled by using the GIMP software, so that the experimental stimulus was of the real size of the participant's hand (i.e., same size trials, 0% of change with respect to the participant's hand size), or could be 3%, 6%, 9%, 12%, 15%, 18% smaller (-) or bigger (+) (i.e., different size trials) than the participant's real hands, for a total of 13 hand dimensions (see Figure 1a). The different hand dimensions (i.e., smaller or bigger than the real size) were on-line created by E-Prime Software (Psychology Software Tools Inc., Pittsburgh, PA), trial-by trial during the task. Each hand stimulus was presented for 1500 ms, followed by a central fixation (white cross) presented on a black screen (see Figure 1b for the experimental timeline). The participants' task was to indicate whether the viewed hand matched («Same» response) or not («Different» response) the size of their own hand; participants were

instructed to give their response, as accurately and fastly as possible, by pressing the right buttom of the PC mouse (using their right hand, the ones ipsilateral to the rTMS side) if they judged the viewed hand as of the same size of their own hand, or the left button of the PC mouse if they considered the seen hand of a different size. At variance with previous studies using a similar task (e.g., Gandevia et al., 1999; Longo et al., 2012a, 2012b; Longo, Long & Haggard 2012), participants had a limited time for responding: this variation was introduced in order to force a 'first-hand' judgement, hence limiting the chance of adopting more cognitive strategies, and as well in consideration of the short-living after effects of the rTMS (about 15 min following a 15 min train of rTMS at 1-Hz; see e.g., Bolognini et al., 2018; Chen, Friedman & Roe, 2003; Knecht, Ellger, Breitenstein, Bernd Ringelstein & Henningsen, 2003). Pictures of the participant's left and right hands were presented in two separate blocks (AB-BA order, counterbalanced across participants); in both blocks, participants were instructed to focus on the felt size of their own left hand (out-of-view, hand contralateral to rTMS side). In each block, 16 trials were presented for each of the 13 hand sizes, for a total of 208 trials. Each block lasted ~8 min, for a total duration of the procedure of ~16 min. Stimuli presentation and randomization were computer controlled by the E-Prime software (Psychology Software Tools Inc., Pittsburgh, PA), used to run the task and to record the participants' responses.

Before the experiment, a training session was performed to allow participants to familiarize with the task. During the experiment, the participants' left and right hands (as well as the PC mouse used for responding) were kept out-of-view, hidden under a wooden panel, in order to prevent an online size matching of the hands. The HST was administered before (baseline) and after the application of 1-Hz rTMS (see below).
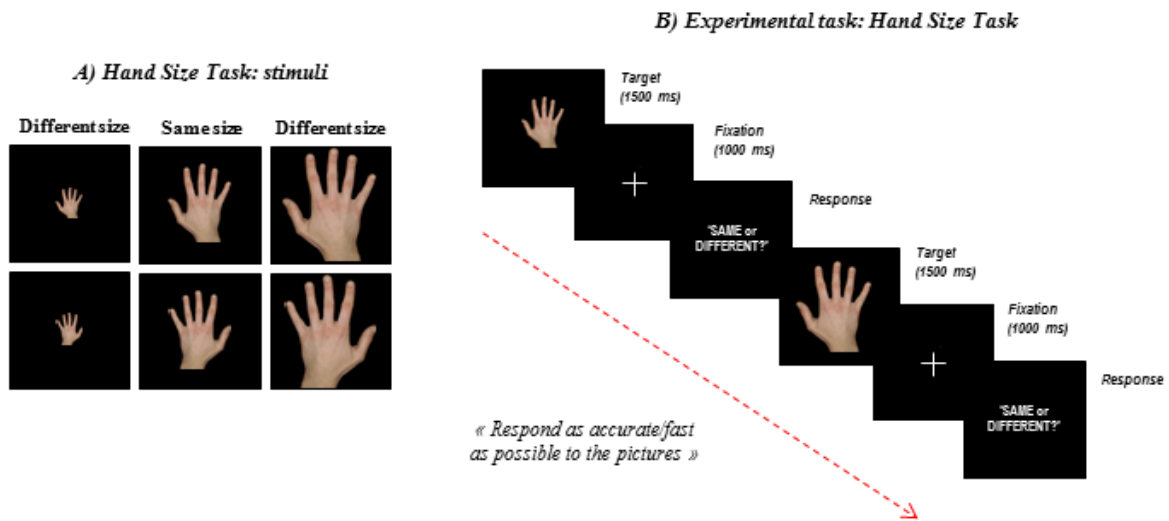
Figure 1. Experiment 1. Hand Size Task - HST. A) Stimuli were pictures of the participant's left and right hands with different sizes, with respect to the participant's individual hand: 0% (*same* size trials), smaller or bigger by 3%, 6%, 9%, 12%, 15% or 18% (*different* size trials). **B)** In each trial, a hand picture (target) was presented; the participants' task was to judge whether the size of the viewed hand matched («Same» response) or not («Different» response) the size of their own (out-of-view) hand (2 forced-choice task). The task was performed before (baseline), and after 15 min of 1-Hz rTMS. Adapted from Giurgola, Pisoni, Maravita, Vallar & Bolognini (2019).

TMS protocol

A Magstim Super Rapid[2] transcranial magnetic stimulator (Magstim Co. Ltd, Whitland, UK) with a figure-of-eight-shaped coil (Ø = 70 mm) for focal cortical stimulation was used to deliver biphasic 1-Hz repetitive TMS (rTMS). rTMS protocol lasted for 15 min, delivering a total of 900 pulses. The TMS intensity was set at 110% of the individual resting motor threshold (rMT, mean = 51% ± 6.52%, range = 42-67% of the maximal stimulator output), defined as the minimum intensity of the TMS stimulator able to elicit five out of ten detectable motor twitches in the contralateral hand (Rossi et al., 2009). The rMT was assessed targeting the optimal scalp position for inducing, with the lowest stimulation intensity, motor twitches in the left hand, by targeting the right primary motor cortex (M1) with single TMS pulses.

In Experiment 1, the coil was positioned over the S1 hand map in the right hemisphere. I firstly used an anatomical procedure to localize the hand area in S1, placing the coil 2 cm backward from the M1 hotspot (e.g. Avenanti, Bolognini, Maravita & Aglioti, 2007; Bolognini, Rossetti, Convento, & Vallar, 2013; Fiorio et al., 2005; Harris, Miniussi, Harris, & Diamond, 2002).

Worth mentioning, recent evidence indicating that the S1-hand map is located ~2 cm lateral and ~0.5 cm posterior to the M1-hand scalp location, at least when the index finger map is localized (Holmes & Tamè, 2019; Holmes et al., 2019; Tamè & Holmes, 2016). However, in the present study I aimed at targeting the hand in S1 (in line with the stimuli presented in the HST).

In addition to the anatomical localization approach, given the imprecision and variability of a mere anatomical localization of S1, I also used a Neuronavigation System, and functional criterion (reduction of tactile sensitivity at the hand palm). In particular, the SofTaxic Evolution navigator system (Version 1.0, http://www.emsmedical.net; see for instance, Bolognini, Rossetti, Maravita, & Miniussi, 2011) was used to reconstruct a virtual volume of each participant's brain. This software allows creating from a template an MRI image of the cerebral cortex in Talairach coordinates, by means of a warping procedure. Parameters for warping the template image were estimated on the basis of four digitized skull landmarks (i.e., nasion, inion and the right/left preauricular points), and 50 uniformly distributed points mapped on the participant's scalp, with a mean error of 2.11 mm and a standard deviation of 2.04 mm. Digitalization and neuronavigation were achieved via a graphic user interface and a 3D optical digitizer (NDI, Polaris Vicra). For each participant, the location of S1 was identified following the Talairach coordinates X = 47, Y = -32, Z = 59 on the MRI template and using a 3D virtual reconstruction of the participant's brain. The coordinates of S1 were derived from previous functional Magnetic

Resonance Imaging (fMRI) studies (e.g. Boakye, Huckins, Szeverenyi, Taskey & Hodge, 2000), and had already been used in previous TMS studies targeting the S1 hand area (e.g., Bolognini et al., 2011; Bolognini, Olgiati, Rossetti & Maravita, 2010; Bolognini, Rossetti, Fusaro, Vallar & Miniussi, 2014; Pisoni, Romero Lauro, Vergallito, Maddaluno & Bolognini, 2018). In previous TMS studies (see, e.g., Bolognini et al., 2010, 2011, 2014; Rossetti, Miniussi, Maravita & Bolognini, 2012), the same Talairach coordinates have been shown to be associated to functional effects, including paraesthesia or induction of tactile extinction by single-pulse TMS to S1. During the stimulation, the correct and stable position of the coil was monitored on-line with the same neuronavigation system, and the coil was kept tangential to the scalp, with the handle pointing laterally 45° away from the mid-sagittal line. This neuronavigation procedure has been used in several previous studies (e.g., Bolognini et al., 2014; Carducci & Brusco, 2012; Pisoni et al., 2018; Tecchio et al., 2014).

Moreover, for each participant, the effective modulation of the S1 hand representation by 1-Hz rTMS was further checked by using a functional method, namely by administering a 2-point discrimination task (2PDT), to assess changes in tactile sensitivity before and after the rTMS protocol (Kennett et al., 2001; Tegenthoff et al., 2005). This ensured an appropriate, functionally-based, localization of S1 hand area.

During the 2PDT, participants were blindfolded and their left hand, contralateral to the rTMs site, was touched on the palm of left hand with 1 or with 2 points using a 2-Point Discriminator (Touch Test® Two-Point Discriminator, North Coast Medical & Rehabilitation Products). Four pairs of pins, separated by 7, 8, 9 and 10 mm, as well as a single pin representing the single touch condition, were used. Participant were required to report whether 1 or 2 pins were perceived. A total of 40 stimuli were given, 10 for each distance for a total duration of ~5 min. The 2PDT was administered before and after 1-Hz

rTMS, along with the HST (experimental task); the order of the two tasks was randomized and counterbalanced across participants (AB-BA). The comparison of the participants' performance at the 2PDT, showed a significant decrement of tactile sensitivity after 1-Hz rTMS over right S1, as compared to the baseline (baseline = 80% ± .06 vs. post-rTMS = 70% ± .14, t_{19}= 2.92, p= .01), confirming the effective stimulation of the somatosensory hand area in S1.

Statistical analyses

The participant's performance at the HST was analyzed with the statistical program R (R Development Core Team, 2008). Responses were entered as dependent binomial variable, coding the «Same» responses as 1 and the «Different» responses as 0. Data were submitted to a series of generalized mixed effects models (Baayen, Davidson & Bates, 2008), using the "lme4" package (version 1.1-5, Bates, Maechler, Bolker & Walker, 2015). First, I assessed if the inclusion of fixed effects or interactions contributed to the model goodness-of-fit. This was tested by likelihood ratio tests (LRT), including only effects which significantly increased the model goodness-of-fit (Gelman & Hill, 2006). The fixed factors were "Time" (factorial, 2 levels: baseline vs. post-rTMS), "Hand Laterality" (factorial, 2 levels: right vs. left hand), and "Hand Size" (from -18% to +18%, as a continuous independent variable); their interactions were also tested. A by-subjects random intercept was included. Parameters from the final, best fitting model are reported, including factors' significance level, based on Satterthwaite's degrees of freedom approximation in the "lmerTest" R package (version 2.0-29, Kuznetsova, Brockhoff & Christensen, 2015).

2.2.2. Results

The model included the main effects of Time, Hand Laterality, and linear, quadratic and cubic effects of Hand Size, as well as the interactions: Time X Hand Size, and Hand Laterality X Hand Size (see Table 1 for results of the LRT procedure for model selection, and for the final model's parameters). The model showed significant effects of Time, and of the linear, quadratic, and cubic trends of the main factor Hand Size. Of main relevance, the Time X Hand Size interaction was significant for the linear, quadratic, and cubic (z=2.34; p=.019) trends of the Hand Size effect (see Table 1). As shown in Figure 2, after rTMS over the right S1, participants overestimated the size of their hand, regardless of which hand was presented (left or right viewed hand) during the HST, increasing their «Same» responses to hands bigger than their real ones (Figure 2).
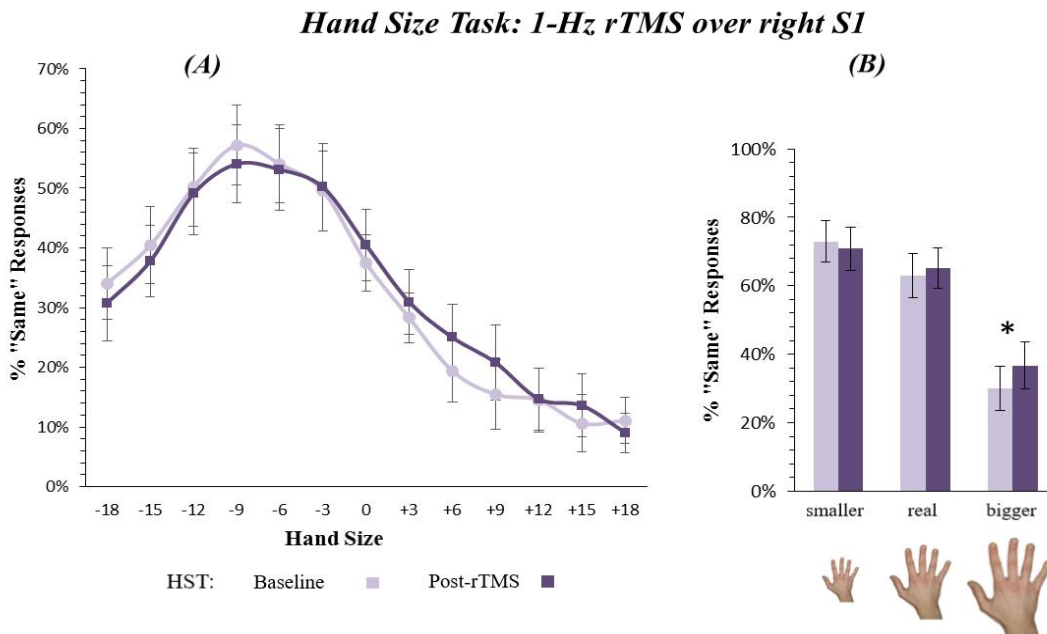

Figure 2. Hand size perceived change by 1-Hz rTMS of the right S1 hand area (Experiment 1). Panel **(A)** shows the increase of «*Same*» responses after right S1 rTMS in trials presenting a hand bigger than the participant's real hand, regardless of the hand laterality (Time x Hand Size interaction, p= .01). X axis = mean percentage of the hand size change, with negative values corresponding to a reduction of the hand size, positive values to an increase; Y axis = percentage of «*Same*» responses. Light violet line = participants' performance before 1-Hz rTMS (baseline); dark violet line = performance after 1-Hz rTMS (post-rTMS). Panel **(B)** recaps the overestimation effect. Error bars represent the Standard Error of the mean (SEM). Adapted from Giurgola et al. (2019).

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HST – LRT goodness-of-fit test

	χ^2	Df	p
Time	.54	1	.46
Hand Laterality	4.22	1	.04
Hand Size	1681.82	3	<.001
Time X Hand Size	16.61	3	<.001
Time X Hand Laterality	.91	1	.33
Hand Laterality X Hand Size	8.15	3	.04
Time X Hand Laterality X Hand Size	2.53	3	.46

HST – Mixed logistic regression

	B	SE	z value	p
Intercept	-0.35	.11	-3.06	.002
Time	-0.13	.05	-2.57	.01
Hand Laterality	-0.04	.05	-0.76	.44
Hand Size (linear trend)	-0.11	.006	-16.48	<.001
Hand Size (quadratic trend)	-0.004	.0003	-12.48	<.001
Hand Size (cubic trend)	.0002	.00003	7.58	<.001
Time X Hand Size (linear trend)	-0.02	.008	-3.21	.001
Time X Hand Size (quadratic trend)	.0007	.0003	2.08	.03
Time X Hand Size (cubic trend)	.00007	.00003	2.34	.01
Hand Laterality X Hand Size (linear trend)	.01	.008	1.35	.17
Hand Laterality X Hand Size (quadratic trend)	-0.00006	.0003	-0.17	.86
Hand Laterality X Hand Size (cubic trend)	-0.000005	.00003	-0.14	.88

Table 1. Results from statistical analysis of Experiment 1. Abbreviations: HST, hand size task; LRT: likelihood ratio tests.

2.3. EXPERIMENT 2 – Somatotopic organization of body's metric properties in S1

Experiment 2 investigated whether the perceptual distortion of the hand size induced by rTMS over the S1-hand map extended to other body-parts, namely the foot, or if it was specific for the body district whose cortical S1 representation was targeted. Critically, S1 cortical map of the foot lies far from the cortical map of the hand, being located in the dorso-medial surface of S1 (Penfield et al., 1950). The prediction was thus made that rTMS to the hand area should not affect the foot cortical somatosensory map, and hence foot size judgements.

2.3.1. Materials and Methods

Participants

Twenty healthy participants (11 females; 18 right-handed; mean age = 24.7 ± 5.1 years; range = 20-30 years), recruited using the same criteria of Experiment 1, took part in Experiment 2. One participant did not complete the experiment, and therefore was excluded from the analyses. In the final sample (N=19), the mean individual rMT value was 54% (± 7.2%, range = 41-67%) of the maximal stimulator output.

Experimental paradigm and statistical analyses

Materials, methods and statistical analyses were identical to those of Experiment 1. The only difference pertained to the experimental tasks, now including the HST with the presentation of the left hand only, and a version of it with foot stimuli (i.e., *Foot Size Task*, FST). These new stimuli depicted the participants' left foot. In both tasks, the size of the stimuli ranged from -15% to +15% (again in steps of 3%; the more extreme dimensions, -/+18% were not included, in order to reduce the number of trials). For both tasks, a total

of 176 stimuli were given (16 for each distance). The order of the two tasks was randomized and counterbalanced across participants (AB-BA), with half of participants starting with the HST and the other half starting with the FST.

Changes in tactile sensitivity brought about by rTMS were assessed with the 2PDT on the left hand and on the left foot, contralateral to the rTMS site: a significant decrease of the hand tactile sensitivity was found after 1-Hz rTMS of S1 hand representation (baseline = 77.19% ± .06 vs. post-rTMS = 66.75% ± .14, t_{18} = 2.83; p<.01). Instead, tactile sensitivity at the foot did not change after the stimulation of the S1-hand map (baseline = 59.47% ± .05 vs. post-rTMS = 57.36% ± .10, t_{18}= .93; p= .4).

2.3.2. Results

With respect to the HST, the best model included the main effects of Time and Hand Size, as well as their interaction (see Table 2 for details). Results showed significant linear, quadratic and cubic trends for the main effect of Hand Size. Furthermore, the interaction between Time, and the linear and cubic (z=7.19; p<.001) trends for the Hand Size effect, resulted significant, as for Experiment 1. As in the previous experiment, «Same» responses increased for hand stimuli with dimension bigger than the participants' real hand (see Figure 3).

With respect to the FST, the final model included only the main effect of Foot Size, with significant linear, quadratic and cubic trends of the main effect of Foot Size. Importantly, the main effect of Time and its interactions did not reach significance (all p>.63; see Table 2 and Figure 3).
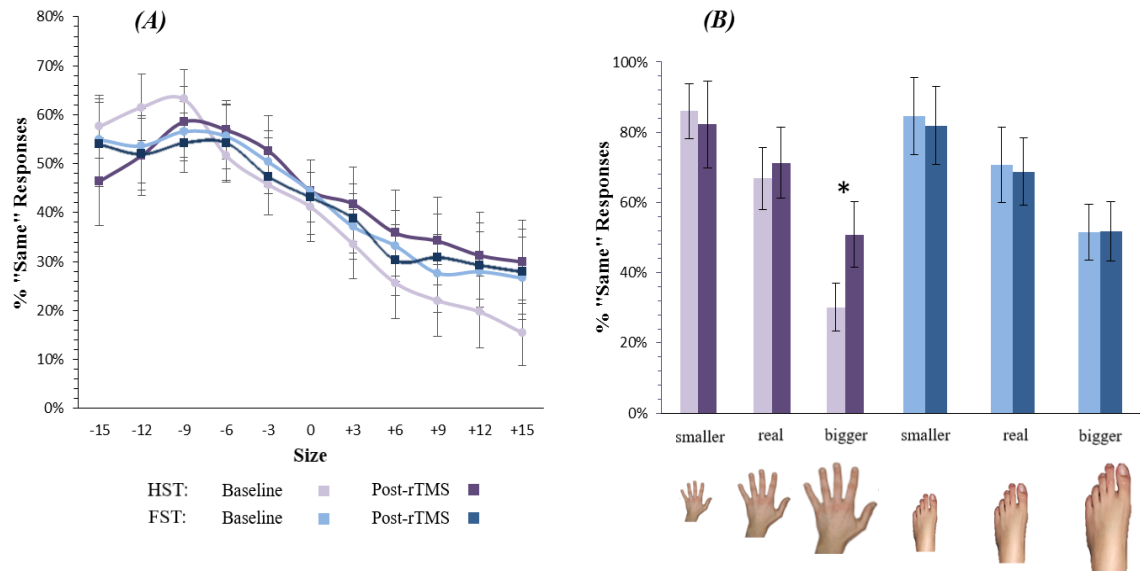
Hand Size Task & Foot Size Task: 1-Hz rTMS over right S1

Figure 3. Hand and foot size perceived change by 1-Hz rTMS of the S1 hand area (Experiment 2). Panel **(A)** illustrates the increase of «*Same*» responses after right S1 rTMS in trials presenting a hand bigger than the participant's real hand (Time x Hand Size interaction, p=.001). Light purple and blue lines = performance before 1-Hz rTMS (baseline) at the HST and FST, respectively; dark purple and blue lines = performance after 1-Hz rTMS at the HST and FST, respectively. See caption to Figure 2 for details (X/Y axis). Panel **(B)** recaps the somatotopic specificity of the overestimation effect. Error bars= SEM. Adapted from Giurgola et al. (2019).

HST – LRT goodness-of-fit test			
	χ^2	Df	p
Time	13.45	1	<.001
Hand Size	446.62	3	<.001
Time X Hand Size	58.92	3	<.001
FST – LRT goodness-of-fit test			
	χ^2	Df	p
Time	.23	1	.62
Foot Size	352.57	3	<.001
Time X Foot Size	1.51	3	.67
HST – Mixed logistic regression			
	B	SE	z value	p
Intercept	-0.11	.14	-0.75	.44
Time	-0.30	.07	-3.80	<.001
Hand Size (linear trend)	-0.75	.09	-7.91	<.001
Hand Size (quadratic trend)	-0.16	.04	-3.83	<.001
Hand Size (cubic trend)	.21	.04	4.31	<.001
Time X Hand Size (linear trend)	-0.33	.13	-2.40	.01
Time X Hand Size (quadratic trend)	.06	.06	.98	.325
Time X Hand Size (cubic trend)	.21	.03	7.19	<.001
FST – Mixed logistic regression			
	B	SE	z value	p
Intercept	-0.28	.16	-1.70	.08
Foot Size (linear trend)	-0.79	.06	-11.38	<.001
Foot Size (quadratic trend)	-0.07	.03	-2.32	.02
Foot Size (cubic trend)	.16	.03	4.56	<.001

Table 2. Results from statistical analysis of Experiment 2. Abbreviations: FST, foot size task; HST, hand size task; LRT: likelihood ratio tests.

2.4. EXPERIMENT 3 – Modulation of metric representation of the body by left S1 rTMS

Experiment 3 aimed at testing a possible hemispheric asymmetry of S1 in modulating the metric properties of one's own hands, by targeting the hand somatosensory map in the left hemisphere.

2.4.1. Materials and Methods

Participants

Twenty healthy participants (17 females; 18 right-handed; mean age = 22.5 ± 2.5 years; range = 19-31 years), selected using the same criteria of Experiment 1, took part in Experiment 3. In this experiment, the mean individual rMT value was 52.7% (± 6.4%, range = 43-63%) of the maximal stimulator output.

Experimental paradigm and statistical analyses

Stimuli, procedures, and statistical analyses were identical to Experiment 1, with the exception of the rTMS target, that was the S1 hand representation in the left hemisphere, localized with the SofTaxic Evolution navigator system and following Talairach coordinates (X = -47, Y = -32, Z = 59, e.g., Boakye et al., 2000). Accordingly, the 2PDT was now delivered to the right hand. Participants performance at the 2PDT showed a significant decrement of right hand tactile sensitivity after 1-Hz rTMS over the left S1 (baseline = 78.91% ± .78 vs. post-rTMS = 67.25% ± .67, t_{19}= 3.88, p= .0009).

2.4.2. Results

The best model included the main effects of Time, Hand Laterality and Hand Size, as well as the Time X Hand Size and the Time X Hand Laterality interactions (see Table 3). The main effects of Time and Hand Laterality reached significance, as in Experiment 1. Additionally, the main linear, quadratic and cubic trends of the main effect of Hand Size were significant. Crucially, as in Experiment 1, the Time X Hand Size interaction was significant for the linear, quadratic and cubic ($z= 1.98$; $p= .046$) trends of the Hand Size effect, showing effects comparable to those found in Experiment 1, by targeting the right S1: after stimulation of the left S1, participants overestimated the size of their hands, as demonstrated by the increased «Same» responses when the viewed hands were bigger than their real one (see Figure 4).

However, after stimulation of left S1, but not of right S1 (see Experiment 1, but also Experiment 2), I found an increase of «Same» responses when the viewed hands matched the size of the participant's hands (i.e., same size trials = 0% of size difference), suggesting an improved recognition of their real hand size. Hence, in order to further verify a possible left-right hemispheric asymmetry of S1 for the estimation of the own hand size, a further analysis was performed, adding as a fix, between-subjects, factor the Hemisphere over which rTMS was delivered (2 levels: right S1 vs. left S1, i.e., Experiment 1 vs. 3 respectively). The LRT test showed significant main effects of Hand Size ($\chi^2=3109.6$, Df=3, p<.001), Time ($\chi^2=7.5$, Df=1, p=.006), and Hemisphere ($\chi^2=139.5$, Df=1, p<.001). The Hand Size X Hemisphere ($\chi^2=152.6$, Df=3, p<.001), and, most importantly, the Hand Size X Time ($\chi^2=49.04$, Df=3, p<.001) interactions were significant. The latter interaction effect confirms findings from the previous analyses. The lack of significant Hand Size X Time X Hemisphere ($\chi^2=2.52$, Df=3, p=.47), and Time X Hemisphere ($\chi^2=1.25$, Df=1, p=.26) interactions rules out the existence of significant differences between rTMS over

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the left or the right S1 for hand size perception. Rather, overall, participants in Experiments 3 gave more «Same» responses (main effect of Hemisphere), but the rTMS effect did not differ between left and right S1.
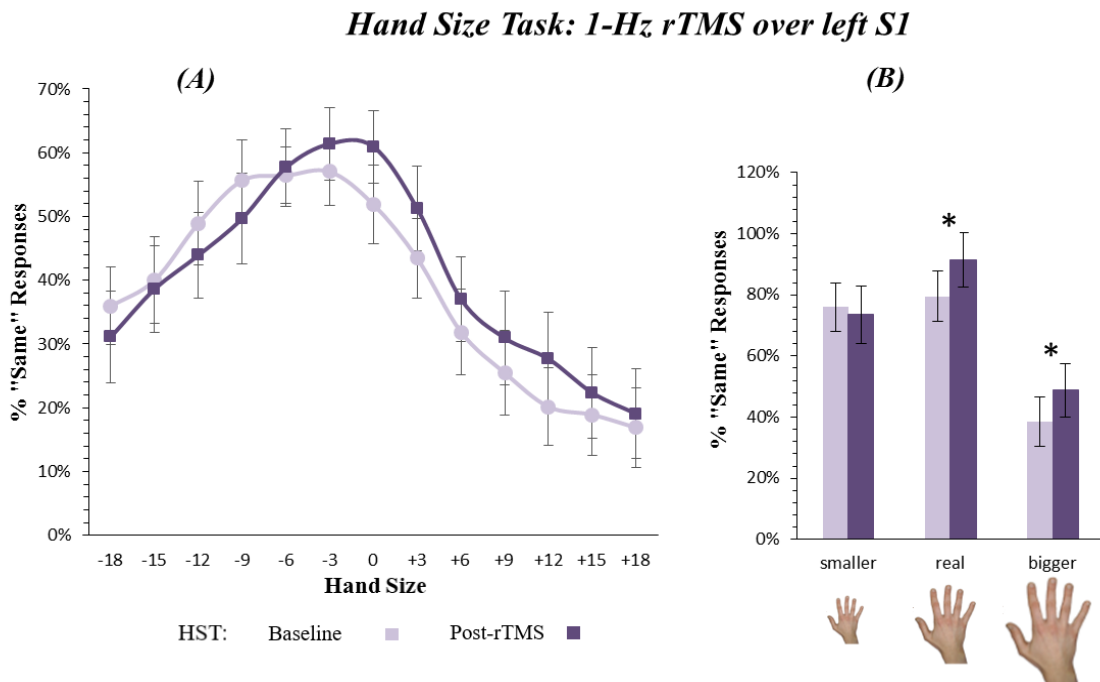

Figure 4. Hand size perceived change by 1-Hz rTMS of the left S1 hand area (Experiment 3). Panel **(A)** depicts the increase of «*Same*» responses after left S1 rTMS in trials presenting a hand bigger than the participant's real hand (Time x Hand Size interaction, p=.04). See caption to Figure 2 for details (X/Y axis). Panel **(B)** recaps the overestimation effect. Error bars= SEM. Adapted from Giurgola et al. (2019).

HST – LRT goodness-of-fit test			
	χ^2	Df	p
Time	9.86	1	.001
Hand Laterality	4.21	1	.039
Hand Size	1242.20	3	<.001
Time X Hand Size	39.09	3	<.001
Time X Hand Laterality	8.55	1	.003
Hand Laterality X Hand Size	1.99	3	.57
Time X Hand Laterality X Hand Size	4.13	3	.24

HST – Mixed logistic regression				
	B	SE	z value	p
Intercept	.12	.13	.91	.36
Time	-0.22	.05	-4.47	<.0001
Hand Laterality	.07	.03	2.05	.04
Hand Size (linear trend)	-0.05	.005	-11.32	<.0001
Hand Size (quadratic trend)	-0.004	.0002	-20.59	<.0001
Hand Size (cubic trend)	.0001	.00002	5.69	<.0001
Time X Hand Size (linear trend)	-0.03	.007	-4.03	<.0001
Time X Hand Size (quadratic trend)	.0008	.0003	2.62	.008
Time X Hand Size (cubic trend)	.00006	.00003	1.98	.04

Table 3. Results from statistical analysis of Experiment 3. Abbreviations: HST, hand size task; LRT: likelihood ratio tests.

2.5. EXPERIMENT 4 – Modulation of metric representation of the body by rTMS of left and right IPL

Experiment 4 aimed at verifying the additional involvement of the IPL of both hemispheres in the observed effects. Indeed, a variety of body representation disturbances occurs after parietal lesions or brain stimulations (Bolognini et al., 2018), among which distorted awareness of the size of the whole body or of body-parts, as well as other forms of spatial size distortion (hyperschematia, see Vallar et al., 2009). Furthermore, applying rTMS to other cortical sites could prove the specificity of the effects of interfering with the activity of S1 in bringing about the effects observed in Experiments 1-3.

2.5.1. Materials and Methods

Participants

Twenty healthy participants (15 females; 18 right-handed; mean age ± SD = 22.3 ± 3.2 years; range = 19-31 years), selected using the same criteria of Experiment 1, entered Experiment 4. One participant could not perform the second rTMS session (see below) and was excluded therefore from statistical analyses. In the final sample, the mean individual rMT value was 55.8% (± 6.2%, range = 43-64%) of the maximal stimulator output for the right IPL, and 55.4% (± 7.2%, range = 42-67%) for the left IPL.

Experimental paradigm and statistical analyses

Stimuli, procedure, and statistical analyses were identical to those of Experiment 1, with the exception of the rTMS target site, which in Experiment 4 was placed over either the right or the left IPL. Adopting a within-subjects design, participants underwent 2 rTMS sessions, during which 1-Hz rTMS was applied over the right or the left IPL. The two experimental sessions were separated by an interval of at least 24 hours, and their order was counterbalanced across participants (AB-BA; i.e., half of the participants started with

the rTMS session over the right IPL, the other half started with the rTMS session over left IPL). The right and left IPL were localized with the SofTaxic Evolution navigator system, following Talairach coordinates ($X = +/-40$, $Y = 52$, $Z = 44$, BA 40) (e.g., Bolognini, Miniussi, Savazzi, Bricolo & Maravita, 2009). As for stimulation of the S1-hand area, 1-Hz rTMS was delivered for 15 min (TMS intensity= 110% of the individual rMT, 900 pulses).

With respect to the statistical analyses, the Hemisphere (right IPL vs. left IPL) was now included among the fixed factors and in interaction with the other effects.

To test possible distant influences of rTMS on S1, I administered the 2PDT. There was no change in tactile sensitivity of the left hand following rTMS of the right IPL (baseline = 80 % ± .09%, vs. post-rTMS = 77.63 ± .17, t_{18}= .51, p= .6), nor of the right hand following the stimulation of the left IPL (baseline = 78% ± .05%, vs. post-rTMS = 75% ± .16%, t_{18}= .72, p= .5). Moreover, there was neither a difference in tactile sensitivity between the two baseline sessions (t_{18}= .82, p= .4), nor between the 2 post-TMS sessions (i.e., right vs. left IPL, t_{18}= .47, p= .6).

2.5.2. Results

The best-fitting model for the HST included the main effects of Time, Hand Laterality, Hand Size and Hemisphere, as well as the Time by Hemisphere interaction (see Table 4). The final model showed a main effect of Time, showing an overall increase of «Same» responses after rTMS (38% ± 16.7), as compared with before the stimulation (baseline= 37% ± 13.6), but regardless of the size of the viewed hand. Moreover, a significant effect of the linear, quadratic and cubic trends of Hand Size was found. The main effect of Hemisphere reached significance, since, in the left IPL sessions, overall participants provided less «Same» responses (36.7% ± 17.2%), than in the right IPL session (38.4% ±

17.6%). Importantly, however, no significant interactions between the factors Time and Hand Size emerged (see Table 4 and Figure 5).
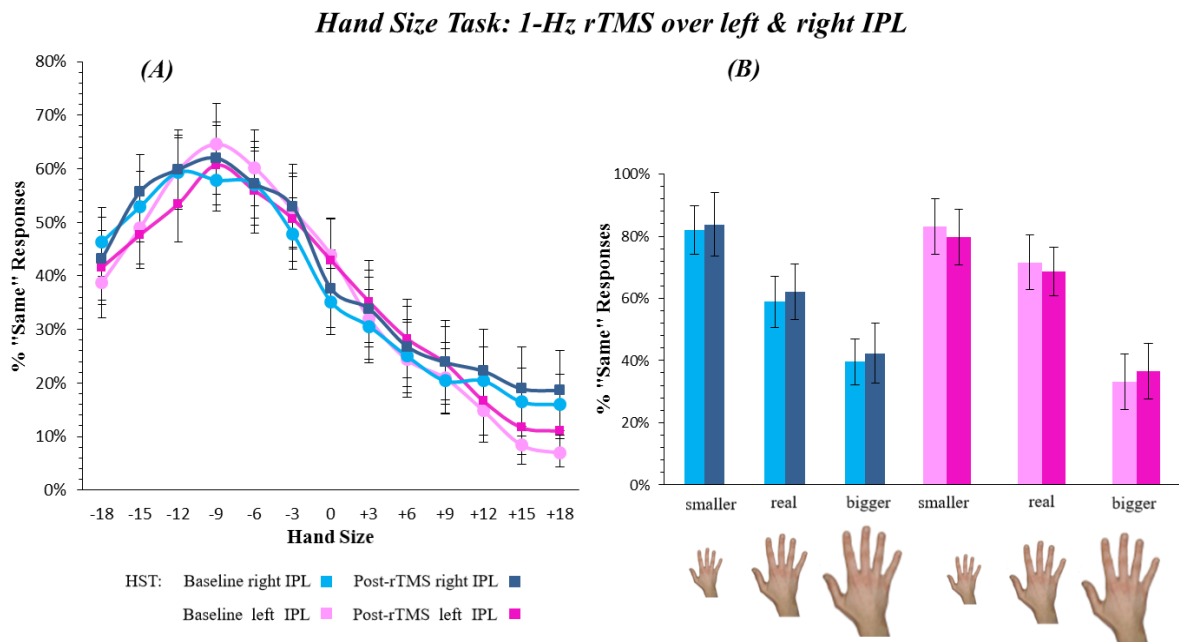

Figure 5. Hand size perceived change by 1-Hz rTMS of IPL (Experiment 4). Panel **(A)** illustrates the results showing no change of the perceived size of the hands after the stimulation of both the left and right IPL (Time x Hand Size x Hemisphere interaction, p= .17). Light pink and blue lines = performance before 1-Hz rTMS over the left and right IPL, respectively. Dark pink and blue lines = performance after 1-Hz rTMS over the left and right IPL, respectively. See caption to Figure 2 for details (X/Y axis). Panel **(B)** summarizes the behavioral effect before and after 1-Hz rTMS. Error bars= SEM. Adapted from Giurgola et al. (2019).

HST – LRT goodness-of-fit test			
	χ^2	Df	p
Time	4.46	1	.03
Hand Laterality	15.55	1	<.0001
Hand Size	1559.32	3	<.0001
Hemisphere	8.83	1	.002
Time X Hand Size	6.77	3	.07
Time X Hemisphere	5.54	1	.01
Hand Size X Hemisphere	2.36	3	.49
Time X Hand Size X Hemisphere	4.97	3	.17
HST – Mixed logistic regression			
	B	SE	z value	p
Intercept	-0.24	.18	-1.35	.17
Time	-0.11	.03	-3.09	.002
Hand Laterality	.03	.02	1.44	.14
Hand Size (linear trend)	-1.43	.03	-41.58	<.0001
Hand Size (quadratic trend)	-0.33	.01	-21.66	<.0001
Hand Size (cubic trend)	.35	.01	19.74	<.0001
Hemisphere	-0.13	.03	-3.77	<.0001
Time x Hemisphere	.09	.05	1.90	.06

Table 4. Results from statistical analysis of Experiment 4. Abbreviations: HST, hand size task; LRT: likelihood ratio tests.

2.6. Discussion

In this study, I aimed at investigating whether an interfering modulation of the metric representation of the body, by affecting somatosensory cortical maps with rTMS, could influence the representation of the size of the participant's own body. Firstly, results show that S1 shapes the metric of body-parts: low-frequency rTMS delivered to the S1 hand area brings about an overestimation of the perceived size of the participant's own hand (Experiment 1). This effect mirrors the phenomenon of *macrosomatoagnosia* (Fredericks, 1969, 1985), a disorder characterized by the feeling that one or more parts of the body are

disproportionately large (Kew, Wright & Halligan, 1998; Podoll, Mühlbauer, Houben, & Ebel, 1998; Podoll & Robinson, 2000; Vallar et al., 2009). Secondly, the effect reflects the somatotopic organization of S1, being body-part specific: targeting the hand representation in S1 leads to an overestimation of the size of the hand, but not of the foot (Experiment 2). Thirdly, the stimulation of S1 of both hemispheres affects the visual estimation of the size of both hands, namely both the hand ipsilateral and that contralateral to the stimulated hemisphere (Experiment 1 and 3). Finally, no perceptual distortion of hand size was found after stimulation of either the right or left IPL, although this region holds higher-order representation of somatosensory information (Huang & Sereno, 2018).

The present results complement and extend the seminal study by Gandevia and co-workers (1999), who showed that the representation of the own body size can be affected in a bottom-up manner by peripheral somatosensory afferents, in a somatotopic-specific way. In their work, authors speculated that perceptual body size distortions induced by acute anaesthesia/deafferentation could be due to a reversible enlargement of S1 neurons' receptive fields, as it occurs in animal after limb amputation or spinal cord transection (Head & Holmes, 1912; Melzack & Bromage, 1973; Merzenich, Kaas, Wall, Nelson, Sur & Felleman, 1983). In human amputees, a shrinking and retraction of the cortical representation of the phantom limb has been documented (Flor, Nikolaisen & Staehelin Jensen, 2006; Grüsser et al., 2001), although this phenomenon has been recently questioned by novel evidence, in both human and non-human primates, showing that limb amputation does not cause a rearrangement of functional sensory representations; rather, the cortical representation of the limb seems to remain stable despite the loss of the peripheral input (Kikkert et al., 2016; Makin & Bensmaia, 2017; Makin, Scholz, Henderson Slater, Johansen-Berg & Tracey, 2015).

The suggestion can be made from my findings is that the perceptual enlargement of the subjective hand is caused by variations of neural activity of S1 by rTMS, which may drive a temporary sort of shrinking of the cortical somatosensory map of the hand. In particular, since low-frequency rTMS usually has an inhibitory effect on neural activity (Bolognini et al., 2018), I propose that this kind of stimulation may bring about a functional contraction of the cortical representation of the hand (as acute peripheral hand deafferentation does; e.g. Calford & Tweedale, 1988; Merzenich et al., 1983), which is behaviorally compensated by the perceptual overestimation of its size, as found in the present set of experiments.

This well fits with evidence showing that body-parts under-represented in S1 (Linkenauger et al., 2015; Mancini et al., 2014) are perceptually overestimated. This phenomenon represents a sort of compensatory mechanism by which the perceptual system distorts the experience of a body part's size to a magnitude that compensates for its differences in the somatosensory cortical maps - *somatosensory homunculus* (Linkenauger et al., 2015; Sadibolova, Ferrè, Linkenauger & Longo, 2019). Accordingly, an abnormal under-representation of the hand in S1, induced by 1-Hz rTMS, seems to be compensated by an over-estimation of its size at the perceptual level.

Peripheral deafferentation brings about changes of perceptual size only on the side ipsilateral to the deafferentation (Gandevia et al., 1999). Conversely, in the present experiments rTMS of S1 affects size representation of both the hand contralateral and of the hand ipsilateral to the stimulated hemisphere. These findings broadly agree with the evidence that, in the monkey's somatosensory cortex, at the level of the hand area, some neurons have bilateral and ipsilateral receptive fields (Iwamura, 2000). Recent evidence from humans also shows substantial integration of tactile information from the two hands in S1 (Tamè, Pavani, Papadelis, Farnè & Braun, 2014; Tamé, et al., 2016). Finally,

receptive fields may increase in the contralateral homologous cortex after acute deafferentation (Calford & Tweedale, 1990), while unilateral S1 rTMS can affect somatosensory processing in the ipsilateral and in the contralateral hands (Bolognini et al., 2018; Eshel, Ruff, Spitzer, Blankenburg & Driver, 2010; Meehan, Linsdell, Handy & Boyd, 2011; Premji, Ziluk & Nelson, 2010; Uguisu et al., 2010).

Thus, the emerging view is that human S1 is more than a simple relay for somatosensory inputs from the contralateral side of the body, playing instead a key role in the integration of such inputs from the two sides of the body (Tamè et al., 2016). Additionally, beyond S1, the secondary somatosensory cortex (S2), and Brodmann's area 5 in the posterior parietal cortex (PPC), also receive dense bilateral afferent projections (Forss, Jousmäki, & Hari, 1995; Lin & Forss, 2002; Sakata, Takaoka, Kawarasaki, & Shibutani, 1973). Therefore, a possible account for the present findings is that rTMS delivered to S1, independent of the stimulated hemisphere, may affect size estimation of both the right and the left hand, possibly through both trans-callosal interactions between the S1s of the two hemispheres, and ipsilateral connections between S1 and S2, which, as noted above, receives dense bilateral afferent projections (Forss et al., 1995). In the light of the distant effects of rTMS through neural connectivity (e.g. Bolognini et al., 2018), the present findings may also reflect the modulation of broader networks involved in the computation of the own body size, of which nevertheless S1 appears to be a key node (Forss et al., 1995; Lin et al., 2002; Sakata et al., 1973).

The present results also demonstrate the role of S1 in the somatotopic representation of body size. Indeed, the stimulation of the S1-hand map brings about an overestimation of the participants' own hand size, without affecting the perceived size of their own foot. In line with this finding, peripheral changes in the somatosensory input from the thumb do not alter the perceived size of the index finger, although they affect the perceived size of

the lips, in keeping with the well-known plastic changes that may occur across the hand-face S1 border (Muret et al., 2016; Muret, Dinse, Macchione, Urquizar, Farnè & Reilly, 2014). Hence, the representation of the size of body-parts in S1 reflects the topographic map of the body surface (Penfield et al., 1950).

In my last experiment (Experiment 4) I assessed the selective involvement of S1 in the observed effects, by verifying whether perceptual distortions of body-parts size could be induced also by the stimulation of posterior parietal regions, namely the left and right IPL. The IPL of both hemispheres is not found to be involved in this process, suggesting that the estimation of the size of body-parts primarily relies on the computation of more elementary somatic signals from body segments in S1. Noteworthy, posterior parietal damage (especially in the right hemisphere) may cause perceptual distortions primarily affecting extra-personal space (Rode, Michel, Rossetti, Boisson & Vallar, 2006; Rode, Revol, Rossetti & Vallar, 2008; Rode, Vallar, Chabanat, Revol & Rossetti, 2018). Conversely, body-part "macrosomatognosia" (Fredericks, 1969, 1985) or "hyperschematia" (Vallar et al., 2009) has been described in patients with vestibular dysfunction (Bonnier, 1905; see Vallar et al., 2003, for review), and following lateral medullar damage in the brainstem (Rode et al., 2012), which also causes somatosensory, body-part specific, impairments, along with a central vestibular dysfunction (Dieterich & Brandt, 2010). It is worth noting that transcranial direct current stimulation (tDCS) of the posterior parietal cortex does not affect telescoping in amputees with a phantom limb (Bolognini, Olgiati, Maravita, Ferraro & Fregni, 2013; Bolognini, Spandri, Olgiati, Fregni, Ferraro & Maravita, 2013; Bolognini et al., 2015), while systematic alterations in the perception of body size occur after spinal cord injury. Critically, in the latter case, patients experiencing phantom sensations may report the feeling of an increased size of the deafferented limb, while a reduction of body-part size is generally not reported (Bors,

1951; Conomy, 1973; Evans, 1962; Longo, Mattioni & Ganea, 2015).

Finally, in all four experiments, in the baseline condition (before rTMS) participants underestimate the perceptual size of their own hands and feet, in accordance with other behavioral evidence documenting the existence of a basal distortion of the perceived hand size in humans (Fuentes et al., 2013; Longo, 2015a; Longo et al., 2010, 2015), also using template matching tasks similar to that employed in the present study (Longo et al., 2012a, 2012b; Longo et al., 2015).

The present study demonstrates that the perceptual representation of the size of the own body-parts may be shaped by local changes of activity in the S1 of either hemispheres, induced by rTMS. The mutual relation between body surface, somatosensory processing and abstract representation of one's own body, including its metric properties, dates back to the suggestions of the existence of a "schema" of the body, starting from the end of the XIX century (Vallar et al., 2003 for review). The present results suggest that the perceptual metric representation of the body involves cortical, somatotopically organized, activity, in S1. This conclusion is in line with the suggestion of a distinction between a "somato-perceptual" representation of the body, built up mainly on external (somatosensory, and also from other modalities, such as vestibular) inputs, and a "somato-representation", based on cognitive processes creating a more abstract body knowledge, including semantic features, beliefs, and attitudes related to the body (Longo et al., 2010; see the distinction between "body schema" and "body image", discussed by Vallar et al., 2003; Head et al., 1911, for the concept of "body schema"; Schilder, 1935, for that of "body image"). In this broader perspective, I then suggest that somato-perception, and, specifically, its component concerning the perceptual representation of the size of body-parts, is essentially based on on-line computations occurring within somatotopic cortical representations in S1.

Representation of body size appears highly dependent upon sensory input processing and, as such, it can be functionally distorted by modulating body-part maps in S1.

3. PLASTIC DISTORTION OF THE OWN BOSY SIZE BY CHANGING THE SENSE OF BODY OWNERSHIP

3.1. Aim of the study

As discussed in the previous chapters, the body model proposed by Longo and colleagues (2010) assumes the existence of an implicit stored representation of the body's metric properties, comprising the size and shape of each body-part, inherently linked to tactile size perception and position sense. One of the core features of this model is that the implicit perceptual representation of the own body-parts (specifically, the representation of the hand structure) results massively distorted. In line with this account, several evidence has documented that the inherent subjective representation of the own hand size appears highly distorted (Fuentes et al., 2013; Giurgola et al., 2019; Linkenauger et al., 2015; Longo, 2015; Longo et al., 2010; Longo et al., 2012a, 2012b; Longo et al., 2015). Moreover, body size representation is plastic and can be modulated, on the one hand, in bottom-up fashion by incoming tactile inputs (Gandevia et al., 1999), on the other hand, by inducing neural excitability shifts at the cortical level (Giurgola et al., 2019). Intriguingly, recent studies investigated the possible influence of body metric alterations over the sense of body ownership. In this regard Pavani and co-workers (2007) developed a modified version of the classical RHI paradigm (Botvinick et al., 1998), using three fake hands differing in their dimension (i.e., one veridical, one reduced and one enlarged image of the hand, respectively). The authors assessed whether the embodiment of a fake hand is influenced by its size, thus altering the sense of body ownership regardless of the rubber hand dimension. Their findings showed that the RHI, as assessed at the level of the

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subjective illusory experience detected by questionnaire measures, occurs regardless of the congruence between the size of the fake hand and that of the participant's real hand. However, the proprioceptive drift induced by the RHI occurred both after the illusory experience with the veridical and the enlarged hand images, but it did not appear after the embodiment of the reduced hand image. These findings suggest that the perception of the body's metric properties selectively influences the multisensory illusory manipulations of self-attribution and embodiment, characterized by an asymmetric tendency to acknowledge either veridical and magnified – not reduced – external body-parts within the own mental body representation (Pavani et al., 2007).

In the same vein, a growing number of studies has shown that multisensory bodily illusions can modulate both tactile size perception and the kinematics of the grasping movements (Banakou et al., 2013; Bernardi et al., 2013; Bruno et al., 2010; De Vignemont et al. 2005; Haggard et al., 2009; Taylor-Clarke et al., 2004). Interestingly, in line with findings from Pavani and colleagues (2007) an asymmetric recalibration of the grasping movements – modulated by the embodiment of enlarged, but not shrunken, hand – has been described (see Bernardi et al., 2013).

This set of evidence examined the relationship between body-part metric representation and the sense of body-part ownership showing that very selective aspects of body metric representation, such as body-parts size, directly influence the multisensory modulation of body ownership. However, the reversed perspective (i.e., the possible effects of the body ownership modulation on body metric representation) has been poorly investigated. Changing in grasping movements kinematics after perceiving the own hand enlarged (Bernardi et al., 2013) seems to suggest that an altered sense of body ownership may at least *implicitly* shape the representation of one's own body metric. Nevertheless, this hypothesis still needs empirical demonstration: to date, the effects of manipulating body

ownership on the plastic distortions of one's own *conscious* body-parts size representation have not been directly assessed.

To address this issue, I have carried out a series of behavioral experiments, aimed at corroborating the link between the sense of body-part ownership and the representation of the size of body-parts. To this aim, a modified version of the RHI procedure (Botvinick et al., 1998) was adopted in order to assess whether and how the embodiment of fake hands of different sizes (i.e., bigger or smaller than the own hand; Experiment 1 and 3, respectively) would induce an updating of one's own hand size representation. I also seek for the selectivity of the effect with respect to the participant's hand exposed to the RHI (Experiment 2). Finally, the bodily selectivity of the effect was assessed by examining whether the embodiment of fake hand with altered size can also affect the perception of the size of objects (Experiment 4).

3.2. EXPERIMENT 1 – Illusory ownership of an enlarged hand shapes the perceived size of the own hand

Experiment 1 assesses whether the embodiment of a fake hand with a size greater than the own hand would affect the perceptual representation of the own hand size.

3.2.1. Materials and Methods

Participants

Fifteen neurologically healthy participants (9 females; mean age ± standard deviation = 22.33 ± 2.87 years; range = 20-28 years) entered Experiment 1. All subjects gave their written informed consent to take part in the study, which was approved by the local Ethical Committee of the University of Milano-Bicocca and conducted in line with the Declaration

of Helsinki. All participants were right-handed as assessed by the standard questionnaire (Oldfield, 1971), and had normal or corrected-to-normal vision. Participants were naïve both to the experimental procedure and to the purpose of the study. Exclusion criteria included history of neurological and psychiatric disorders.

Experimental paradigm

The RHI followed the original protocol of Botvinick and co-workers (1998). A wooden box (90 x 50 x 15 cm) was employed; it consisted of 3 parts (left, central and right sides of the box) by two panels arranged vertically. The box was positioned in front of the participants, at 15 cm of distance. Participants positioned their left and right hands in the left and the right side of the box, respectively, with the palm facing down and the fingers stretched out, while the rubber hand was placed in the central side of the box, aligned with the participant's left shoulder. The central side of the box was open, so that subject could view the rubber hand, while the other sides were always covered to take out of sight the subject's own hands. The rubber (left) hand and the participant's left hand were horizontally aligned, with the middle finger of the rubber hand and the middle finger of the participant's left hand kept at a fixed distance of 30 cm. The subject's shoulders and upper-limbs were covered by a black towel, so that the rubber hand appeared as an extension of the participant's own left arm. During the RHI, participants were gently touched with a paintbrush on their left middle finger, receiving 120 seconds of synchronous (strokes were delivered spatially and temporally in phase) or asynchronous (strokes spatially and temporally out of phase; i.e., control condition) stroking of both the real hand and the rubber hand (~1 stroke every second).

Participants were exposed to a fake hand of the same size (Real size RHI, Rs-RHI; Figure 1a, central panel) or bigger size (Bigger size RHI, Bs-RHI; Figure 1a, right panel) of the own hand. Fake hands were created with 3D printer: for the Rs-RHI, the hand was of 30

cm (height) X 16 cm (width); such dimensions reflect the mean size of an adult's hand. For the Bs-RHI, the fake hand was magnified of 50 (height= 45 cm; width= 25 cm).

Each participant underwent 4 experimental sessions, differing for the size of the fake hand, and the synchrony of the visuo-tactile stroking: 1) Rs-RHI with synchronous stroking, or 2) asynchronous stroking, 3) Bs-RHI with synchronous stroking, or 4) asynchronous stroking. Each session was separated by an interval of at least 24 hours and counterbalanced between participants. The order of the sessions was randomized across participants. In each session, after the RHI induction, participants compiled the "Embodiment questionnaire" (Botvinick et al., 1998; see Table 1a), which assesses the occurrence of the illusory embodiment of the rubber hand, and the "Disembodiment questionnaire" (Longo, Schüür, Kammers, Tsakiris & Haggard, 2008; see Table 1b), which assesses the illusory sense of disownership of the own hand.

Table 1a. Embodiment questionnaire (Botvinick et al., 1998)

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1. It seemed as though the touch I felt was caused by the paintbrush touching the rubber hand
2. It seemed as if I were sensing the touch of the paintbrush in the location where I saw the rubber hand touched
3. I felt as if the rubber hand was my hand

Table 1b. Disembodiment questionnaire (Longo et al., 2008)

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1. It seemed like I was unable to move my hand

2. It seemed like a couldn't really tell where my hand was

3. It seemed like my hand had disappeared

Table 1. Embodiment and Disembodiment questionnaires. The Embodiment (Tab. 1a) and Disembodiment (Tab. 1b) questionnaires comprised 3 statements (Botvinick et al., 1998; Longo et al., 2008) assessing the illusory embodiment of the rubber hand and the illusory disembodiment of the own hand. Participants had to judge the vividness of their feeling of dis/ownership by using a 7-points Likert scale, rating their agreement/disagreement with each statement (from -3 = strong disagreement, to +3 = strong agreement).

Moreover, before (baseline) and after (post-RHI) the RHI, participants underwent the HST developed in the previous TMS experiments (see Chapter 2; Giurgola et al., 2019), a 2-forced-choice visual perceptual task developed to assess perceptual representation of one's own hand size. Details about the HST are described in the previous Chapter (see paragraph 2.2.1., page 34). The only difference with Study #1 was that now hand stimuli were scaled in order to be of the same size, 0% (i.e., same size trials), or smaller (-) or bigger (+) (i.e., different size trials: from -15% to +15% in steps of 3%), than the participant's hand dimension (see Figure 1b for a selection of experimental stimuli). For each hand size (total=11), 12 trials were given (total = 132 trials; task duration = ~6 min). Moreover, only pictures of the participants' left hand were presented (i.e., the one exposed to the RHI).

The HST and the 2 questionnaires were given in a counterbalanced order across participants (AB-BA order; for the experimental procedure, see Figure 1c).
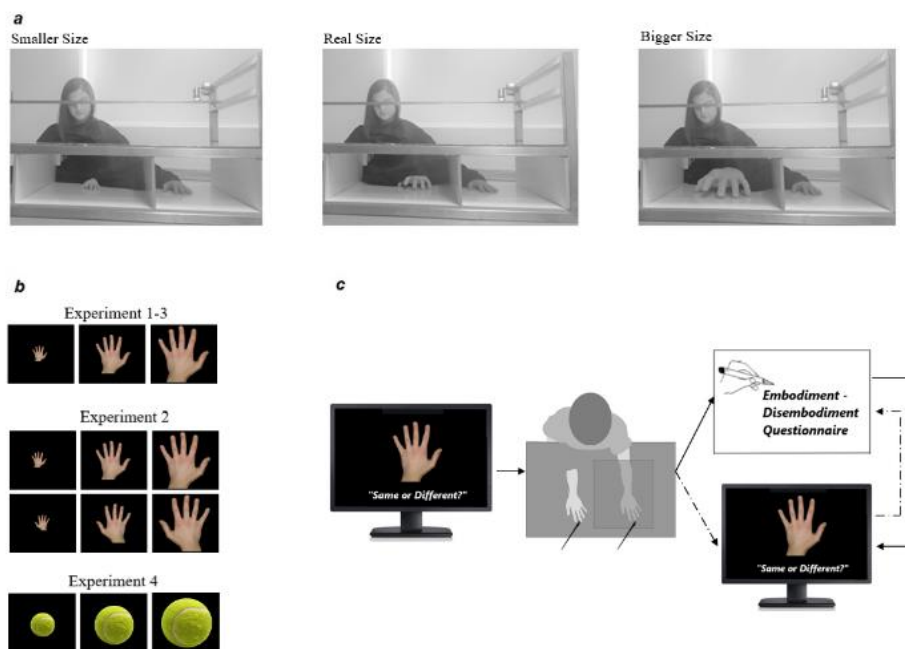
Figure 1. Experimental procedure. (a) Participants underwent the classical RHI procedure (Botvinick et al., 1998), receiving 120 sec of synchronous/asynchronous stronking of both their left hand and the fake hand, which could be of the same size (Real size RHI, Rs-RHI) or bigger size (Bigger size RHI, Bs-RHI) of the own hand (Experiments 1, 2, 4). In Experiment 3, the Rs-RHI and a smaller fake hand (Smaller size RHI, Ss-RHI), were adopted. **(b)** Pictures of the stimuli used in the Hand Size Task (HST, Experiment 1,2,3) and in the Object Size Task (OST, Experiment 4). **(c)** Schematic representation of the experimental procedure: the HST or the OST were administered before and after each RHI session; after the RHI induction, the Embodiment and Disembodiment questionnaire were administered.

Statistical analyses

For both Embodiment and Disembodiment questionnaires, scores (calculated as the mean value of the 3 statements) were analysed with the Friedman ANOVA test (i.e., nonparametric repeated measures comparisons) to assess for interaction effects; when appropriate, paired comparisons were carried out using the Wilcoxon signed rank test.

Performance at the HST was analysed using the statistical program R (R Development Core Team, 2008). Responses were entered as dependent binomial variable, coding the «Same» responses as 1 and the «Different» responses as 0. The "lme4" package (version 1.1-5, Bates et al., 2015) was employed to submit data to a series of generalized mixed effects models (Baayen et al., 2008). First, the likelihood ratio tests (LRT) assessed whether the inclusion of fixed effects or interactions contributed to the model goodness-of-fit, including only effects which significantly increased the model (Gelman et al., 2006). As fixed factors, Time (pre- vs. post-RHI), RHI (Synchronous Rs-RHI, Asynchronous Rs-RHI, Synchronous Bs-RHI, Asynchronous Bs-RHI), Hand Size (at the HST: from -15% to +15%, as continuous independent variable), as well as their interactions, were tested. A by-subjects random intercept was included. Parameters from the final, best-fitting, model are reported, including factors significance level based on Satterthwaite's degrees of freedom approximation in the "lmerTest" R package (version 2.0-29, Kuznetsova et al., 2015). The model included the main effects of Time, RHI and Hand Size, as well as their interactions (see Tables 2 for results of the LRT procedure for model selection, and for the final model's parameters).

3.2.2. Results

The analysis of the Embodiment questionnaire showed a significant effect (Friedman $\chi^2 =$ 20.35, p<.001), with a difference between synchronous and asynchronous conditions for either the Rs-RHI (1.91 ± 1.04 vs. -0.62 ± 2.26, p= .004) and the Bs-RHI (1.66 ± 1.13 vs. -0.66 ± 1.87, p= .003); importantly, scores did not differ in the Rs-RHI and the Bs-RHI (p= .26), indicating that the embodiment of the rubber hand occurred independently of its size. At the Disembodiment questionnaire a significant effect was found (Friedman $\chi^2 = 14.08$, p= .002), with a difference between synchronous and asynchronous conditions for either the Rs-RHI (-0.24 ± 1.25 vs. -1.44 ± 1.36, p= .01) and the Bs-RHI (-0.57 ± 1.19 vs. -1.86 ± 1.32, p= .005); again, scores did not differ in the Rs-RHI and the Bs-RHI (p= .14) sessions, indicating that that a feeling of disembodiment of the own hand occurred independently of its size.

With respect to the HST, the main critical finding was the significant Time by Hand Size by RHI interaction (z=-3.21; p<.001; see Table 2 for full results). As shown in Figure 2, the synchronous Bs-RHI induced an overestimation of the own hand size, indexed by increased «Same» responses to the view of a hand bigger than the participant's own hand (Figure 2).
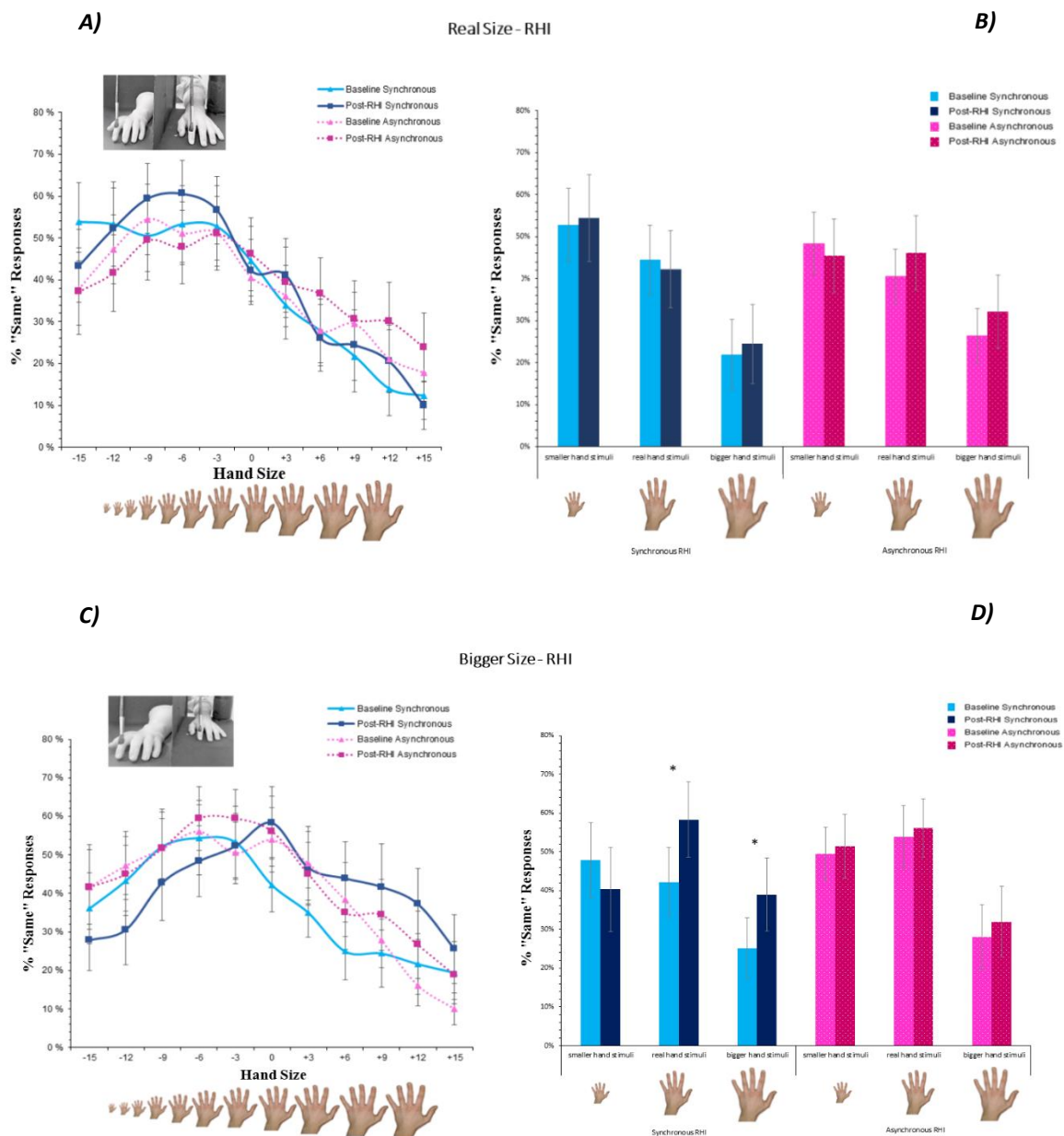
Figure 2. Results from Experiment 1: HST. Perceived change of the own left hand size after RHI procedure with Real size (Real size RHI, Rs-RHI; panel **A**) and Bigger size (Bigger size RHI, Bs-RHI; panel **C**) rubber hands. Panel **C)** shows increased «Same» responses (Y-axis) after the embodiment of the bigger fake hand in the synchronous condition in trials presenting a hand bigger than the participant's real hand (Time X Hand Size X RHI interaction, $p<.001$). X axis= percentage of the hand size changes with respect to the participant's own hand; negative values= reduced hand size; positive values= increased hand size. Light pink and blue lines= participants' performance before RHI (baseline); dark pink and blue lines= performance after RHI; continuous lines= synchronous RHI, dotted lines= asynchronous RHI. Panel **B)** summarizes the absence of hand size change after Rs-RHI; panel **D)** recaps the overestimation effect after Bs-RHI. Error bars= Standard Error of the mean (SEM).

HST – LRT goodness-of-fit test			
	χ^2	Df	*p*
Time	12.57	1	<.001
Hand Size	592.53	1	<.001
Rhi	10.67	3	.01
Time X Hand Size	33.72	1	<.001
Time X Rhi	1.77	3	.62
Hand Size X Rhi	92.15	3	<.001
Time X Hand Size X Rhi	17.58	3	<.001
HST – Mixed logistic regression			
	B	SE	z value	*p*
Intercept	-0.31	.17	-1.83	.06
Time	-0.14	.06	-2.12	.03
Hand Size	-0.04	.005	-8.08	<.001
Rhi (synchronous Bs-RHI)	-0.06	.06	-0.96	.33
Rhi (asynchronous Rs-RHI)	-0.17	.06	-2.57	.01
Rhi (synchronous Rs-RHI)	-0.18	.06	-2.58	.009
Time X Hand Size	-0.01	.007	-1.94	.05
Time X Rhi (synchronous Bs-RHI)	-0.07	.09	-0.77	.43
Time X Rhi (asynchronous Rs-RHI)	.06	.09	.67	.50
Time X Rhi (synchronous Rs-RHI)	.05	.09	.50	.61
Hand Size X Rhi (synchronous Bs-RHI)	.04	.007	5.73	<.001
Hand Size X Rhi (asynchronous Rs-RHI)	.007	.007	.98	.32
Hand Size X Rhi (synchronous Rs-RHI)	-0.02	.007	-3.81	.001
Time X Hand Size X Rhi (synchronous Bs-RHI)	-0.03	.01	-3.21	<.001
Time X Hand Size X Rhi (asynchronous Rs-RHI)	-0.0005	.01	-0.05	.95
Time X Hand Size X Rhi (synchronous Rs-RHI)	.006	.01	.59	.55

Table 2. Results from statistical analysis of Experiment 1. Abbreviations: HST= hand size task; LRT= likelihood ratio tests; Rs-RHI= Real size RHI; Bs-RHI= Bigger size RHI.

3.3. EXPERIMENT 2 – Selectivity of the hand size distortion for the hand exposed to the Rubber Hand Illusion

Experiment 2 assesses whether the perceptual distortion of the hand size induced by the RHI is specific for the left hand exposed to the illusion or whether it extends even to the right, unexposed, hand.

3.3.1. Materials and Methods

Participants, experimental paradigm and statistical analyses

Fifteen healthy right-handed participants (13 females; mean age = 25.01 ± 2.78 years; range = 19-28 years) entered Experiment 2. Stimuli, procedures, and statistical analyses were identical to Experiment 1, the only difference was that in Experiment 2 the HST showed both the participant's right (unexposed to the RHI) and left (exposed) hands (see Figure 1b). Pictures of left and right hands were presented in two separate blocks (AB-BA order, counterbalanced across participants). In this experiment, participants underwent only 1 session, namely the Bs-RHI with synchronous stroking (see above), hence the following factors were included in the analysis of the HST: Time, Hand Size, Hand Laterality (left, right), as well as their interactions.

3.3.2. Results

Scores at the Embodiment (mean =1.42 ± 1.55) and Disembodiment (mean= -0.33 ± 1.69) questionnaires were similar to those found in Experiment 1, thus confirming the occurrence of a reliable RHI with a bigger size fake hand [i.e., no differences between Experiment 1 and Experiment 2 in the Bs-RHI synchronous condition emerged neither at the Embodiment questionnaire (p=.73) nor at the Disembodiment questionnaire (p=.57)].

With respect to the HST, the Time by Hand Laterality by Hand Size interaction reached significance (z=2.54; p=.01), showing a selective overestimation of the own left hand, the one exposed to the RHI, but not of the right hand (see Table 3 for details; see Figure 3). However, after the RHI, a non significant (p= .07) increase of «Same» responses when the right unexposed-hand matched the size of the participant's hands (i.e., same size trials, 0% size variation) emerged, suggesting a better recognition of their real hand size.
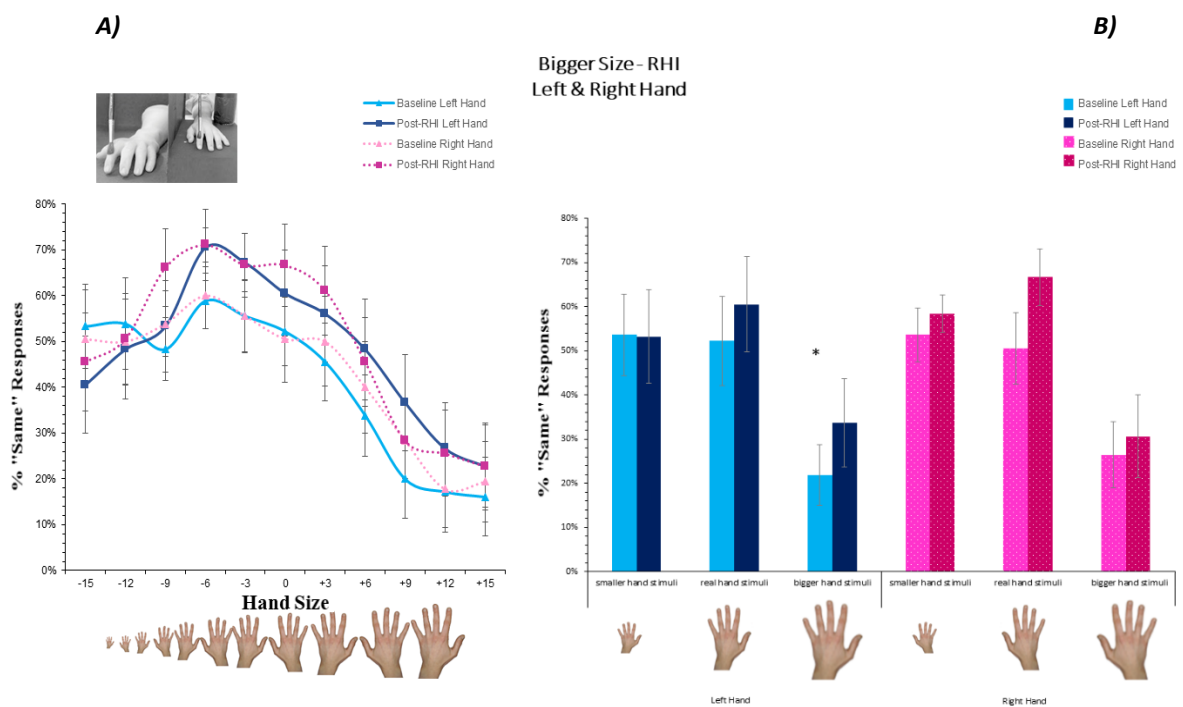
Figure 3. Results from Experiment 2: HST. Left and right hand's perceived size change by synchronous/asynchronous RHI stimulation of the participant's left hand by using the Bigger Size fake hand (Bs-RHI). The graph (panel **A**) illustrates the results showing selective change of the perceived size of the left hand, the only one exposed to the RHI (Time X hand Size X Hand Laterality interaction, p=.01). Light pink and blue lines= participants' performance before RHI (baseline); dark pink and blue lines= performance after RHI. Continuous lines= percentage of «Same» responses when the participant's left hand was presented during the HST; dotted lines= percentage of «Same» responses when the participant's right hand was presented in the HST. See caption to Figure 2 for details (X/Y axis). Panel **B**) recaps the overestimation effect. Error bars= SEM.

HST – LRT goodness-of-fit test			
	χ^2	Df	*p*
Time	43.31	1	<.001
Hand Size	421.08	1	<.001
Hand Laterality	3.13	1	.07
Time X Hand Size	12.16	1	<.001
Time X Hand Laterality	.01	1	.88
Hand Size X Hand Laterality	.11	1	.73
Time X Hand Size X Hand Laterality	6.49	1	.01
HST – Mixed logistic regression			
	B	SE	z value	*p*
Intercept	-0.03	.20	-0.15	.87
Time	.32	.07	4.63	<.001
Hand Size	.05	.005	10.23	<.001
Hand Laterality (left)	.07	.07	1.12	.26
Time X Hand Size	.005	.007	.68	.49
Time X Hand laterality (left)	.03	.09	.29	.76
Hand Size X Hand Laterality (left)	-0.01	.007	-2.01	.04
Time X Hand Size X Hand Laterality (left)	.03	.01	2.54	.01

Table 3. Results from statistical analysis of Experiment 2. Abbreviations: HST= hand size task; LRT= likelihood ratio tests.

3.4. EXPERIMENT 3 – Illusory ownership of a hand reduced in size does not shape the perceived size of the own hand

Experiment 3 assesses whether the embodiment of a fake hand of smaller size than the own hand would shrink the perceptual size of the own hand.

3.4.1. Materials and Methods

Participants, experimental paradigm and statistical analyses

Fifteen healthy right-handed participants (11 females; mean age = 21.35 ± 1.15 years; range = 20-24 years) entered Experiment 3. Stimuli, procedures and statistical analyses were identical to Experiment 1, apart from the size of the fake hand, which could be of the same size (Rs-RHI) or smaller than the own hand (see left and central panels of Figure 1a). The size of the fake hand was reduced of 50% with respect to the standard hand (smaller size RHI, Ss-RHI; height= 15 cm, width= 7 cm). Participants underwent 4 experimental sessions, differing for the size of the fake hand, and the synchrony of the visuo-tactile stroking, namely: 1) Rs-RHI with synchronous or 2) asynchronous stroking, 3) Ss- RHI with synchronous or 4) asynchronous stroking.

3.4.2. Results

As in Experiment 1, scores at the Embodiment questionnaire showed a significant effect (Friedman χ^2 = 26.51, p<.001), with a difference between synchronous and asynchronous conditions for either the Rs-RHI (1.31 ± 1.14 vs. -1.06 ± 1.48, p= .001) and the Ss-RHI (1.55 ± .86 vs. -1.4 ± 1.56, p= .001); no difference between the Rs-RHI and the Ss-RHI conditions was found (p= .31), hence confirming that the embodiment of the rubber hand occurred independently of its reduced size. At the Disembodiment questionnaire, I found a significant effect (Friedman χ^2 = 22.62, p= <.001), with a difference between synchronous and asynchronous stroking for either the Rs-RHI (-0.2 ± 1.69 vs. -1.55 ± 1.31, p= .006) and the Ss-RHI (-1 ± 1.43 vs. -1.88 ± 1.14, p= .004); for the synchronous conditions of the Rs-RHI and Ss-RHI, scores were different (p= .01), indicating that the smaller rubber hand caused a lower feeling of disembodiment of the hand with the real size.

With respect to the HST, the final model included only the main effects of Hand Size and RHI, as well as their interaction. The Time by Hand Size by RHI interaction did not reach significance (p= .10, see Table 4 for details), thus showing that the embodiment of the smaller fake hand did not affect the perceptual estimation of the own hand size (see Figure 4).
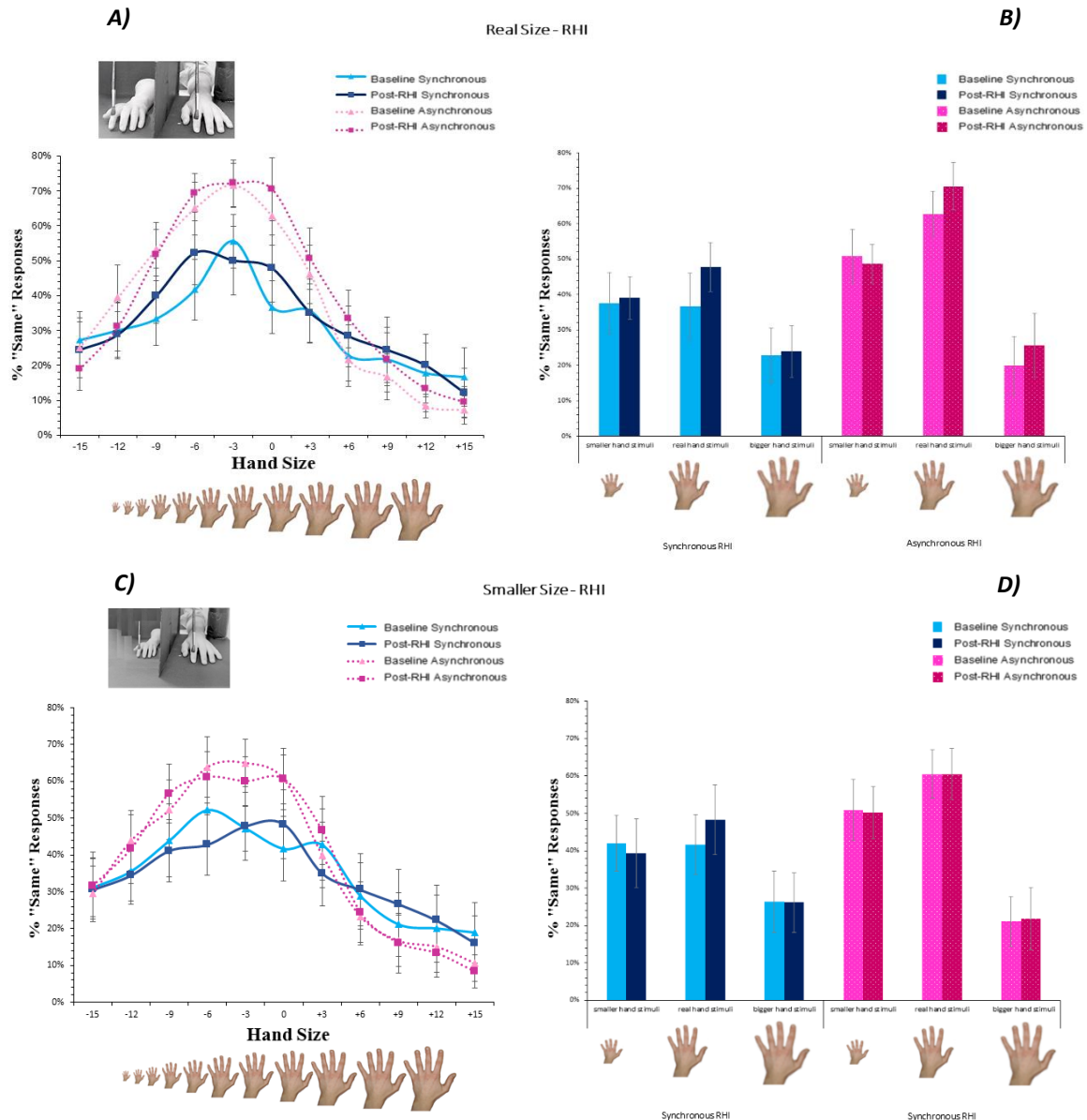
Figure 4. Results from Experiment 3: HST. Perceived change of the own left hand size after RHI procedure with Real Size (Real size RHI, Rs-RHI; panel **A**) and Smaller Size (Smaller size RHI, Ss-RHI; panel **C**) rubber hand. Light pink and blue lines= participants' performance before RHI (baseline); dark pink and blue lines= performance after RHI. Continuous lines= percentage of «Same» responses in synchronous RHI conditions; dotted lines= percentage of «Same» responses in asynchronous RHI conditions. Panel **B)** and **D)** summarize the results showing no changes of the perceived size of the own left hand after the RHI neither with the Rs-RHI neither with the Ss-RHI (Time X Hand Size X RHI interaction, p= .10). See caption to Figure 2 for details (X/Y axis). Error bars= SEM.

HST – LRT goodness-of-fit test			
	χ^2	Df	*p*
Time	1.70	1	.19
Hand Size	541.19	1	<.001
Rhi	62.89	3	<.001
Time X Hand Size	2.59	1	.10
Time X Rhi	3.35	3	.33
Hand Size X Rhi	49.67	3	<.001
Time X Hand Size X Rhi	6.09	3	.10
HST – Mixed logistic regression			
	B	SE	z value	*p*
Intercept	-0.55	.15	-3.64	<.001
Hand Size	-0.06	.003	-16.22	<.001
Rhi (synchronous Ss-RHI)	-0.15	.04	-3.03	.002
Rhi (asynchronous Rs-RHI)	.04	.04	1.006	.31
Rhi (synchronous Rs-RHI)	-0.27	.05	-5.49	<.001
Hand Size X Rhi (synchronous Ss-RHI)	.02	.005	5.55	<.001
Hand Size X Rhi (asynchronous Rs-RHI)	.009	.005	1.85	.06
Hand Size X Rhi (synchronous Rs-RHI)	.03	.005	5.91	<.001

Table 4. Results from statistical analysis of Experiment 3. Abbreviations: HST= hand size task; LRT= likelihood ratio tests; Rs-RHI= Real size RHI; Ss-RHI= Smaller size RHI.

3.5. EXPERIMENT 4 - Illusory ownership of an enlarged hand does not affect the estimation of the size of objects

Experiment 4 investigates whether the illusory ownership of a bigger rubber hand also affects the ability of visually estimating the size of an object (namely, a tennis ball) held in the left hand exposed to the RHI.

3.5.1. Materials and Methods

Participants, experimental paradigm and statistical analyses

Fifteen healthy right-handed participants (12 females; mean age = 23.13 ± 2.69 years; range = 21-30 years) participated in Experiment 4. Procedures, and statistical analyses were identical to Experiment 1, with the exception of the size estimation task: now stimuli were pictures of a tennis ball (Figure 1b), instead of the participant's own hand; this version of the task was named Object Size Task (OST). Stimuli of the OST were scaled as to be of the same size of a real tennis ball size (diameter = 6.54 cm; same size trials), or smaller or bigger (i.e., different size trials: from -30% to +30% in steps of 6%). These dimensions were choosen following a pilot study (number of participants = 10) showing that differences between object's sizes of 3%, as those used in the HST, were too difficult to be detected by participants. As in the HST, for each of the 11 sizes, 12 trials were presented (total= 132 trials). Statistical analyses were identical to those conducted for the HST in Experiment 1, except for the fact that now the model included the factor Ball Size (from -30% to +30%) as continuous independent variable.

During the entire duration of the OST, participants were instructed to hold a real tennis ball (diameter = 6.54 cm) in their left hand; the participants could not see the ball, nor the own hands, which were hidden under a wooden panel.

3.5.2. Results

A RHI occurred in either the Rs-RHI and Bs-RHI sessions, as documented by scores at the Embodiment questionnaire (Friedman χ^2 = 26.76, p<.001), with a difference between synchronous and asynchronous conditions for either the Rs-RHI (1.46 ± 1.21 vs. -1.02 ± 1.72, p= .002) and the Bs-RHI (1.24 ± 1.42 vs. -1.17 ± 1.56, p= .003); importantly, scores did not differ in the Rs-RHI and the Bs-RHI (p= .16); hence, the RHI occurred regardless

of the fake hand size. At the Disembodiment questionnaire, the significant effect (Friedman χ^2 = 19.31, p= <.001) showed a difference between synchronous and asynchronous stroking for either the Rs-RHI (-1.24 ± 1.56 vs. -2.24 ± .79, p= .79) and the Bs-RHI (-1.6 ± .96 vs. -2.64 ± .49, p= .003), with no differences between the synchronous conditions (p= .36): again, the disembodiment of the own hand occurred independently of the fake hand size.

With respect to the OST, the final model included only the main effect of Ball Size, as well as the Time by RHI and the Ball Size by RHI interactions. Instead, the Time by Ball Size by RHI interaction did not reach significance (p=.64; see Table 5 for details), hence the embodiment of the tennis ball did not affect the own hand size perception (see Figure 5).
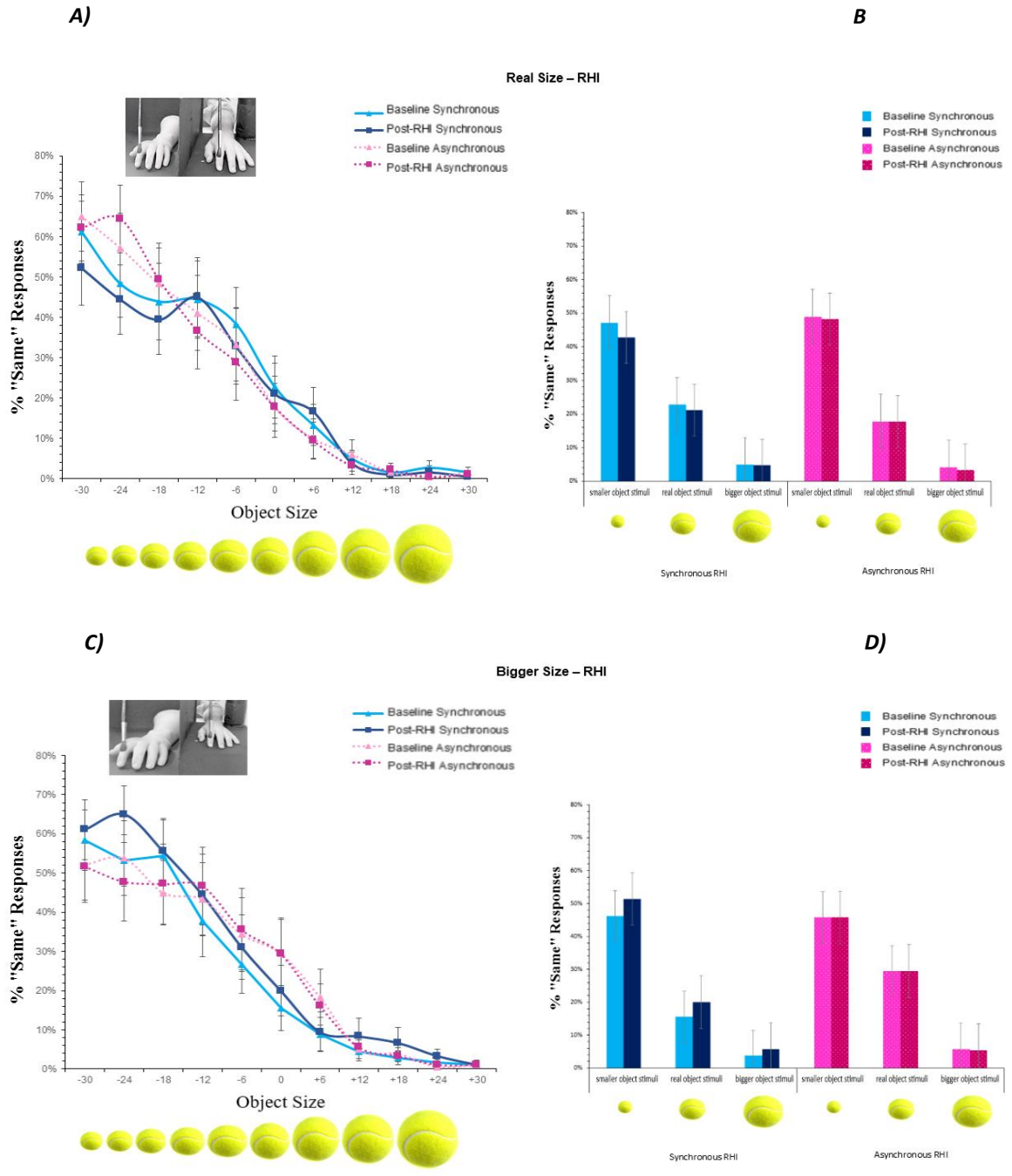
Figure 5. Results from Experiment 4: OST. Perceived change of the tennis ball size after RHI procedure with Real Size (Real size RHI, Rs-RHI; panel **A**) and Bigger Size (bigger size RHI, Ss-RHI; panel **C**) rubber hand. The graphs summarize the behavioral effect at the OST, before (baseline, light lines) and after (post-RHI, dark lines) the RHI procedure. Continuous lines represent percentage of «Same» responses in synchronous RHI conditions, dotted lines in asynchronous RHI conditions. Panel **B)** and **D)** summarize the results showing no changes of the perceived size of the tennis ball after the RHI stimulation, as compared to the baseline, neither with the Real Size RHI (Rs-RHI) neither with the Bigger Size RHI (BS-RHI, panel **C**; Time X Ball Size X RHI interaction= .64). X axis= percentage of the ball size change, with negative values corresponding to a reduction of the ball size, positive values to an increase; Y axis= percentage of «Same» responses. Error bars= SEM.

HST – LRT goodness-of-fit test			
	χ^2	Df	*p*
Time	0.10	1	.74
Ball Size	2793.36	1	<.001
Rhi	4.11	3	.25
Time X Ball Size	.21	1	.64
Time X Rhi	15.37	3	.001
Ball Size X Rhi	34.74	3	<.001
Time X Ball Size X Rhi	1.66	3	.64
HST – Mixed logistic regression			
	B	SE	z value	*p*
Intercept	-1.58	.24	-6.41	<.001
Time	-0.003	.10	-0.03	.97
Ball Size	-0.07	.004	-18.87	<.001
Rhi (synchronous Bs-RHI)	.008	.10	.08	.93
Rhi (asynchronous Rs-RHI)	-0.34	.11	-3.06	.002
Rhi (synchronous Rs-RHI)	-0.20	.10	-2.01	.04
Time X Ball Size	-0.001	.005	-0.28	.77
Time X Rhi (synchronous Bs-RHI)	-0.34	.15	-2.25	.02
Time X Rhi (asynchronous Rs-RHI)	.12	.15	.77	.43
Time X Rhi (synchronous Rs-RHI)	.13	.14	.89	.37
Ball Size X Rhi (synchronous Bs-RHI)	-0.01	.005	-2.53	.01
Ball Size X Rhi (asynchronous Rs-RHI)	-0.02	.006	-4.27	<.001
Ball Size X Rhi (synchronous Rs-RHI)	-0.002	.005	-0.38	.69
Time X Ball Size X Rhi (synchronous Bs-RHI)	-0.002	.008	-0.23	.81
Time X Ball Size X Rhi (asynchronous Rs-RHI)	.007	.008	.86	.38
Time X Ball Size X Rhi (synchronous Rs-RHI)	-0.003	.008	-0.40	.68

Table 5. Results from statistical analysis of Experiment 4. Abbreviations: HST= hand size task; LRT= likelihood ratio tests. Rs-RHI= Real size RHI; Bs-RHI= Bigger size RHI.

3.6. Discussion

In the present study, I investigated the relationship between the perceptual representation of body-part size and the sense of body-part ownership, assessing whether and how modulating the sense of ownership of one hand could shape how we perceive the size of that hand. Findings show that the embodiment of a fake hand occurs regardless of the fake hand dimension (bigger or smaller than the participant's hand size); however only the embodiment of a bigger fake hand, but not that of a smaller ones, influences the metric representation of the participant's own hand. In particular, in healthy adults, the embodiment of a fake hand bigger than the own hand causes an overestimation of the perceived size of the participant's own hand (Experiment 1 & 2), as assessed by a visual perceptual task (HST). This effect is specific for the hand exposed to the RHI (i.e., the left hand), since it does not occur for the unexposed (right) hand (Experiment 2). Results also show an asymmetric recalibration of the own hand size perception following the RHI: indeed, the embodiment of a fake hand smaller than the participant's own hand does not shrink the perceptual size of the own hand (Experiment 3). Finally, the illusory ownership of a bigger rubber hand does not affect the ability of visually estimating the size of an object (here, a tennis ball) held in the (left) exposed hand to the RHI (Experiment 4). Thus, the perceptual distortion of the hand size induced by the visuo-tactile stimulation does not extend to non-corporeal stimuli different from the hand, showing the selectivity of the bodily perceptual distortions induced by manipulating the sense of body ownership. Notably, in Experiment 1, 2 and 3, before inducing the RHI (baseline condition) participants tended to underestimate the size of their own hand; this confirms the results of the TMS experiments presented in the previous chapters (see also Giurgola et al., 2019), and it is also in line with other behavioral evidence confirming the existence of basal systematic distortions of body metric representation as an intrinsic feature of healthy adult

cognition (Fuentes et al., 2013; Longo et al., 2010; Longo et al., 2012a, 2012b; Longo, 2015; Tamè et al., 2017).

My results extend findings from previous studies assessing the relationship between body metric representation and body ownership (Banakou et al., 2013; Bernardi et al., 2013; Bruno et al., 2010; De Vignemont et al. 2005; Haggard et al., 2009; Pavani et al., 2007; Taylor-Clarke et al., 2004). Crucially, these findings provide novel evidence that altering the sense of body ownership by inducing it towards magnified body districts, in turn modulates the *conscious* representation of the own body-parts size in the same direction, thus resulting in perceptual distortions of the own hand metric representation, which is perceived bigger (Experiment 1, 2). The lack of integration of the fake hand within the own body representation in the asynchronous condition excludes the possibility that the mere visual perception of the hand would shape body size representation. The suggestion can be made from these findings is that top-down influences related to the mental representations of the own body may play a crucial role in updating the pre-existing perceptual representation of the own body-parts size. It is well accepted that bottom-up factors, such as the incongruence between visual, tactile and proprioceptive information, are critically involved in the induction of the RHI (Ehrsson, Holmes & Passingham, 2005; Ehrsson, Spence & Passingham, 2004; Tsakiris et al., 2005). However, here I propose that a merely bottom-up interpretation of the observed results cannot explain the present findings since any modulation of the own conscious hand size representation occurred at the HST, following the embodiment of a fake hand smaller than the own (despite the occurrence of the illusory ownership of the fake hand during the synchronous visuo-tactile stimulation, as assessed by the embodiment/disembodiment questionnaires; see results from Experiment 3). If the modulation of the hand size perception induced by the RHI were purely due to bottom-up factors, we should expect that subjects underestimated the

size of the own hand at the HST following the visuo-tactile stimulation of both their real hand and the smaller rubber hand (i.e., a complementary effect to the hand size overestimation, found after the embodiment of the bigger rubber hand), but this was not the case. By contrast, a selective, clearly shaping of the metric properties of the own hand emerged after the illusory ownership of the bigger fake hand. A possible interpretation of these findings is that participants tended to acknowledge enlarged rather than reduced body districts within the own pre-existing mental representation due to ontogenetic reasons. As suggested by De Vignemont and colleagues (2005, page 1288), *"ontogenetic development tends in the direction of growing and cannot normally be reversed"*. Hence, typical developmental changes in perceived body size may implicitly induce asymmetric expectations about the visual perceptual updating of the own body size. Furthermore, visual experience could explain why subjects are more likely to accommodate magnified than shrunken body images. Indeed, it is possible to visually perceive an enlargement of the own hand image by putting it close to the face, while a complementary relevant shrinkage cannot be perceived since the maximum reachable distance is the arm-length distance. The overestimation effect described in my study after the illusory ownership of the enlarged hand seems to mimic the subjective distortions reminiscent of 'macrosomatoagnosia' ('hyperschématie', Vallar et al., 2009) described in brain-damaged patients, a body illusion characterized by altered perception of the own body-parts as bigger than their real size (De Vignemont, 2010; Podoll et al., 1998; Podoll et al., 2000; Vallar et al., 2009). It is worth to notice that also the neuropsychological literature suggests that macrosomatoagnosia appears to be more frequent than 'microsomatoagnosia', a neurological condition in which patients complain to perceive the own body as smaller than the real size (Mauguiere & Courjon, 1978).

It has been also documented that the *implicit* modulation of the body image through multisensory illusions in turn shapes the body-referenced tactile perception of external objects touching the physical body (Banakou et al., 2013; Bruno et al., 2010; De Vignemont et al., 2005; Haggard et al., 2009; Taylor-Clarke et al., 2004), as well as the kinematics of reaching-to-grasp movements towards external objects (Bernardi et al., 2013; Bruno et al., 2010; Haggard et al., 2009). My findings well fit with evidence from Bernardi and co-workers (2013), showing that viewing the own hand enlarged alters the movement kinematics reducing the grip aperture towards objects, while the vision of the own shrunken hand does not modulate the grasping kinematics. Changing in movements kinematics after perceiving the own hand enlarged (Bernardi et al., 2013) seems to probe that altering body ownership *implicitly* shapes one's own body metric properties. In light of my results, I suggest that the implicit modulation of the own body representation, inferred by tactile perception and kinematics movements studies, reflects the *conscious* updating of the own body metric representation.

In the last experiment (Experiment 4) I assessed the possible effects of body ownership manipulation on body metric distortions by examining the occurrence of object size perceptual alterations after inducing the RHI with the bigger fake hand (Experiment 4). As in Experiment 1 and 2, after the synchronous visuo-tactile stimulation participants confirm to experience the illusory ownership of the bigger fake hand, as reported by the embodiment and disembodiment questionnaires. However, this does not affect the visual estimation of the object size (i.e., the tennis ball) held in the hand exposed to the RHI. Thus, the alteration of the sense of body ownership through the embodiment of an enlarged hand does not extend to perception of the size of non-corporeal stimuli, speaking in favor of selective bodily perceptual distortions induced by manipulating body ownership. Previous evidence in literature has shown effects of multisensory illusions in shaping

tactile perception of external objects (Banakou et al., 2013; Bruno et al., 2010; De Vignemont et al., 2005; Haggard et al., 2009; Taylor-Clarke et al., 2004), which might appear against the present findings. However, there are methodological differences, which are related to the different aim of such study. The main pertains to the experimental task, here the OST: participants held the object in their left hand, which – as in the previous Experiments 1, 2 and 3 – was hidden from the view, and were asked to judge the size of the object presented on the PC screen in haptic passive perception condition.

In conclusion, the present series of experiments demonstrates the tight link between the sense of ownership and body size, showing that the way we perceive the size of the our body-parts is shaped by our sense of ownership over the estimated body-part.

4. DEVELOPMENTAL CHANGES OF THE PERCEPTION OF THE BODY-PARTS SIZE

4.1. Aim of the study

As discussed in the introduction, and further confirmed by the studies described in the two previous chapters, perceptual distortions of body and body-parts representations constitute an intrinsic feature of healthy adult cognition (Longo et al., 2010; Tamè et al., 2017). However, the question remains as to whether such distortions in body size and shape arise during the developmental course: to date, very few studies have directly assessed perceptual bodily distortions in children. For example, Le Cornu Knight, Cowie & Bremner (2017) investigated tactile distance estimation (i.e., Weber's law) in children aged between 5 and 7 years. In their study, children were asked to adjust the distance between two tactile stimuli presented to the left forearm and hand. Results showed that children, just as adults, perceived tactile distances as smaller when the two stimuli were presented within the boundaries of a single body-part (i.e., stimuli that were presented on the arm or on the hand) and perceived the two stimuli as spaced farther apart when they were presented on two different body-parts (e.g., on the wrist and on the hand). The authors suggested that this stability of body distortions could be due to the fact that, while the single body-parts change in size and proportion (given that children's bodies rapidly grow across development), the relationship between the proportions of the different body-parts – as well as the relative location of the different body-parts – remain quite stable. Le Cornu Knight and colleagues (2017) also showed that, as in adults, perceived tactile distances appear larger on the hand than on the arm, which is likely the result of a higher density of

skin receptors in the hand than in the arm (Longo et al., 2011; Taylor-Clarke et al., 2004). However, contrary to adults, children overestimated tactile distance, while adults commonly tend to underestimate it (De Vignemont, Majid, Jola & Haggard, 2009).

Other developmental studies conducted in younger children showed that by 30 months of age, toddlers possess a rudimentary topographic representation of their own body shape, structure and size (Brownell, Nichols Svetlova, Zerwas & Ramani, 2010). In the study by Brownell and colleagues (2010), toddlers were administered five different tasks assessing their own body topography and body size; however, all experimental tasks reflected toddlers' bodily self-awareness, rather than measuring potential body distortions. For example, in one of the tasks designed to assess body size perception, toddlers were invited to put on doll clothes that were clearly too small for them to wear. The attempts of toddlers to actually put the clothes on were taken as evidence of immaturity of bodily self-awareness.

Bodily self-awareness has been the focus of recent studies conducted in preschool children (age 4-5 years), in which multisensory bodily illusions have been used to investigate the development of the body image and schema. For example, by means of the RHI, several studies have shown that while the sense of body ownership is already adult-like by age of 4 years (Cowie, Makin & Bremner, 2013; Nava, Bolognini & Turati, 2017), the sense of body position still develops up to 10 years of age (Cowie, Sterling & Bremner, 2016). Intriguingly, a recent study examined the relationship between body size changes and corresponding updates in body self-consciousness, investigating to what extent children are able to update their own body representation in order to match the changing body size (Filippetti & Crucianelli, 2019). In the study by Filippetti et al. (2019), 6- to 8- year-old children were exposed to the RHI, while watching either a regular (child-like) or a bigger (adult-like) size fake hand, being stroked in synchronous or asynchronous way with their

own hand. The synchronous – but not the asynchronous – stroking with both the regular and the bigger rubber hand modulated the sense of body ownership, but regardless of the fake hand size. Thus, visuo-tactile inputs influenced body self-consciousness in 6- to 8-years old children, regardless of the perceived variations of the body metric properties.

Perceptual bodily distortions in children have been directly examined in a very recent study by Cardinali, Serino & Gori (2019) demonstrating that children aged 6 to 10 years tend to underestimate the size of the own hand. Crucially, this bias seems to increase with age and to be selective for the body, since it does not extend to object size estimation (Cardinali et al., 2019).

Notwithstanding the importance of uncovering how the representation of the body, and of its parts, develops in human being, studies in this field are still at a preliminary stage of evidence: it is yet to be understood whether perceptual bodily distortions are present and reliable in early childhood (i.e., since preschool age) and how they potentially differ from adult's distortions, thus proving a more in-depth insight into the malleability – or rather stability – of such representations. Thus, by conducted 2 experiments, I have investigated the metric properties underlying body-parts representation in preschool children (3 to 6 years old), as compared to that of young adults, taking advantage of the experimental paradigm (the HST) used in the previous studies (see Chapters 2 & 3, Giurgola et al., 2019).

4.2. EXPERIMENT 1

Experiment 1 investigated the existence of perceptual distortions of the own hand size in healthy children, which were consistently reported in adults either in the neuroscientific literature (see Chapter 1) and confirmed by my previous experiments with the HST (Chapters 2 & 3).

4.2.1. Materials and Methods

Participants

The sample includes 90 healthy children (39 females; 72 right-handed; mean age ± standard deviation = 5.2 ± 6.56 years; range = 3-6 years) and 78 healthy adults (55 females; 72 right-handed; mean age ± standard deviation = 23.48 ± 3.66 years; range = 18-42 years). Twelve children did not complete the experiment and were therefore excluded from statistical analyses (hence the final sample comprised 78 children). Children were recruited from two kindergartens around the city of Milan ('Bruno Munari' and 'Via Gallina di Bareggio', San Martino di Bareggio, Italy). Adults were students recruited at the University of Milano-Bicocca (Italy).

The study was approved by the local Ethical Committee of the University of Milano-Bicocca and conducted in line with the Declaration of Helsinki. Handedness was assessed by the standard questionnaire (Oldfield, 1971); all participants had normal or corrected-to-normal vision. Participants were naïve both to the experimental procedure and to the purpose of the study. The parents of the children gave written informed consent before the children were tested.

Experimental paradigm

Participants underwent the HST described in Chapter 2 & 3 (see paragraph 2.2.1., page 34 for details). For adults, the experimental task was identical to that of Study #2 (see paragraph 3.2.1., page 62; see also Figure 1a for a selection of adult's stimuli, and Figure 1b for the experimental procedure). Instead, in children the number of stimuli and the procedure were slightly modified in order to facilitate the task. In particular, for each hand size (N = 11), 6 trials were presented (total = 66 trials; task duration = ~15 min). Furthermore, the stimuli were presented in two different blocks (i.e., 33 trails for each

block), separated by a 5 minutes interval. Moreover, differently from the adult group, stimuli presentation was not time-limited, so that each trial lasted until the child's response, which was followed by a white fixation cross presented at the center of the screen (Figure 1c). Finally, for the children group, in each trial the response button was pressed by the experimenter, after the participant's verbal response.
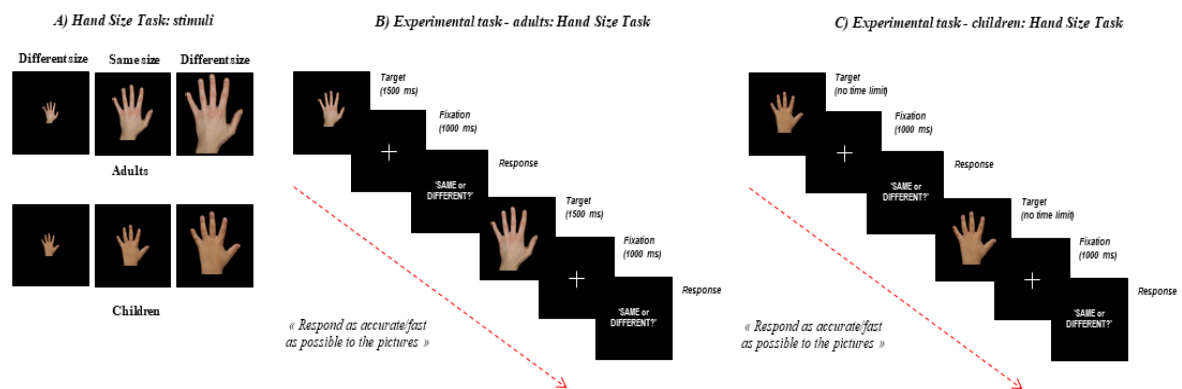
Figure 1. HST 1. A) Stimuli were pictures of the participant's left and right hands with different sizes, with the respect to the participant's individual hand: 0% (*same* size trials), smaller or bigger by 3%, 6%, 9%, 12% or 15% (*different* size trials). **B)** For adults, in each trial, a hand picture (target) was presented for 1500 ms; the participants' task was to judge whether the size of the viewed hand matched («Same» response) or not («Different» response) the size of their own (out-of-view) hand (2 forced-choice task). **C)** For children, stimulus presentation was not time limited.

Statistical analyses

Statistical analyses were performed using JASP Software (see Marsman & Wagenmakers, 2017; Wagenmakers et al., 2018).

I used a Bayesian approach to analyse data, thus comparing the predictive adequacy of two competing statistical models, i.e., the likelihood of either the null or alternative hypothesis. In general, the Bayesian framework offers a series of advantages in comparison to the more standard frequentist approach. First of all, it compares the predictive adequacy of two competing statistical models and provides a redistribution of probability between these competing accounts. Second, it capitalises on prior knowledge to construct a more

informative test. To quantify the evidence in favour of one or the other hypothesis, the Bayesian framework uses the Bayes factor, which is determined by comparing the hypotheses' abilities to predict the observed data (Etz & Vandekerckhove, 2018), with the posterior odds favouring more or less strongly one hypothesis than the prior odds. Furthermore, there is now consensus on the approximate classification scheme for the interpretation of the Bayes Factor (BF_{10}, see Lee & Wagenmakers, 2013), by which $BF_{10} > 3$ are considered as moderate evidence for H_1, and $BF_{10} < 1/3$ are considered as moderate evidence for H_0. $BF_{10} > 10$ are considered as strong evidence in favour of H_1, and $BF_{10} < 1/10$ are considered as strong evidence in favour of H_0[1].

In this study, for each participant I calculated the mean proportion of «Same» responses provided on each hand size (N = 11, from -15% to +15%). To detect differences between groups (children vs. adults), I performed a series of Bayesian Independent samples t-tests comparing the «Same» responses for each hand size. Furthermore, to document whether children and adults presented distortions of the perceived hand size, for both groups I made a series of Bayesian Paired samples t-tests comparing the «Same» responses for each hand size (i.e., smaller and bigger, different size trials: from -15% to +15%) against the «Same» responses given when the size matched the real size of the participants' hand (i.e., same size trials, 0% variations).

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[1] *Please note that even adopting a non-bayesian statistical approach, as that used in the previous experiments (see Chapters 2-3), the same results were obtained.*

4.2.2. Results

The Bayesian Independent samples t-tests between children and adults are summarised in Table 1. In particular, the analysis showed that the proportion of «Same» responses of children and adults mostly differed when the size of the hand presented was bigger than the participant's real hand (see Figure 2). Indeed, children reported more «Same» responses than adults particularly when the hand size was 6% ($BF_{10} = 12.76$) and 12% ($BF_{10} = 19.47$) bigger than their real hand (see Table 1). On the contrary, when the presented hand was smaller than the real hand, the difference in responses between adults and children for all hand sizes was between a BF_{10} of 0 and 1, which is interpreted as moderate evidence in favour of H_0. It should be noted that when the presented hand matched the participant's hand size (i.e., same size trials, 0% variations) the difference in «Same» responses between the two groups achieved a $BF_{10} = 0.17$, supporting moderate evidence of H_0. Thus, any difference between groups emerged when participants judged the real size of their own hand.

Bayesian Independent samples t-tests		
Hand Size	BF_{10}	error %
-15	0.351	4.075e -6
-12	0.274	5.2423 -6
-9	0.767	1.646e -6
-6	0.809	1.527e -6
-3	0.182	7.6893 -6
0	0.174	8.015e -6
+3	2.294	3.299e -7
+6	12.758	4.080e -9
+9	4.215	1.046e -7
+12	19.473	4.473e -9
+15	3.941	1.203e -7

Table 1. Bayesian Independent samples t-tests comparing percentage of «Same» responses for each hand size between children and adults.
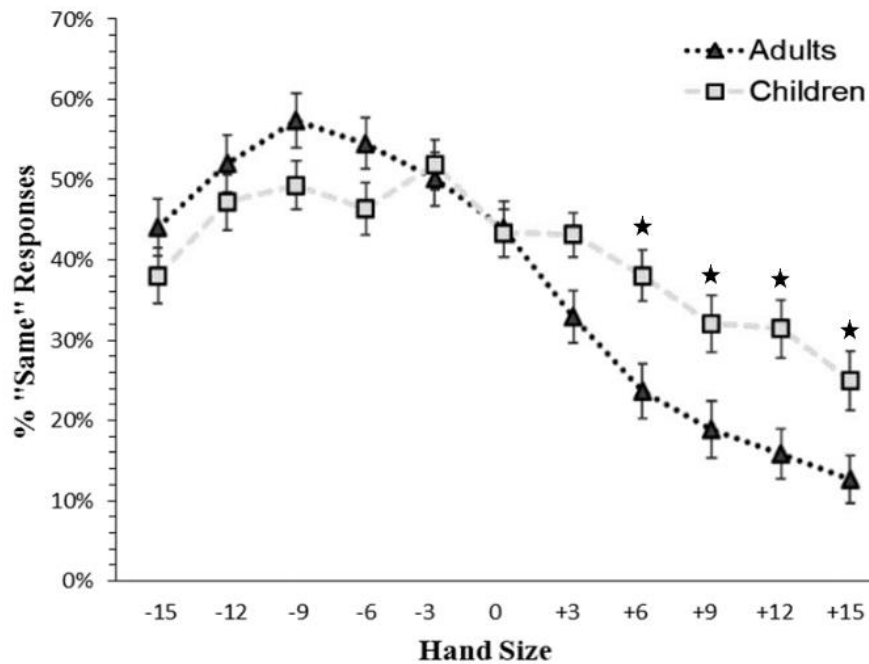
Figure 2. HST. Hand size perception for children and adults. X axis = percentage of the hand size change with respect to the participant's own hand; negative values corresponding to a reduction of the hand size, positive values to an increase. Y axis = percentage of «Same» responses for each hand size. Grey line = children's performance; black line = adults' performance. Error bars = SEM.

To further explore the potential distorted perception of own hand size within each group, the proportion of «Same» responses for the different hand sizes was separately analysed for children and adults by comparing the ten different hand sizes (i.e., five smaller and five bigger, respectively) to the real hand size (i.e., 0% variations). The Bayesian Paired samples t-tests for children are reported in Table 2. Specifically, the analyses revealed that children tended to slightly underestimate the size of their hand, since they reported a similar proportion of «Same» responses as when the seen hand was smaller than their own, and less «Same» responses when the seen hand was bigger than their own. While there was moderate evidence in favour of H_0 when the size of the hand was between 15% and 6% smaller than the real hand (all BF_{10} between 1/10 and 1/3; see example in Figure 3, left

panel), evidence in favour of H_1 was particularly strong when the seen hand was 9% (BF_{10} = 13.90), 12% (BF_{10} = 12.08), and 15% bigger than the real hand (BF_{10} = 3507.87, see example in Figure 3, right panel).

Bayesian Paired samples t-tests			
Hand Size	**Real Hand**	**BF_{10}**	**error %**
-15	0	0.231	5.848e -6
-12	0	0.168	1.008 -5
-9	0	0.340	3.059e -6
-6	0	0.168	1.007e -5
-3	0	1.540	1.150e -6
+3	0	0.125	1.625e -5
+6	0	0.611	1.674e -6
+9	0	13.904	3.471e -7
+12	0	12.082	3.815e -7
+15	0	3507.875	2.836e -9

Table 2. Bayesian Paired samples t-tests comparing percentage of «Same» responses for the ten different hand sizes (i.e., five smaller and five bigger than the real hand, respectively) to the real hand size (i.e., 0% variations) in children.
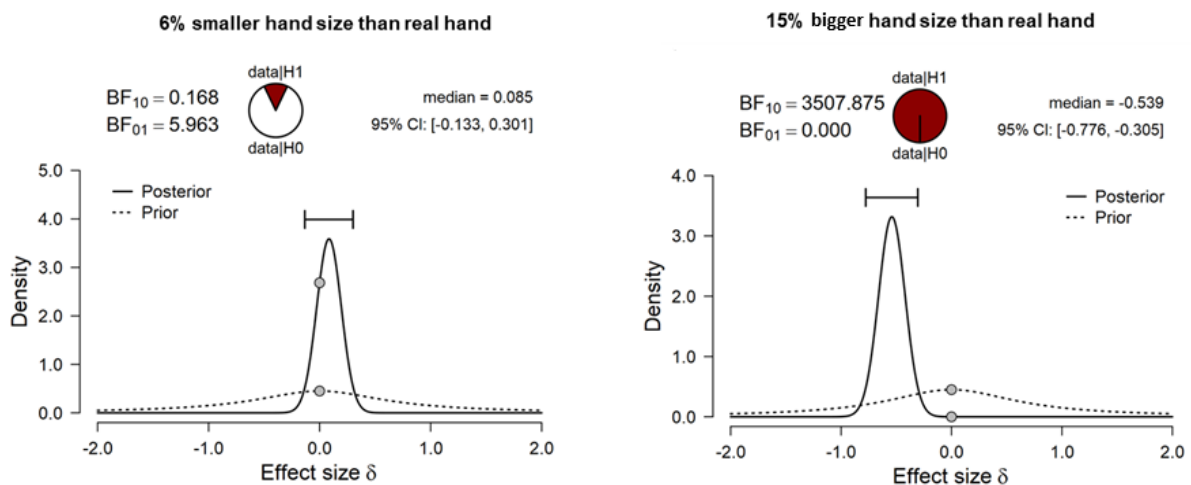
Figure 3. Example of prior and posterior distribution for the comparison between the proportion of «Same» responses in children, when the hand was 6% smaller (left panel) or 15% bigger (right panel) than their real hand.

For adults, the Bayesian Paired samples t-tests are reported in Table 3 and show that participants clearly underestimated the size of their hand particularly when it was 9% (BF_{10} = 5.51) and 6% (BF_{10} = 8) smaller than their real hand. On the contrary, the proportion of «Same» responses strongly decreased as soon as adults saw the size of their hand becoming bigger. Indeed, there was extreme evidence in favour of H_1 for all the comparisons between the bigger hand sizes and their real hand (all $BF_{10} > 1636$, see Figure 4 for an example of the distribution).

Bayesian Paired samples t-tests			
Hand Size	Real Hand	BF_{10}	error %
-15	0	0.125	1.625e -5
-12	0	0.349	2.925 -6
-9	0	5.514	6.205e -7
-6	0	8.000	4.975e -7
-3	0	2.753	8.937e -7
+3	0	1636.775	6.036e -9
+6	0	919439.641	5.541e -12
+9	0	1.720e +6	4.319e -9
+12	0	3.467e +7	2.811e -14
+15	0	6.188e +8	7.161e -16

Table 3. Bayesian Paired samples t-tests comparing percentage of «Same» responses for the ten different hand sizes (i.e., five smaller and five bigger than the real hand, respectively) to the real hand size (i.e., 0% variations) in adults.
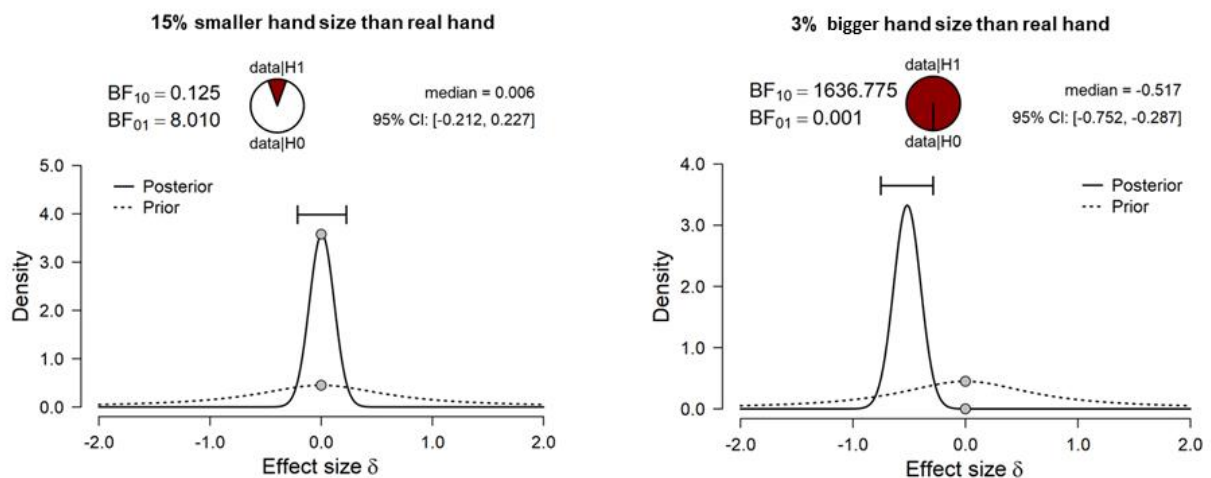
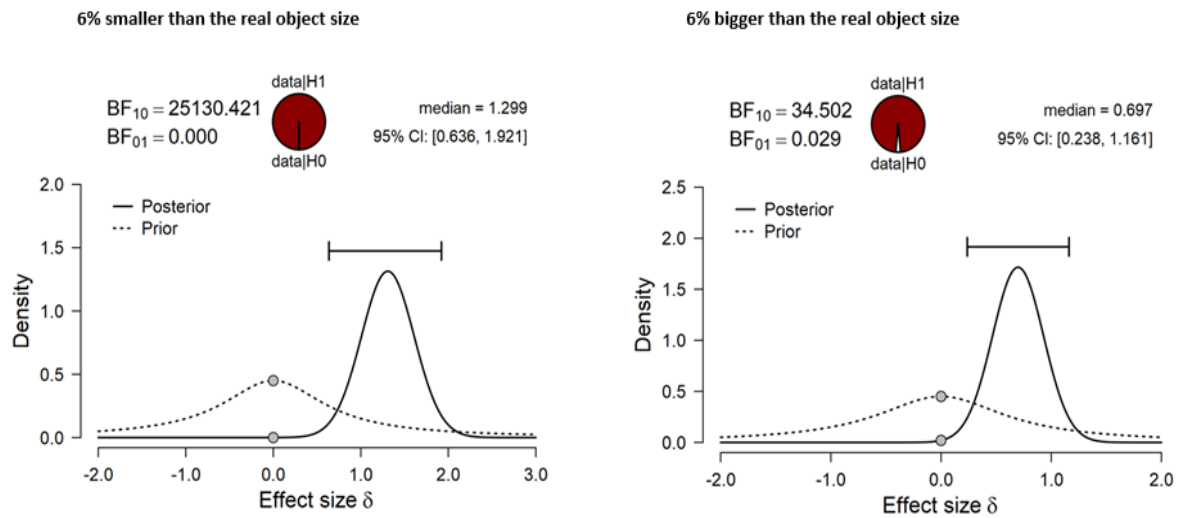**Figure 4.** Example of prior and posterior distribution for the comparison between the proportion of «Same» responses in adults, when the hand was 15% smaller (left panel) or 3% bigger (right panel) than their real hand.

4.3. EXPERIMENT 2

Experiment 2 represents a control experiment aimed at assessing whether the previous findings are specifically related to the estimation of the hand size. Hence, I have explored whether the perception of the size of an object (a tennis ball), held in the hand, is also different in children as compared to adults.

4.3.1. Materials and Methods

Participants

Thirty healthy right-handed children (13 females; mean age = 5.58 ± 5.67 years; range = 4-6 years) and twenty-one healthy right-handed adults (18 females; mean age = 25.09 ± 4.91 years; range = 21-42 years) took part in Experiment 2. Six children were not able to complete the task and were therefore excluded from statistical analyses (hence the final sample comprised 24 children). Children were recruited at the kindergarten 'G. Gattinoni' (Mantegazza, Milan, Italy), while adults were students recruited at University of Milano-Bicocca. All participants were recruited by using the same criteria of Experiment 1.

Experimental paradigm

Procedures and statistical analyses were identical to Experiment 1, with the only difference of using the OST employed in Study #2. For adults, the OST was identical to that of Study #2 (see Chapter 3, paragraph 3.5.1., page 76 for details; see also Figure 5a for the experimental procedure); instead, in order to administer it in children, the experimental paradigm was slightly modified. Specifically, for each ball size (total = 11), 6 trials were presented; moreover, as in Experiment 1, only for children trials were presented in two separate blocks without time limit and the experimenter pressed the right («Same» response) or the left («Different» response) mouse button, according to the children's verbal response (Figure 5b).
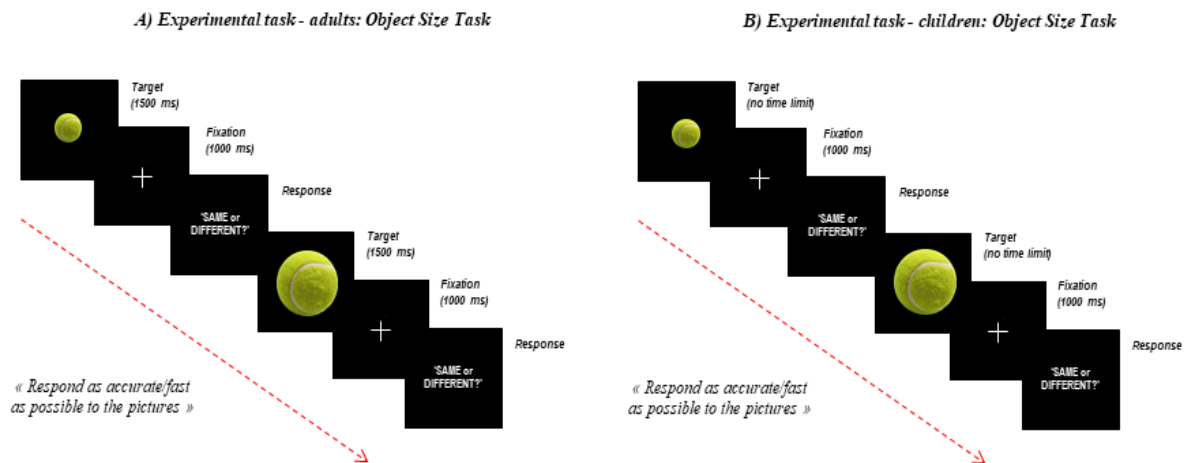
Figure 5. OST. A) For adults, in each trial, a tennis ball picture (target) was presented for 1500 ms; the participants' task was to judge whether the size of the viewed ball matched («Same» response) or not («Different» response) the size of the ball held in the hand own (out-of-view). **B)** For children, stimuli presentation was not time limited.

4.3.2. Results

The analyses performed in Experiment 2 mimicked the ones of Experiment 1.

As depicted in Table 4, the differences between groups were strongly in favour of H_1 when the object seen by participants was 30% (BF_{10} = 20.94), 24% (BF_{10} = 6.08) and 18% (BF_{10} = 7.31) smaller than the object held in their hand. This was caused by adults providing more «Same» responses than children; that is, adults tended to underestimate the size of the object more than children.

On the contrary, when the size of the ball was bigger than the ball held in the participants' hand, the pattern reversed: this time, there was strong evidence in favour of H_1 when the ball was 6% (BF_{10} = 76.43) and 12% (BF_{10} = 11) bigger than the real ball, since children reported more «Same» responses than adults. That is, children overestimated more than adults the size of the object (see Figure 6).

Bayesian Independent samples t-tests		
Object Size	BF_{10}	error %
-30	20.936	3.462e -4
-24	6.085	3.611 -4
-18	7.314	0.002
-12	0.328	0.020
-6	3.357	0.001
0	1.087	1.328e -4
+6	76.433	1.992e -6
+12	11.003	4.126e -4
+18	3.341	0.001
+24	1.306	3.759e -4
+30	1.055	2.564e -4

Table 4. Bayesian Independent samples t-tests comparing percentage of «Same» responses for each ball size between children and adults.
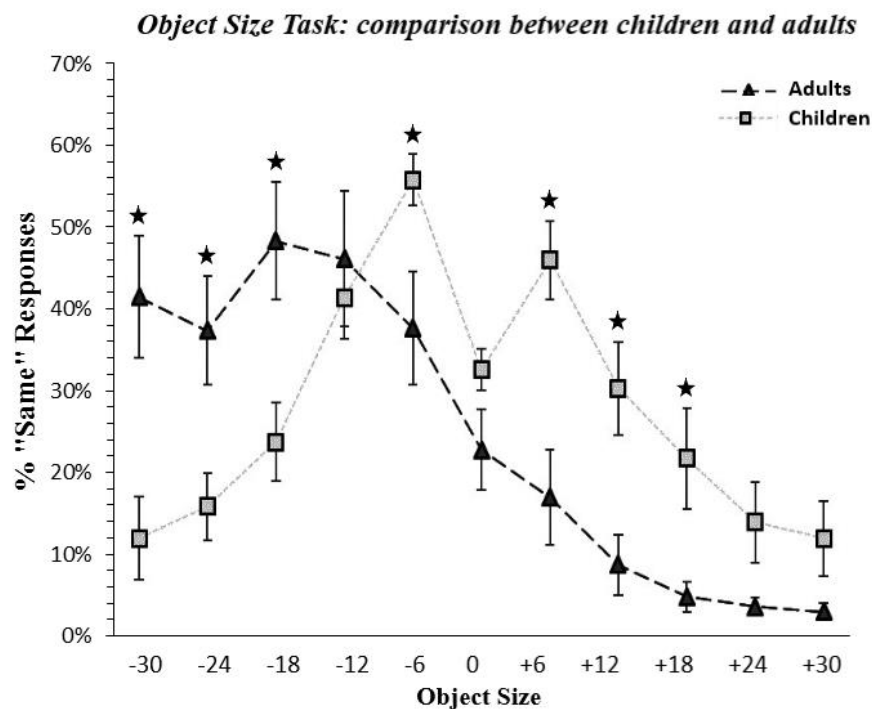
Figure 6. OST. Object size perception for children and adults. X axis = object size change; negative values corresponding to a reduction of the object size, positive values to an increase. Y axis = percentage of «Same» responses for each ball size. Grey line = children's performance; black line = adults' performance. Error bars = SEM.

To further explore the distorted visual representation of the object size within group, the proportion of «Same» responses for the different ball sizes was separately analysed for children and adults by comparing the ten different sizes (i.e., five smaller and five bigger, respectively) to the real size (i.e., 0% variations) of the object participants held in their hand.

Table 5 reports Bayesian Paired samples t-tests in children, which showed strong evidence in favour of H_1 when the size of the seen object was 30% ($BF_{10} = 11.15$), 24% ($BF_{10} = 8.64$), and 6% ($BF_{10} = 25130.42$, see Figure 7, left panel) smaller than the real object. There was also a very strong evidence in favour of H_1 when the seen object was 6% ($BF_{10} = 34.50$, see Figure 7, right panel), 24% ($BF_{10} = 54.39$) and 30% ($BF_{10} = 272.47$) bigger than the object held in the hand. That is, children showed on average accurate estimation of the object size, irrespective of whether it was bigger or smaller with respect to the real object.

Bayesian Paired samples t-tests			
Object Size	Real Object Size	BF_{10}	error %
-30	0	11.150	3.646e -4
-24	0	8.646	3.251 -4
-18	0	0.678	1.098e -4
-12	0	0.574	1.130e -4
-6	0	25130.421	5.441e -9
+6	0	34.502	2.042e -4
+12	0	0.240	0.035
+18	0	1.197	9.926e -5
+24	0	54.387	1.331e -4
+30	0	272.475	1.309e -5

Table 5. Bayesian Paired samples t-tests comparing percentage of «Same» responses for the ten different ball sizes (i.e., five smaller and five bigger than the real ball, respectively) to the real ball size (i.e., 0% variations) in children.

Figure 7. Example of prior and posterior distribution for the comparison between the proportion of «Same» responses in children, when the object was 6% smaller (left panel) or 6% bigger (right panel) than the real object.

For adults, Table 6 reports Bayesian Paired samples t-tests, showing that adults' differences between the different seen object sizes and the real object was very strongly in favour of H_1 when the seen object was 12% ($BF_{10} = 29.39$), 18% ($BF_{10} = 126.72$), 24% ($BF_{10} = 129.10$), and 30% ($BF_{10} = 88.57$) bigger than the real object. On the contrary, the differences between the smaller seen object and the real object only moderately supported the H_1, such as when the size of the seen object was 18% ($BF_{10} = 9.48$) and 12% ($BF_{10} = 5.04$) smaller than the real object (see Figure 8 for an example of the distribution).

Bayesian Paired samples t-tests			
Object Size	Real Object Size	BF$_{10}$	error %
-30	0	0.801	0.006
-24	0	0.665	0.009
-18	0	9.478	8.286e -4
-12	0	5.045	0.002
-6	0	2.627	0.002
+6	0	0.691	0.009
+12	0	29.392	1.580e -4
+18	0	126.722	2.249e -6
+24	0	129.102	2.115e -6
+30	0	88.575	6.635e -6

Table 6. Bayesian Paired samples t-tests comparing percentage of «Same» responses for the ten different ball sizes (i.e., five smaller and five bigger than the real ball size, respectively) to the real size (i.e., 0% variations) of the ball held in adult's hand.
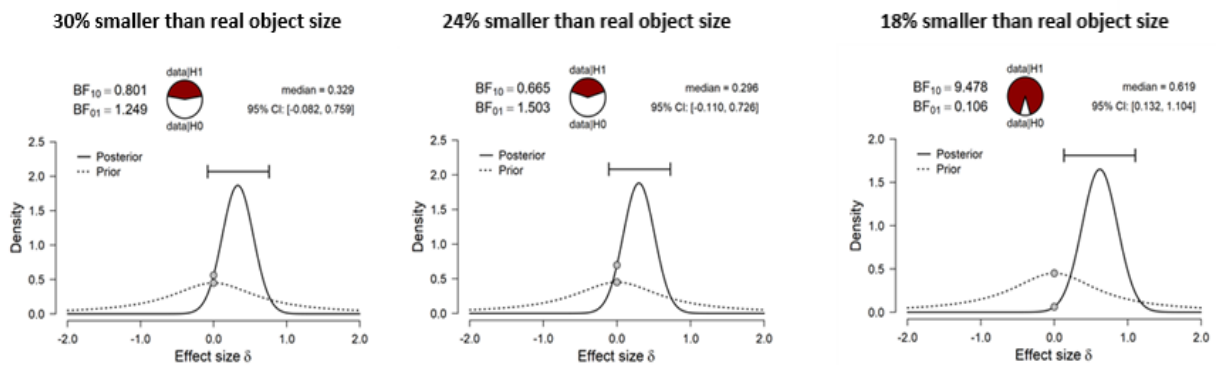
Figure 8. Example of prior and posterior distribution for the comparison between the proportion of «Same» responses in adults when the object was 30% (left panel), 24% (central panel) or 18% (right panel) smaller than the real object.

4.4. Discussion

The present study investigated whether perceptual bodily distortions in healthy cognition occur earlier in childhood, and whether such distortions are selective for body perception

(Experiment 1) or, conversely, they extend to object's size estimation (Experiment 2). I assessed the subjective ability of visually perceiving the own hand dimension in a group of 3 to 6 years old children, as compared to adults. Firstly, findings from the HST show that both children and adults tend to underestimate the perceptual size of the own hand. Indeed, when asked to recognize the size of their own hand among different scaled hand pictures, participants tend to indicate the viewed hand as matching the size of their own when the presented image is scaled in order to appear smaller than participant's real hand size. Thus, results from Experiment 1 reveal that children aged between 3 and 6 years already present bodily perceptual distortions that are similar to that observed in adults. Furthermore, the pattern shown by adults corroborates findings from several behavioural studies showing a fundamental distortion of the perceived dimension of the own hand in healthy individuals (Fuentes et al., 2013; Longo, 2015; Longo et al., 2010); indeed, the present results provide further support of the existence, in healthy adults, of an underestimation of the size of their own hand, at least in visual perceptual tasks (Giurgola et al., 2019). Interestingly, the present results also well fit with evidence using template matching task similar to the HST adopted here, typically used to assess the metric properties of the own body (Longo et al., 2012).

However, the Bayesian approach adopted in the present study shows that, by comparing children and adults' size perception of the own hand, children tend to slightly overestimate the size of their own hand as compared to adults. That is, children differ from adults in hand size estimation, mostly when the seen hand is bigger than their own. By contrast, the difference between groups when the hand was smaller than their real one was in favour of H_0, thus suggesting that already by age 3 years, children tend to underestimate the size of their own hand. However, when the distorted perception of own hand size was separately observed in children and in adults, while adults clearly reported the seen hand to be of the

same size of their own when viewing hands smaller than their own, children's performance revealed a more attenuate tendency to underestimate the size of the own hand. The suggestion can be made from these findings is that body distortions occur very early in childhood, showing an asymmetric tendency to underestimate the own body-size. It could be speculated that this pattern of asymmetry develops gradually during the lifespan, characterizing bodily distortions even in preschool children, up to sharpening in adult life. This explanation well fits with longitudinal studies on body size estimation. For example, Gardner, Friedman, Stark & Jackson (1999) investigated the perceived body size in children aged 6 through 14 years. In their study, children were presented with videos showing their life-size frontal image and they were asked to adjust its width according to size of the own body, as subjectively felt. The authors collected data annually for three years, beginning at ages 6, 9, and 12. Overall, children resulted accurate in estimating their body dimension, showing average overestimation of less than 2%. Crucially, overestimation decreased within each age group during the three years of the study.

Interestingly, the idea that the tendency to underestimate the own body size develops gradually across the lifespan finds further supports in a recent study by Cardinali and co-workers (2019). In their study, body size representation resulted asymmetrically distorted in children aged between 6 and 10 years. Specifically, when children were asked to judge the own hand size, using both visual or haptic modalities, they underestimated the size of the own hand; notably, such bias was found to increase with age (i.e., younger children were more accurate in estimating their own hand size than the older ones). My study, where the visual metric representation of the own hand was explored in 3- to 6- year-old children, shows an attenuate tendency to underestimate the size of the own hand by children; this distortion appears less pronounced than that of 6- to 10- year-old children, as reported by Cardinali et al. (2019). Thus, it is possible to propose that the underestimation

of the own body size, which probably reflects the somatotopic organization of S1 (Linkenauger et al., 2015), represents a sort of compensation mechanism for body-parts that are over-represented in S1 (and M1) maps, such as the hands; such compensatory distortion could already be present in new-borns, in turn supporting an innate representation of the body.

The fact that typically developing children show body distortions that are similar to adults is important to determine whether such body distortions can be considered a sign of a healthy development or a pathological one. For instance, studies have shown that children with autism present altered motor representations. In particular, leg/trunk and upper limb/hand representations in the primary motor cortex (M1) appear less distinct in children affected by autism as compared to healthy controls (Nebel et al., 2012) and this anomalous organization may be associated with many of the fine and gross motor deficits observed in autism. Thus, it could be speculated that autistic children may also present altered representation of body-parts, as the localization of activity within M1 evoked by a motor task commonly reflect the body-part involved in the task (Grafton, Woods, Mazziotta & Phelps, 1991).

The present study extends findings about body distortions in adults to children, suggesting that such body metric alterations start to develop at least by 3 years of age.

Results from the control task (i.e., OST, Experiment 2) demonstrate that the perceptual distortions observed in the HST are selective for the own body-part representation and such distortions do not extend to external non-corporeal objects estimation. This is in line with previous findings showing that perceptual distortions in size estimation task do not appear when participants are required to judge non-corporeal objects of the same size as their own body-parts (Linkenauger et al., 2015). Specifically, Linkenauger and co-workers (2015) employed a visual estimation task to examine the perceptual distortions of body-

parts sizes. The authors investigated whether distortions of body perception occur only when participants are required to compare one body-part to another, or whether they extend to the comparison between the length of body-parts and a non-corporeal object as a meter. Results revealed remarkable distortions in the perceived size of body proportions that were specific to the viewing of one's own body. Indeed, such distortions occurred when subjects compared the length of one body-part to another, but they did not emerge when subjects estimated the size of a body-part with respect to a non-corporeal object, or when judging non-corporeal objects of the same dimension as the own body-parts.

The comparison between the two groups shows some differences in their ability of visually estimating the dimension of objects. Indeed, when both groups were required to judge the size of the tennis ball presented as bigger than that held in the hand, children overestimated its dimension, as compared to adults. This pattern of results was complementary to that observed when participants had to estimate the size of the ball in trials representing it smaller than its real size: in this case, children tended to underestimate the size of the tennis ball held in the hand, as compared to adults. Crucially, when children's ability to estimate objects' size was separately observed, children showed - on average - accurate object size estimation ability, irrespective of whether the object presented was smaller or bigger with respect to the real object dimension. This demonstrates, also in preschool children, the selectivity of the bodily perceptual distortions that do not extend to non-corporeal stimuli. Finally, this well fits with findings from Cardinali et al., (2019) showing that in 6- to 10- years old children underestimation is specific for the body and it does not extend to object size judgements.

Overall, these results are in accordance with previous evidence demonstrating that distortions of body representation are specific for the perception of the metric properties of the own body and are not limited to neurological or psychiatric disorders, since

misperception of the metric properties of the body characterize also healthy cognition (Longo, 2015; Longo et al., 2015). Here I demonstrate that such bodily distortions occur earlier in childhood.

5. GENERAL DISCUSSION

The series of experiments illustrated in the present doctoral thesis focused on the cognitive and neural signatures underlying the metric properties of body-parts representation, providing novel clues on how we perceive our body-parts size and how they are represented in our brain.

In Chapter 2, by adopting a neurophysiological approach, through a set of four experiments I explored the effects of modifying the somatosensory cortical excitability on the metric representation of the own body-parts (Study #1). Taking advantage of non-invasive brain stimulation techniques such as rTMS, I demonstrated the causal role of S1 in the perceptual processing of body-parts size. In healthy, neurologically unimpaired individuals, targeting the cortical hand representation in S1 maps of both hemispheres with rTMS leads to bodily distortions (i.e., overestimation) of the perceived size of the own left and right hands (Experiment 1-3), in a somatotopic manner which does not generalize to other body-parts (the foot, Experiment 2). The fact that cortical excitability shifts in IPL of both hemispheres do not alter body size perception (Experiment 4) confirms the causal, selective implication of S1 in the construction and updating of one's own body metric representation.

In Chapter 3, the flexible nature of body-parts size representation was confirmed by adopting a behavioral approach aimed at modulating the sense of body ownership, in order to investigate its effects on body metric representation (Study #2). By carrying out four experiments in healthy adults, I showed how the embodiment of external hands bigger (Experiment 1, 2) but not smaller (Experiment 3) than the own hand causes a selective overestimation of the own hand dimension, that does not extend to non-corporeal stimuli (Experiment 4).

Finally, in Chapter 4 (Study #3) I provided further support to the existence of bodily perceptual distortions in healthy cognition, showing the probably innate nature of such distortions that occur earlier in childhood, develop during the lifespan (Experiment #1) and are specific for the own body size estimation without impacting on object size perception (Experiment #2).

Overall, my findings well fit with previous evidence in literature, which has documented distortions and misperceptions of the inherent subjective representation of the own body-parts size (Fuentes et al., 2013; Linkenauger et al., 2015; Longo, 2015; Longo et al., 2010; Longo et al., 2012a, 2012b; Longo et al., 2015). Moreover, they extend the knowledge on the cognitive and neural mechanisms involved in body-parts size processing.

In this regard, Study #1 complements previous evidence on local peripheral deafferentation showing that the own body size can be modulated, in bottom-up fashion, by incoming tactile inputs (Gandevia et al., 1999): by adopting a reversed perspective, I showed how the perceived size of the own body-parts can be shaped by plastic, dynamic and reversible changes of body-parts maps within S1. Indeed, changes of the central somatosensory maps by rTMS alter the perceived size of the participant's own hands, probably due to adjustments in the receptive fields of S1 neurons representing the hand, as peripheral hand deafferentation does (Merzenich et al., 1983). This provides evidence to a new understanding of S1, showing how it represents a key site for body size processing, causally involved in the topographical representation of the metric properties of the body surface. To the best of my knowledge, this is the first demonstration that reliable perceptual distortions of own body-parts size can be induced by the alteration of body-parts representations at the cortical level. Hence, new insights about the functional role of S1 in body perception are proposed, suggesting that S1 is more than a simple relay for unilateral tactile inputs. Traditional studies have depicted S1 body maps as fixed and

reflecting the physical location of peripheral stimulation, in the form of the somatosensory homunculus (Penfield et al., 1937, 1950). Here I challenge this view, going beyond this over-simplistic perspective and proposing a more complex functional role for S1, the first cortical site involved in tactile information processing. In line with new perspectives supporting the role of S1 in the integration of bilateral somatosensory inputs both at early (i.e., via trans-callosal connections between S1 of both hemispheres, as well as via ipsilateral thalamo-cortical interactions) and later (via ipsilateral connections between S1 and S2) stages (Tamè et al., 2014; Tamè et al., 2016), my findings are consistent with the idea that S1 is a key cortical site for the integration of ipsilateral and contralateral somatosensory information from both sides of the body. In particular, the fact that unilateral S1 stimulation affects size estimation of both the left and the right hands, suggests that the neural representations of the body metric in S1 is not exclusively contralateral, as if the size update of one hand may be automatically passed onto the other one (Tamè et al., 2016). Note that, in spite of questioning the classical conceptualization by which S1 elaborates *primarily* incoming inputs from the contralateral side of the body, here I point out that S1 does not *exclusively* process contralateral somatosensory signals. This well fits with neurophysiological studies in monkeys and neuroimaging studies in humans showing that that neural representation of the body in S1 is not purely contralateral (Blatow, Nennig, Durst, Sartor & Stippich, 2007; Iwamura, Tanaka, Iriki, Taoka & Toda, 2002; Iwamura, Taoka & Iriki, 2001; Reed, Qi & Kaas, 2011). Crucially, as illustrated in Study #1, S1 of both hemispheres contributes to the ongoing estimation of the own body-parts size. Overall, results from Study #1 not only corroborate the straight link between body representation and somatosensation, but also shed new light on the role of S1 in the construction and maintenance of the body metric, relating this low-level primary sensory cortex to higher-order processes subtending awareness of body size.

The evidence discussed so far points at the plastic properties of body metric representation, endorsing its dynamic and flexible nature. In support to this proposal, I demonstrated how the perceptual representation of the own body size can be shaped both by inducing neural excitability shifts at the cortical level (Study #1), as well as by manipulating bodily experiences, in particular by modulating the sense of body-parts ownership (Study #2, Chapter 3). Thus, capitalizing on findings from Study #1, I explored whether modulating the relationship between the sense of body-parts ownership and body metric representation could corroborate the straight link between the somatosensory system and body size (Study #2).

The malleability of the sense of body ownership has been previously highlighted through experimental research, which has demonstrated an asymmetric tendency to embody enlarged body districts but not reduced ones (De Vignemont et al., 2005; Haggard et al., 2009; Pavani et al., 2007). In this regard, it has been shown that an altered sense of body ownership may at least *implicitly* shape the representation of one's own body metric (Banakou et al., 2013; Bernardi et al., 2013; Bruno et al., 2010; De Vignemont et al., 2005; Haggard et al., 2009; Pavani et al., 2007; Taylor-Clarke et al., 2004). Through four behavioral experiments, in Study #2 I explored the sense of ownership towards magnified and reduced representations of the hand; crucially, I examined body size perceptual changes following exposure to altered representations of the body (through the RHI paradigm; Botvinick et al., 1998). Hence, my study extends the knowledge about the relationship between the sense of body ownership and body metric representation, providing novel evidence about the effects of manipulating body-parts ownership on the plastic distortions of one's own *conscious* body-parts size representation. Following cross-modal conflicts applied to participants' own hand, my study shows how the internal mental representation of the own body size can be quickly and directly updated in order to reflect

the nature of such distortions. The modulation of the hand metric representation following the embodiment of a bigger – but not smaller – fake hand seems to suggest that the recalibration of the own hand size perception could be due to top-down influences related to the own mental body representations, which may play a key role in updating the pre-existing perceptual conscious representation of the own body-parts size. Interestingly, the asymmetric tendency to acknowledge enlarged – rather than reduced – body-parts within the own pre-existing mental representations could occur due to developmental reasons, since typical developmental changes in perceived body size tend in the direction of growing (De Vignemont et al., 2005). However, the perceptual representation of the own body-parts size during development has been so far poorly investigated. Thus, I faced this issue in Study #3, where I explored hand size perceptual representation in typically developing preschool children. Specifically, I examined whether children's bodily representation may mimic body size perceptual distortions similar to that documented in healthy adults by previous evidence (Fuentes et al., 2013; Longo, 2015; Longo et al., 2010), and illustrated also in the present dissertation (Study #1 & #2). Findings from Study #3 suggest that perceptual distortions of body-parts representations arise during the developmental course; indeed, children aged 3 to 6 years tend to underestimate the own hand size, as adults do. This bias appears more attenuated in children as compared to adults, speaking in favour of the flexible, plastic nature of such body-parts size representation: given the different levels of hand under-estimation in the two groups, it could be speculated that the asymmetric tendency to underestimate the own body-size develops gradually across the lifespan through plastic processes, up to becoming stable in adults life. Interestingly, my findings seem to support the key role of S1 in the construction and updating of the own body metric representation, above discussed for Study #1: it is plausible proposing that under-estimation of the own body size mimics the somatotopic

organization of S1 (Linkenauger et al., 2015), according to which body districts that are over-represented in somatosensory and motor maps (like the hands), are perceptually underestimated due to cognitive compensation mechanisms. Thus, the existence of compensatory bodily distortions earlier in childhood suggests the innate nature of such distortions, that could find their cortical anatomical basis in S1 maps.

Concluding remarks and future directions

Taken together, findings from my doctoral thesis converge in showing the extremely malleable nature of one's own body-parts size representation, shedding new light on its the plastic properties: body size is flexible and it is characterized by dynamics alterations that emerge gradually across the typical development; intriguingly, misperception of the metric properties of the own body-parts can be induced both by behavioral and by cortical manipulations. Thus, far to emerge exclusively in relation to psychiatric or neurological diseases, alterations of the own body size and shape representation appear regardless of brain damage or experimental conditions.

However, the link between the somatosensory system and the knowledge of the metric properties of the body is well supported also by neuropsychological evidence suggesting that body size can be distorted in neurological patients (De Vignemont, 2010; Vallar et al., 2009). For example, distortions and misperceptions of one's own body constitute a conspicuous feature of numerous serious clinical diseases, including phantom limbs (Bolognini et al., 2013; Melzack, 1992; Ramachandran et al., 1998), somatoparaphrenia (Vallar et al., 2009), xenomelia (Brugger, Lenggenhager, & Giummarra, 2013; Geoch, Brang, Song, Lee, Huang & Ramachandran, 2011), out-of-body and autoscopy experiences (Blanke, Landis, Spinelli & Seeck, 2004), spinal cord injuries (Scandola, Aglioti, Avesani, Bertagnoni, Marangoni & Moro, 2017) and above all in case of micro- and macro-

somatoagnosia (De Vignemont, 2010; Leker, Karni & River, 1996; Podoll, et al., 1998; Podoll et al., 2000; Vallar et al., 2009). Psychiatric conditions such as anorexia nervosa – in which disturbances of body size and shape constitute key features – are characterized by extremely malleable body representations as well. This is well documented by stronger susceptibility to the RHI in anorexic patients as compared to healthy individuals (Keizer, Smeets, Postma, van Elburg & Dijkerman, 2014). Multisensory illusions, like the RHI, have been reported to attenuate anorexic patients' disturbances (Keizer et al. 2014), thus contributing to make the internal body representation less biased and more in line with the own veridical body size.

It would be a challenge for future research to further investigate body metric representation alterations in neurological and psychiatric conditions. New insight about the functional role of S1 in body perception, as well as new perspectives about the role of multisensory bodily experiences in shaping body size representation, could encourage novel approaches targeting the dynamic aspects of body representation, with potential both for clinical assessments and for future therapeutic interventions.

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