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From Senses to Body and Back: Bidirectional Relation between Body Representation and Sensory Processing

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Abstract

Our body is generally perceived as a unique entity through which we can successfully interact with the external environment. Moreover, the body is particularly special as it can be considered both the object and subject of all experiences. Indeed, through our senses, we can act and interact in the environment but also perceive ourselves from the "inside." Since the perception and knowledge of our body come from different receptors and sensory modalities, numerous aspects are involved in representing our body. Body representation is intrinsically multimodal. Indeed, different sensory signals reach multimodal areas where the multisensory integration occurs to generate the sense of body ownership, i.e., the feeling that one's own body belongs to oneself. Furthermore, sensory information is combined to generate multiple body representations: different weights assigned to different sensory modalities originate distinct body representations. The exchange between senses and body representation seems to be bidirectional. Indeed, body representation would also play a role in influencing the information processing of different sensory modalities. Therefore, representations of different body features, such as shape, size, proportions, and posture, can result from integrating various sensory information. At the same time, the body representation can be the reference in processing sensory signals, thus influencing the perception of the external world. The present doctoral thesis aims to highlight this critical bidirectional relation between body representation and sensory processing: multisensory integration can modify body representation, and, simultaneously, body representation may influence perceptual phenomena.

Accordingly, the first part of the thesis focuses on how the sensorimotor representation of one's own body in space and the representation of the space surrounding the body are constantly updated and modulated based on incoming sensory information (Study 1 and 2). Specifically, Study 1 reveals that a conflict between tactile and visual information can influence the perception of one's own body and of the potential space of action, emphasizing the reciprocity of the interaction between body and senses. Whereas Study 2 suggests how simply holding a tool in the hand, without performing any movement, can affect the morphological body representation (i.e., online incorporation of the tool).

The second part of the thesis aims to test how body representation influences the processing of incoming sensory information (i.e., haptic and visual). More specifically, Study 3, using the established size-contrast aftereffect (i.e., Uznadze haptic Illusion), reveals that the proprioceptive information about the arms position could modulate haptic size perception. Finally, Study 4 shows how visual size processing differs in the presence of bodily stimuli during the Uznadze visual Illusion, emphasizing the importance of the body in influencing sensory processing. In conclusion, the results of the experiments in this thesis highlight the critical reciprocal influence between the perception of the body and the external world, supporting the idea of a bidirectional relation between how the body is represented and how incoming sensory information is processed.

Riassunto

Il nostro corpo è percepito solitamente come un'entità unica attraverso la quale possiamo interagire con successo con l'ambiente esterno. Inoltre, il corpo è particolarmente speciale, poiché è sia l'oggetto che il soggetto di ogni esperienza. Infatti, attraverso i nostri sensi, possiamo agire e interagire nell'ambiente ma anche percepire noi stessi dall' "interno". Poiché la percezione e la conoscenza del nostro corpo provengono da diversi recettori e modalità sensoriali, numerosi aspetti sono coinvolti nella rappresentazione del corpo. Le rappresentazioni del corpo sono intrinsecamente multimodali. Ad esempio, il senso di *ownership* verso il proprio corpo, cioè la sensazione che il proprio corpo appartenga a se stessi, deriva dall'integrazione dei diversi segnali sensoriali che raggiungono le aree multimodali. Inoltre, le informazioni sensoriali vengono combinate per generare rappresentazioni corporee multiple: pesi diversi assegnati a diverse modalità sensoriali danno origine a rappresentazioni corporee distinte. Lo scambio tra sensi e rappresentazione corporea sembra essere bidirezionale. In effetti, la rappresentazione corporea avrebbe anche un ruolo nell'influenzare l'elaborazione delle informazioni provenienti da diverse modalità sensoriali. Pertanto, le rappresentazioni di diverse caratteristiche corporee, come la forma, le dimensioni, le proporzioni e la postura, possono derivare dall'integrazione di varie informazioni sensoriali. Allo stesso tempo, la rappresentazione corporea può essere il riferimento nell'elaborazione delle informazioni sensoriali, influenzando così la percezione del mondo esterno. La presente tesi di dottorato si propone di sottolineare questa relazione bidirezionale tra rappresentazione corporea ed elaborazione sensoriale: l'integrazione sensoriale può modificare la rappresentazione corporea e, allo stesso tempo, la rappresentazione corporea può influenzare l'elaborazione percettiva.

In accordo, la prima parte della tesi si concentra su come la rappresentazione sensomotoria del proprio corpo nello spazio e la rappresentazione dello spazio circostante il corpo siano costantemente aggiornate e modulate in base alle informazioni sensoriali in arrivo (Studio 1 e 2). In particolare, lo Studio 1 mostra che un conflitto tra informazioni tattili e visive può influenzare la percezione del proprio corpo e dello spazio potenziale di azione, enfatizzando la reciprocità dell'interazione tra corpo e sensi. Mentre, lo Studio 2 suggerisce come il semplice mantenimento in mano di uno strumento, senza eseguire alcun movimento, possa influenzare la rappresentazione morfologica del corpo (cioè, incorporazione online dello strumento).

La seconda parte della tesi (Studio 3 e 4) mira a verificare l'influenza della rappresentazione corporea sull'elaborazione delle informazioni sensoriali in entrata (cioè aptiche e visive). In particolare, lo Studio 3, utilizzando il noto *aftereffect* delle dimensioni (Illusione aptica di Uznadze) mostra che le informazioni propriocettive relative alla posizione delle braccia possono modulare la percezione aptica della dimensione degli stimoli. Infine, lo Studio 4 considera come l'elaborazione visiva delle dimensioni differisca in presenza di stimoli corporei durante l'Illusione visiva di Uznadze, sottolineando l'importanza del corpo come riferimento nell'elaborazione sensoriale.

In conclusione, i risultati degli esperimenti di questa tesi evidenziano l'influenza reciproca tra la percezione del corpo e del mondo esterno, avvalorando l'idea di una relazione bidirezionale tra come il corpo è rappresentato e come le informazioni sensoriali in entrata sono elaborate.

Chapter 1.

General Introduction

General Introduction

We perceive the world around us and ourselves within it,

with, though, and because of our living bodies

Seth, A. (2021).

Our body is normally perceived as a unique entity through which we can interact successfully with the external environment. Moreover, the body is special as it can be considered both the object and subject of all experiences. Indeed, through our senses, we can act and interact in the environment and also perceive ourselves from the "inside." Therefore, the way we represent our body is intrinsically multisensory, deriving from the integration of visual, tactile, proprioceptive, vestibular, and auditory information. Since the perception and knowledge of our body come from different receptors and sensory modalities, numerous aspects are involved in representing our body. A key element of our body representation is self-awareness, which is the feeling that one's own body parts belong to oneself (i.e., sense of body ownership). However, there is no clear, unified definition of Body Representation, and this concept has been the focus of several debates. Given the multiple modalities through which we can relate to our bodies (e.g., vision, touch, proprioception, semantics), a single definition may not be sufficient to deal with such variety, and multiple forms of body representations have been proposed. In Chapter 1, I will first consider the main models of body representation that have been described. Then, I will focus on the multisensory nature of body representation and its features. Finally, I will focus on the contribution of individual senses in building and shaping the different types of body representation and how, in turn, body representation is a reference in the processing of sensory information processing.

1.1 Taxonomies of Body Representations

The classic distinction between body representations introduced by Head and Holmes (1911) considered the *Postural Schema* (i.e., perception of body position or passive movements) and *Superficial Schema* (i.e., involved in localizing sensations on the skin surface). With the term “schema,” the authors refer to a proprioceptive, plastic, and online model of one’s own body. Since this early work, many theories and taxonomies based on neuropsychological patients with body representation disorders have been proposed (e.g., Medina & Coslett, 2010; Paillard, 1999; Schwoebel & Coslett, 2005; Sirigu et al., 1991).

Different models have suggested a dyadic taxonomy according to Head & Holmes (Dijkerman & de Haan, 2007; Gallagher, 2005; Head & Holmes, 1911; Paillard, 1999). Thus, body representation would be described by two main components: the *Body Schema* (i.e., body sensorimotor representations for action) and the *Body Image* (i.e., perceptual, conceptual, or affective/emotional representation). For example, Paillard (1999) and, then, Dijkerman and de Haan (2007) re-proposed a dichotomy in line with the one suggested for perception by Milner and Goodale (1995): Body Schema as the dorsal system ("where", i.e., representation of the body position in space used for action) and the Body Image as the ventral system ("what," perceptual representation of body features used for perception). At the same time, Carruthers (2008) suggested a different kind of dichotomy considering an online and offline body representation. The online and synchronic representations are built moment by moment from sensory input, allowing to perceive the body in its current state consciously. The offline representations are constructed from both sensory input and memories to represent the body in its typical form.

Also, a triadic classification has been proposed to address the heterogeneity of the Body Image construct (Schwoebel & Coslett, 2005; Sirigu et al., 1991). Crucially, Schwoebel & Coslett (2005) considered a *Body Schema* similarly defined as a dynamic sensorimotor representation of the body in space used for action based on proprioception and motor information. Secondly, a *Body Structural Description* defines body-part boundaries and proximity relations. It is primarily built on visual information, but even on somatic clues (visual body map). Finally, *Body Semantics* involves conceptual and linguistic aspects and defines the functional and relational information of body parts.

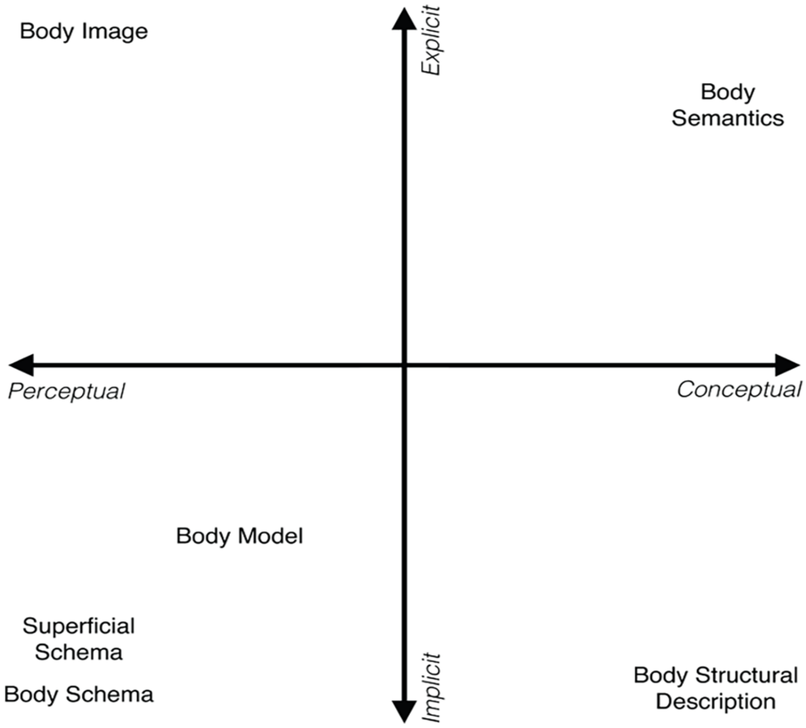
Finally, Longo and colleagues (2010a) pointed out the peculiarity of the body, proposing a further duality of our body representation. Indeed, the body can be primarily the subject of our experience from a first-person perspective, allowing us to feel the sensation from the "inside." On the other hand, the body can also be considered a physical and biological object, similar to other objects about which we have conceptual knowledge. Thus, based on this duality, body representations are divided according to two possible classes: first, body representations that mediate *somatoperception* (i.e., building of higher-level percepts of one’s own body), and second, those relate to *somatorepresentation* (i.e., abstract knowledge about bodies). According to Longo et al. (2010a), *somatoperception* is based on integrating multisensory inputs to construct online perceptual representations of the body and somatic stimuli. Whereas *somatorepresentation* is related to cognitive processes to build abstract knowledge and attitudes about one’s body as a unique object and the body in general. Thus, *somatoperception* includes the Body Image, the Body Schema, the Superficial Schema, and the Body Model. While *somatorepresentation* comprises the Body Semantics and the Body Structural Description. In the following paragraph, I will describe each type of body representation specifically.

1.1.1 Types of Body Representations

According to the model of Longo (2016), in this section, I will describe each type of body representation, starting from the representations related to *somatoperception* and, subsequently, those involved in *somatorepresentation* (Figure 1.1).

Figure 1.1

A schematic model about the relation between body representations (image from Longo, 2016).



Body Schema

Body Schema has been intensely investigated since the first conceptualization by Head and Holmes (1911). Body schema can be considered as a dynamic postural and sensorimotor representation involved in action and interaction with the environment (Dijkerman & de Haan, 2007; Gallagher, 2005; Paillard, 1999). It is mainly based on proprioception and on motor command information (i.e., afferent and efferent information) (Schwoebel & Coslett, 2005). Since posture and body movements continuously change, the Body Schema constantly updates its representation to track the body's posture to allow for proper motor control. Thus, Body Schema can be considered a dynamic pre-conscious system that monitors the body posture moment by moment to guide and control actions. In addition, it is a plastic representation that can be easily modified. Indeed, previous studies have found modulations of body schema due to active movements (Bassolino et al., 2015; D'Angelo et al., 2018; Romano et al., 2019; Tajadura-Jiménez et al., 2012). For instance, numerous studies have shown that using a tool to interact with objects placed outside one's reaching possibility increased the perceived length of this sensorimotor arm representation (Cardinali et al., 2009; Sposito et al., 2012). The prominent idea is that, after active training, the tool is included in the body schema, i.e., tool embodiment (Iriki et al., 1996; Maravita & Iriki, 2004; Martel et al., 2016). Thus, it is possible to consider two main functions of the Body Schema: the first is to provide an accurate description of the body, and the second is to guide action (de Vignemont et al., 2021).

The concept of Body Schema first emerged from patients affected by deafferentation (i.e., the loss of tactile and proprioceptive information; Paillard, 1999; Cole & Paillard, 1995). These patients have usually lost the automaticity of movement, which cannot be performed without constant attentional and visual control. Other examples of Body Schema disorders include optic ataxia (i.e., a deficit in reaching objects; Perenin & Vighetto, 1988; Rossetti & Pisella, 2018), spatial disorientation of the body (Kase et al., 1977), and apraxia (i.e., sensorimotor disorders that affect learned skills movements; Ramón et al., 2000).

Kanayama and Hiromitsu (2021), in line with Dijkerman and de Haan (2007), proposed that Body Schema could be related to the functionality of the dorso-dorsal stream through which sensorimotor information is unconsciously elaborated to execute actions ("how system"). Moreover, previous studies considered somatosensory cortices, the intraparietal sulcus (Corradi-Dell'Acqua et al., 2009; Ehrsson et al., 2005), the lateral intraparietal (Fasold et al., 2008; Snyder et al., 1998), and the superior parietal (Pellijeff et al., 2006; Wolpert et al., 1998) as the possible neural substrates of Body Schema.

Body Image

Body Image can be defined as the conscious and perceptual image of our body's physical structure and composition in terms of size and shape (Dijkerman & de Haan, 2007; Gallagher, 2005; Paillard, 1999; Rossetti et al., 1995). It also includes perceptual, conceptual, and emotional aspects, attitudes, and beliefs about one's body (Gallagher, 2005). It is based on both conceptual understanding and perceptual experience, relying primarily on visual but also somatosensory information. Therefore, contrary to Body Schema, Body Image is a conscious and explicit perception of the body that could be both perceptual and conceptual and could be related specifically to one's own body o to bodies in general. It is normally more stable than Body Schema, but, at the same time, it is plastic to adapt to contingent changes in the size and shape of the body, including both slow and quick plasticity. Recently, Pitron & Vignemont (2017) proposed that the Body Schema is prior to the building of Body Image. Indeed, since sensory processing evolved first to achieve sensory control of movements and only later to provide conscious perceptual experiences and internal models of the world accessible to other cognitive systems, it is likely that Body Schema evolutionarily precedes Body Image.

Classically, a Body Image disorder has been identified in neuropsychological patients suffering from numbsense (i.e., tactually guided movements preserved in the presence of a tactile deficit). Indeed, patients are not consciously aware of any touch, but they are able to point toward the location at which they were touched (Paillard et al., 1983; 1999). Within Body Image disorders are also included eating disorders such as Anorexia Nervosa (Bruch, 1974) or neuropsychological disorders such as Body Integrity Identity Disorder (i.e., feeling of alienation and overcompleteness and desire for amputation or paralysis of healthy limbs, Blom et al., 2012) or Somatoparaphrenia (i.e., attribution of this body part as belonging to someone else, Vallar & Ronchi, 2009; Romano & Maravita, 2019).

Finally, it appears that conscious Body Image derives primarily from activity in the posterior parietal cortex and not simply from somatosensory processing (Berlucchi & Aglioti, 2010; Bisiach et al., 1986; Longo et al., 2010a). Indeed, Dijkerman and de Haan (2007) also proposed that the perception processing involved in body image is related to the stream from the somatosensory areas to the intraparietal sulcus and the posterior insula.

Body Model

The Body Model is a perceptual representation of the size and shape of the body (i.e., metric properties of body parts). This representation is essential in the sensory processing of somatic stimuli, such as during the spatial localization of touch and body or to perceive the size and shape of tactile objects (Longo et al., 2010a). Indeed, in these tasks, it is necessary to link the sensory processing on the skin with the body. To date, however, the neural mechanisms underlying this representation remain unclear. In contrast to body image, which shares several aspects, it is mostly implicit. Moreover, this representation appears to be highly distorted, as evidenced in both proprioceptive (Gurfinkel & Levick, 1991; Longo & Haggard, 2010b) and tactile tasks (Weber's Illusion; Weber, 1834,1996). For example, Longo and Haggard (2010b) revealed a highly distorted map of the represented structure by asking participants to point toward the knuckle and tip of each finger of an unseen hand (see paragraph 1.3.1 for more details). Therefore, the Body Model would be more related to the characteristics of the primary somatotopic representation of the body characterized by strong distortions. In contrast, Body Image would constitute a more explicit and veridical representation of the body. It has also been shown that these two representations can interact: tactile perception can indeed be modulated by high-level changes in body representation, such as those induced by proprioceptive (de Vignemont et al., 2005) or visual (Taylor-Clarke et al., 2004) illusions.

Superficial Schema

The Superficial Schema is a representation aimed at recording somatosensory inputs on the skin surface, mediating the localization of sensations on the body surface. It allows linking the locations of primary somatotopic maps to those on the skin surface. Indeed, the Superficial Schema is involved in several tasks, such as the somatic localization of touch on the body surface and the processing of objects touching the skin in terms of spatial location and metric properties (Longo et al., 2010b). For example, in the localization of a touch on the skin, both a localization of the stimulus within a somatotopic map in the primary somatosensory cortex (SI, Poeck & Orgass, 1971) and a connection with positions on the body surface are required.

The first evidence of a Superficial Schema disorder was shown by Head and Holmes (1911) in patients with atopognosia. Patients were able to report a touch and body posture but with an inability to judge the exact location on the skin where the touch occurred. Therefore, in the face of a preserved primary somatotopic representation of touch, the impairment consisted in linking the somatotopic skin organization to the external body map.

Thus, superficial schema seems to involve the somatotopic maps in the SI and interact with additional processes in parietal areas (Denny-Brown et al., 1952). Indeed, TMS applied on primary sensorimotor cortices (Seyal et al., 1997) or the anterior parietal cortex (Porro et al., 2007) can disrupt tactile localization.

Body Structural Description

The Body Structural Description is a map of the body based mainly on visual information. It is a structural and topological knowledge of the body, referring to the spatial organization of body parts and their relationships (Buxbaum & Coslett, 2001). Patients with body structural description impairment suffer from Autotopagnosia, as it has been described first by Sirigu and colleagues (1991). In this bodily disorder, there is an impairment of the visuo-spatial representation of body structures, thus, patients are unable to localize body parts after a verbal command.

Neuroimaging studies revealed that the ability of spatial localization of body parts is correlated with the activation of the intraparietal sulcus (Corradi- Dell'Acqua et al., 2008), with the antero-medial inferior parietal lobule (Rusconi et al., 2014) and the left temporal lobe (Schwoebel & Coslett, 2005). For instance, Corradi-Dell'Acqua and colleagues (2008) showed an activation of the left superior parietal cortex when participants pointed to parts of their bodies. Thus, these studies suggest the involvement of the ventro-dorsal stream ("where system") and specifically of the left parietal cortex in the Body Structural Description.

Body Semantics

Body Semantics refers to an encyclopedic and lexical-semantic knowledge about one's own body and bodies as a category, including naming, features, and functions of body parts, as well as their categorical relations (Coslett et al., 2002; Kemmerer & Tranel, 2008). Deficits of Body Semantics lead to impairments of lexical-semantic knowledge related to the body, as shown in numerous neuropsychological patients (e.g., body-specific aphasia). For instance, Suzuki et al. (1997) described a patient with an impaired understanding of body part names but with a preserved pointing toward body parts when described functionally or associated with other objects. Thus, the deficit impaired specifically lexical information about body part names, with a spared body functional knowledge and cultural associations.

The neural basis of the Body Semantics still needs to be clarified. Naming body parts seem to be more lateralized in the left hemisphere, and previous studies showed an involvement of the inferior parietal (Kemmerer & Tranel, 2008; Suzuki et al., 1997), inferior frontal (Kemmerer & Tranel, 2008), and anterior temporal (Dennis, 1976) cortices. In addition, Downing et al. (2001) showed that the extrastriate body area (EBA, selectively involved in the visual processing of the human body) might be involved in the organization and transfer of semantic bodily information to the IT cortex (i.e., the final stage of the ventral visual pathway). Therefore, the ventral system, including the EBA, could be involved in representing body semantics (Kanayama & Hiromitsu, 2021).

1.2 Multisensory representation of my body in space: Body Schema, Body Ownership and Peripersonal Space

As emerged from the previous section, each representation is based on the integration of different sensory information. Thus, body perception is intrinsically multisensory, and sensory stimuli are constantly integrated, rather than processed in isolation, to shape our representation of the body (Stein & Meredith, 1993). Therefore, this section will focus on how different sensory information is integrated to form rich and coherent body representations. Indeed, as shown above, how we represent our bodies relies heavily on inputs from different sensory modalities (Ehrsson et al., 2005b; Green & Angelaki, 2010). Different body representations are constructed depending on the type of sensory information and how they are integrated (Azañón et al., 2016; de Vignemont, 2010; Schwoebel & Coslett, 2005). For instance, Body Schema results from the combination of somatosensory, proprioceptive, and visual inputs (i.e., afferent signals) informing about the posture of body-parts and position in space integrated with information about motor control processes (i.e., efferent signals) (Head & Holmes, 1911; Schwoebel & Coslett, 2005).

1.2.1 Principles of Multisensory Integration

The multisensory integration process is primarily based on principles of spatial and temporal congruence (Pavani et al., 2000; Matsumiya, 2014; Stein & Stanford, 2008). Indeed, two multisensory stimuli are more likely to be integrated if they occur within a limited time interval and if they come from the same portion of space or body (Stein & Meredith, 1983). Moreover, multisensory integration follows the optimal weighting principle. Indeed, the weight of sensory input differs depending on its reliability (Matsumiya, 2019; Noel et al., 2018; Samad et al., 2015). This principle determines, in a statistically optimal way, the weight of the contribution of each sensory modality in creating the final percept, maximizing accuracy and minimizing variance in estimates (Ernst & Banks, 2002; van Beers et al., 2002). At last, the final multisensory percept is then referred to the prior knowledge accumulated with the experience (Körding et al., 2007; Wozny et al., 2008). Therefore, body representations are constructed based on the integration of signals of different sensory modalities and on stored body representations that are priors to shape future ones. The weight of past body representations depends on the novelty of the present situation: in the case of new bodily situations, information from multisensory integration is prioritized since previous experiences are less reliable. For example, Body Schema informs about the body position in the space by generating an estimate based on the weighted integration of different sensory cues and biomechanical body constraints (i.e., representation of postural and mechanical features of one's own body). In addition, this representation is continuously updated and refined based on the motor feedback of the performed action.

1.2.2 The sense of Body Ownership

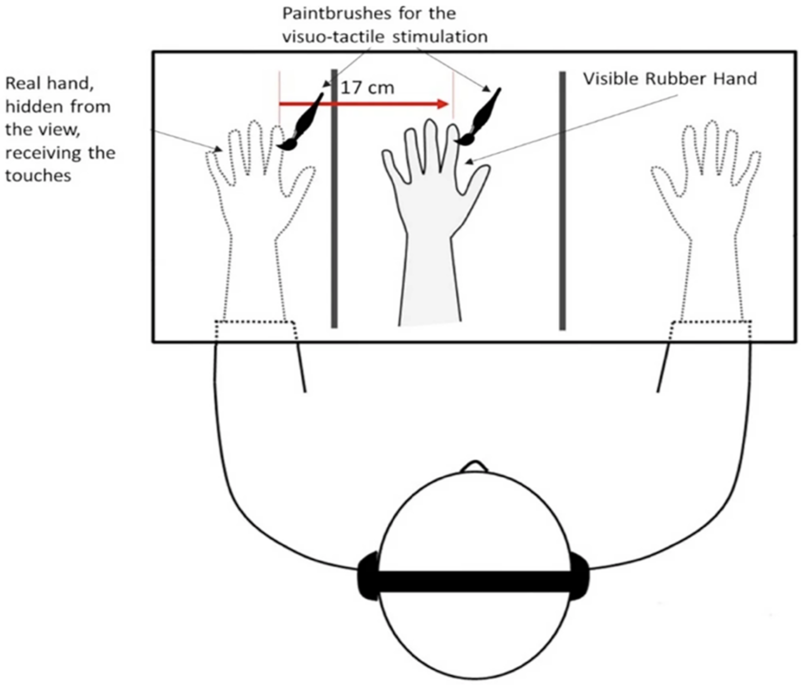
An aspect of body representation that is truly multisensory is the sense of Body Ownership (Ehrsson, 2012). Body Ownership is a perceptual status of one’s own body and a feeling that one’s own body and its parts belong to oneself (De Vignemont, 2011; Tsakiris, 2010b). The sense of body ownership derives from the integration of visual, tactile, and proprioceptive bodily signals according to the principles of temporal and spatial congruence (Avillac et al., 2007; Gentile et al., 2013; Lloyd et al., 2003; Makin et al., 2007). It has been proposed that Body Ownership results from the localization of bodily information on a multimodal body map (i.e., Body Schema), grounding the position of multisensory bodily information in space (de Vignemont, 2007). The close relationship between Body Ownership and Body Schema is shown by a famous bodily illusion in which the position sense of one's own hand is influenced by the vision of a rubber hand (Rubber Hand Illusion; Botvinick & Cohen, 1998). During the Rubber Hand Illusion (RHI), the participants’ hand is hidden from view while an artificial hand is placed in front of the observers in an anatomically compatible position (Figure 1.2). Two different paintbrushes simultaneously stroke the participants’ real hand and the rubber hand. After a short period, the participants perceived the rubber hand as belonging to their own body, and the perceived position of their hand shifted toward the rubber hand (i.e., proprioceptive drift) but only if the two paintbrushes were stroking synchronously. Thus, when the visual feedback of stroking the rubber hand is synchronous with the visual feedback of the real hand, the perception of a common cause for visual and tactile stimuli is elicited, inducing the sense of Body Ownership toward the fake hand (Samad et al., 2015).

Crucially, Ehrsson and colleagues (2005b) investigated the neuronal correlates underlying the sense of Body Ownership. During the RHI, the ventral premotor and the left intraparietal cortex were more activated during the synchronous than the asynchronous stroking. Moreover, the activation in the ventral premotor cortex correlated with subjective feelings of ownership.

Notably, the induction of ownership sensations toward the fake hand is also related to anatomical and spatial constraints (Blanke et al., 2015), confirming the link between Body Ownership and Body Schema. Indeed, the illusion seems to be susceptible according to the anatomical features of the body. For instance, the illusion is not induced in the presence of an anatomically implausible posture (Ide, 2013; Tsakiris & Haggard, 2005) or if the rubber hand is placed outside the space surrounding the body, i.e., the Peripersonal Space (PPS; Lloyd, 2007; Preston, 2013). Thus, as highlighted by Blanke and colleagues (2015), to bind multisensory inputs to one's body and feel ownership, multisensory signals must occur within the limited space surrounding the body and under its anatomical constraints. The body has become, indeed, the reference frame of multisensory perception, according to which sensory information coming from the body and the space near the body are processed. Accordingly, PPS is closely related to self-consciousness since it defines “the space of self” (Serino, 2019). In the next paragraph, I will go through the concept of Peripersonal Space, focusing on the peculiar features of the fronto-parietal network of bimodal neurons that respond both to tactile stimuli on the body and visual/auditory signals in the space surrounding the body.

Figure 1.2

Example of Rubber Hand Illusion set up (Image from Romano et al., 2021).



Note. Only the Rubber Hand is visible during the induction of the illusion.

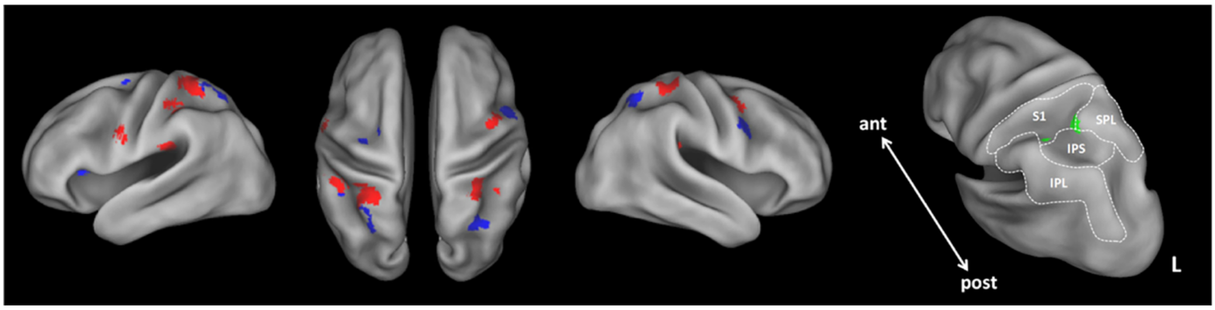
1.2.3 Peripersonal Space

The Peripersonal Space (PPS) is the portion of space immediately surrounding the body, encoded by a fronto-parietal network of multisensory neurons with somatosensory receptive fields centered on a specific body part (di Pellegrino et al., 1997; Ladavas et al., 1998; Rizzolatti et al., 1997b). Indeed, in both monkeys and humans, there are neurons that combine somatosensory stimuli presented on the body with visual/auditory stimuli presented in the space surrounding the body. Thus, these neurons are characterized by a tactile receptive field anchored on a specific body part and visual/auditory receptive field centered on the same part but extending in the space for a specific distance (Graziano & Cooke, 2006; Ladavas & Serino, 2008; Rizzolatti et al., 1997a). For example, neurophysiological studies on monkeys have shown the presence of neurons in the posterior parietal cortex, such as in the ventral intraparietal area (VIP) (Avillac et al., 2007; Duhamel et al., 1998) and area 7b (Leinonen et al., 1980). Neurons with similar properties have also been found in the premotor cortex, specifically in areas 6 and F4 (ventral premotor cortex) (Matelli et al., 1985; Rizzolatti et al., 1981a, b) and in the putamen (Graziano & Gross, 1993). Neuroimaging studies have suggested a similar system for multisensory PPS representation in humans. The metanalysis work of Grivaz and colleagues (2017) reported activation in the temporo-parietal junction (IPL), specifically in the superior parietal, temporo-parietal, and ventral premotor regions (Figure 1.3, in red). For instance, Makin and coworkers (2007) showed stronger activation of the posterior intraparietal parietal sulcus (IPS), the lateral occipital cortex (LOC), and the premotor cortex (PMC) during the approaching of a stimulus toward the participant’s hand as compared to a distant stimulus (70 cm far away from the hand). These brain regions also integrate multisensory stimuli when presented within the arm-centered peripersonal space (Gentile et al., 2011). Furthermore, Brozzoli et al. (2011), through a fMRI adaption paradigm, identified a reduced activation of the inferior parietal lobe (i.e., supramarginal gyrus), the dorsal and ventral PMC, the cerebellum, and the putamen when consecutive visual stimuli were presented near the hand. This pattern was not present with far stimuli.

Overall, these neuroimaging studies highlight that the representation of near-body space derives from an extensive cortical network, mainly fronto-parietal, involved in the multisensory processing of stimuli and centered on specific body parts.

Figure 1.3

Peripersonal Space and Body Ownership activation regions (figure from Grivaz et al., 2017; redrawn from Serino, 2019).



Note. Activation regions in PPS representation (red) and Body Ownership (blue) and their common activation regions. SPL superior parietal lobule, S1 primary somatosensory cortex, IPL inferior parietal lobule, IPS intraparietal sulcus.

1.2.4 The Space of Self: Peripersonal Space and Body Ownership

As shown previously, the spatio-temporal coherence of multisensory signals from the body and the space surrounding the body can be manipulated, leading to changes in the feeling of ownership. Furthermore, previous studies showed that inducing the illusion of Body Ownership toward a virtual body located in a location different from the participant's actual position (i.e., full body illusion, Petkova & Ehrsson, 2008) involves a translation of the PPS toward the virtual body (i.e., an extension of the PPS boundary) (Noel et al., 2015; Serino et al., 2015). Thus, synchronicity during visuotactile stroking on the body would shift the visual receptive field of the multisensory neurons, allowing to extend multisensory properties to the rubber hand or the virtual body. For this reason, the PPS system seems to be directly involved in bodily self-consciousness. Accordingly, it has been shown that the induction of the RHI (i.e., during the visuo-tactile stroking) activates the ventral premotor and posterior parietal cortex (similar to PPS activations) and that the change in ownership feelings correlated with these activations (Brozzoli et al., 2012b; Ehrsson et al., 2004; Makin et al., 2007). Moreover, Grivaz and colleagues (2017) compared activation regions found in neuroimaging studies underlying both PPS representation and Body Ownership feelings. Regions of overlapping between PPS and Body Ownership consist of a fronto-parietal network, including superior parietal lobule (SPL), intraparietal sulcus (IPS), and area 2 in the primary somatosensory cortex (Figure 1.3). Moreover, these areas were found to be mostly connected. These results match the previous activations that emerged during tasks assessing PPS and Body Ownership (Blanke et al., 2015; Brozzoli et al., 2012a; Gentile et al., 2013; Makin et al., 2008).

Thus, these studies show that the integration of multimodal bodily inputs in the peripersonal space is a crucial element for the sense of Body Ownership. Indeed, manipulation of the spatio-temporal principles regulating multisensory integration in the PPS can induce modifications in ownership feelings towards one's own body. At the same time, the boundaries of PPS also change to incorporate new portions of space that are perceived as belonging to oneself.

1.2.5 The Space to Act: Peripersonal Space and Body Schema

Peripersonal Space can be considered a sensorimotor interface to interact with objects near the body (Brozzoli et al., 2012b; de Vignemont & Iannetti, 2015; di Pellegrino, 2015). Thus, to interact successfully in the environment, PPS involves different neural computations that allow the alignment of the coding of multimodal stimuli within a single body-centered frame of reference (Serino et al., 2019). This mechanism allows encoding limb position and significant visual information around it simultaneously, in order to successfully plan and perform actions toward objects (Graziano & Gross, 1998; Pellegrino & Làdavas, 2015). Indeed, as shown previously, single-unit recordings in macaques showed that the visual receptive fields in the ventral premotor cortex are spatially anchored to the arm and follow the change in limb position (Graziano et al., 1997, 1999; Graziano & Cooke, 2006). Moreover, the direction of the eyes or the head does not modulate the response (Fogassi et al., 1996). In humans, the anterior intraparietal sulcus, premotor cortex, and putamen contain selective neurons for visual encoding of stimuli presented near the hand. Also, this encoding is remapped following the movement of the hand in space (Brozzoli et al., 2012a).

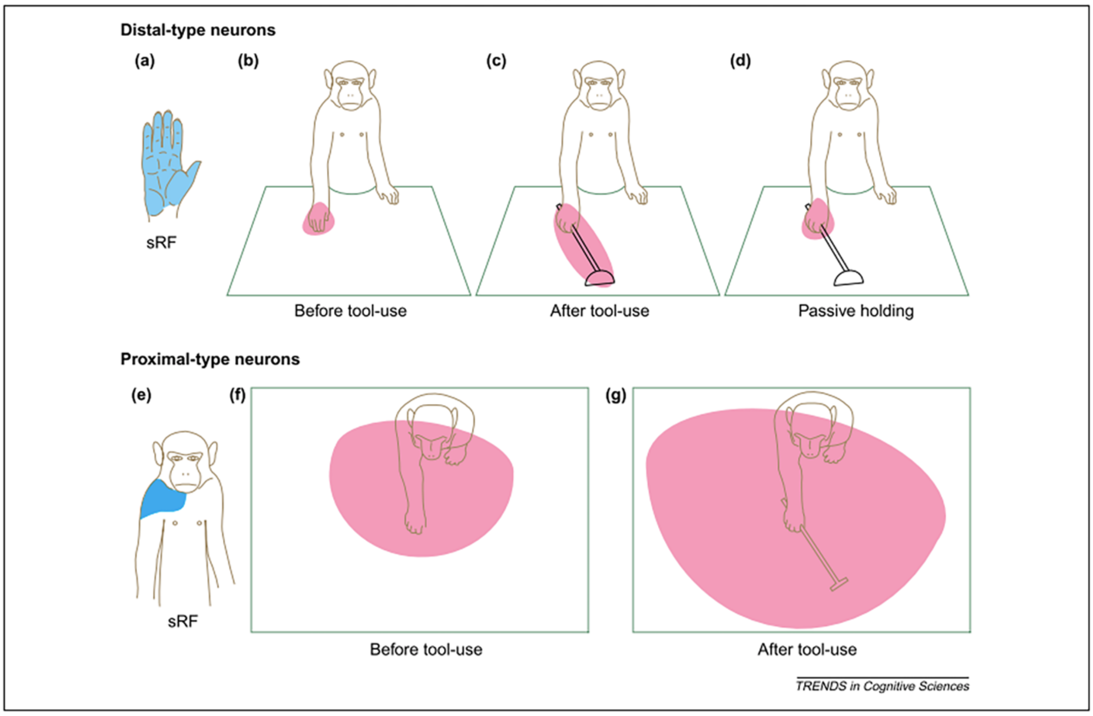
The multisensory fronto-parietal network seems to be strictly connected with areas underlying sensorimotor functions (Cardellicchio et al., 2011; Colby,1998; Makin et al., 2009; Rizzolatti et al., 1997; Serino et al., 2009a). For instance, head or limb movements are elicited by electrical stimulation of neurons in VIP and ventral premotor cortex (F4) regions (Cooke et al., 2003; Graziano et al., 2002). While the presentation of visual (Makin et al., 2009) or auditory (Serino et al., 2009c) stimuli in the PPS transiently modulated the hand’s representation in the primary motor cortex, as shown in single-pulse TMS studies. In addition, Cardellicchio and colleagues (2011) revealed that the excitability of the left primary motor cortex is specifically enhanced when objects are presented within PPS compared to extrapersonal space. Overall, these studies suggest that the representation of the PPS engages the motor system. In particular, it could involve a motor pre-activation without actual limb movement to prepare for successful actions towards objects presented within the PPS. Thus, PPS could be considered a dynamic sensorimotor interface regulating interactions between the body and the external space. PPS representation would be constantly updated to deal with the different body schema configurations and the possible outcome of action toward objects (Coello & Iachini, 2021).

Peripersonal Space and Body Schema

Since the importance of the position sense of one's body for PPS and the sensorimotor aspects of this spatial representation, a link between PPS and Body Schema has been proposed (Holmes & Spence, 2004; Martel, 2016). Indeed, the representation of a body part position in space is crucial to grasp and reach for objects within the external environment nearby the body. Specifically, Longo and Lourenco (2006) showed that the individual arm length is related to the extension of the space immediately surrounding the body. Moreover, different kinds of manipulation altering PPS seem to affect Body Schema. Crucially, the plasticity of the body and space representation has been widely investigated using the tool-use paradigm. Indeed, after a training with the tool, both Body Schema and PPS representation seem to change (di Pellegrino & Làdavas, 2015; Maravita & Iriki, 2004; Martel et al., 2016). It has been argued that the tool would be incorporated into the Body Schema, leading to an extension of both the sensorimotor body representation and the PPS (e.g., Cardinali et al., 2009; Iriki et al., 1996; Maravita & Iriki, 2004; Martel et al., 2016; Sposito et al., 2012). The seminal study by Iriki et al. (1996) is the first work showing this plasticity. In this study, macaques were trained for two weeks to use a rake to get the food closer (i.e., physical extension of the action potentials). The neural response was recorded from bimodal neurons in the intraparietal cortex (Figure 1.4). The authors found an extension of the visual receptive field in these visuo-tactile neurons after 5 minutes of tool training such that the entire length of the tool was included. In contrast, any change was found after the mere holding of the rake in the hand. The authors suggest that the rake may represent a functional elongation of the arm, and the extension found in the visual receptive field of the bimodal neurons could be the neural substrate of the "use-dependent assimilation of the tool" (Maravita & Iriki, 2004). After this pivotal work, many studies focused on confirming tool-use plasticity in PPS with different tasks (Bourgeois et al., 2014; Canzoneri et al., 2013; Holmes, 2012; Maravita et al., 2002; Witt et al., 2005; Witt & Proffitt, 2008). For instance, Bourgeois et al. (2014) investigated the effect of tool-use in reachability judgments using two tools of different lengths (70 cm vs. 10 cm). The distance at which objects are considered reachable is extended only after using the 70cm-long tool, while the reaching space did not change after training with the tool of 10 cm. This finding indicates that only the long tool actually provides a functional arm extension as a result of the sensorimotor incorporation of the tool.

Figure 1.4

Changes in bimodal receptive field properties following tool-use (Image from Maravita & Iriki, 2004).



Note. The somatosensory receptive fields (sRF) of cells in this region were identified by light touches, passive manipulation of joints or active hand-use. The visual RF (vRF) was defined as the area in which cellular responses were evoked by visual probes (the most effective ones being those moving towards the sRF). (a) sRF (blue area) of the 'distal type' bimodal neurons and their vRF (pink areas) (b) before tool-use, (c) immediately after tool- use, and (d) when just passively grabbing the rake. (e) sRF (blue area) of 'proximal type' bimodal neurons, and their vRF (pink areas) (f) before and (g) immediately after tool-use.

Whereas the first work that showed a modulation of the Body Schema after a tool-use training was reported by Cardinali and colleagues (2009). In this study, the tool training consisted of reaching and grasping an object using a 40 cm-long mechanical grabber with the right arm. Before and after the tool-use, kinematics of free-hand and tool-use grasping actions were recorded. The authors found an alteration of the kinematics of the free hand grasping movements, characterized by longer latencies and a maximal amplitude decrease. In a following experiment, blindfolded subjects were touched on their right arm in one of three possible locations (i.e., elbow, wrist, middle fingertip), and, after each stimulation, they had to point towards the location felt with their left index. After tool training, participants located stimulations on the elbow and middle fingertip as if they were more distant. Both findings together showed that the use of the tool would modify Body Schema, leading to a change of the intrinsic properties of the arm morphology (i.e., somatosensory representation) in terms of an increased arm length.

1.3 Sensory modalities and Body Representations

As described in paragraph 1.1.1, body representations have distinct functions and are built on specific sensory information, allowing to interact with the external world properly. Indeed, different kinds of sensory information (e.g., visual, tactile, proprioceptive, auditory, and vestibular information) build and shape body representations throughout everyday experiences. In this section, I will first explore the specific role of different sensory modalities in the construction of body representations. Specifically, I will focus on the contributions of touch, vision, and proprioception in building and shaping the different body representations. Then, I will consider how body representations, in turn, are crucial in processing sensory information.

1.3.1 Contribution of each sense in building and shaping Body Representations

Touch

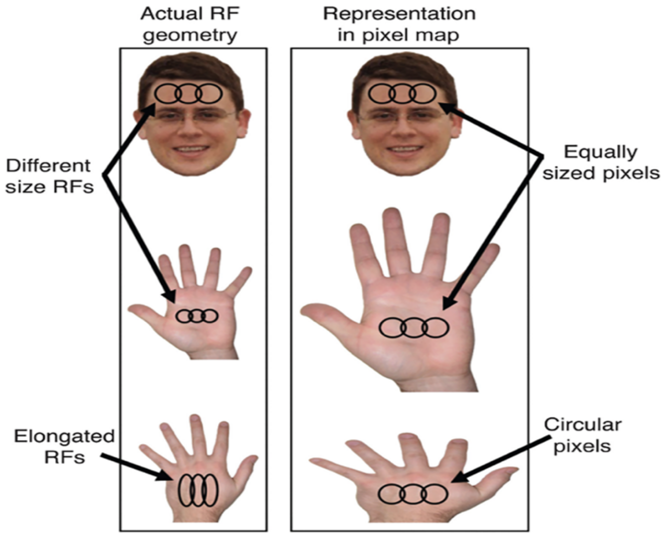
Touch is the sensory modality most intrinsically linked to the body. Indeed, the receptor organ for touch (i.e., the skin) constitutes the surface of the physical body and consists of 16-18% of the body mass (Montagu, 1978). For this reason, touch is commonly defined as "the bodily sense" (Azañón et al., 2016; Serino & Haggard, 2010). Somatosensory inputs from different peripheral receptors (e.g., mechanoreceptors, thermo-receptors, and nociceptors) are transmitted to the contralateral primary (SI), maintaining the spatial organization of the skin. Indeed, SI contains a somatotopic map of the body, i.e., the so-called *somatosensory homunculus* (Penfield & Boldrey, 1937), such that a tactile stimulus delivered on a particular part of the body systematically elicits a response in a specific region of SI (e.g., Shoham &

Grinvald, 2001; Yang et al., 1993). Moreover, body parts with higher tactile acuity are largely represented in the homunculus representation (Weinstein, 1968).

Thus, touch and body are strictly interdependent, and tactile signals specifically contribute to creating and shaping body representations. For instance, as shown in paragraph 1.1.1, the Superficial Schema is based especially on somatosensory input since it is a mapping between somatotopic maps and the location on the skin surface. Furthermore, even if Body Image is based mainly on visual information, somatosensory inputs are also crucial to shape it. As proposed by Dijkerman and de Haan (2007), the perception processing involved in Body Image starts from the somatosensory areas towards the intraparietal sulcus and the posterior insula. Also, the Body Model seems to be strictly dependent on tactile information. Crucially, the relation between the Body Model and tactile information can emerge considering the perception of the tactile distance of paired stimuli delivered on the body. Indeed, by relying only on tactile information, the computation of the distance between two points on the body can be obtained by integrating the somatosensory input with the stored metric properties of the body parts (i.e., Body Model). Thus, investigating how the distance between two tactile stimulations is perceived would provide information about how the Body Model is shaped. As shown in Weber's Illusion (1834/1996), the same distance between two points is estimated differently according to the body part considered. Indeed, the tactile distance in a body part with higher tactile spatial sensitivity is systematically overestimated compared to body parts with lower tactile acuity. It would suggest that the body model is, in general, distorted according to the properties of the tactile receptive field on the skin (e.g., tactile spatial acuity in this example). Indeed, since the sensitive skin surface is magnified in the *somatosensory homunculus*, as a consequence, the perceived dimension would also be enlarged. The distortion of the Body Model based on tactile information is also confirmed by comparing the same distance across different orientations on the same body part. Crucially, estimations of the distance of paired touches on the hand dorsum oriented across the width are overestimated compared to the same distance oriented along the dorsum length (Longo & Haggard, 2011). Again, the distortion mimics the anisotropic geometry of the receptive tactile field (i.e., smaller receptive field medio-laterally than proximo-distally) in the somatosensory cortex of the hand. Longo and Haggard (2011) proposed the “Pixel Model” to interpret these effects. In this model, receptive fields are considered as the basic unit to perceived tactile distance (i.e., pixel); thus, the distance is computed by counting the pixel number between two stimulated activation peaks (Figure 1.5). The crucial role of tactile inputs in shaping body size representation is confirmed, also considering body representation modulations after a change in the volume of afferent information (Di Russo et al., 2006; Gandevia & Phegan, 1999; Moseley, 2005; Serino & Haggard, 2010). For example, when the sensitivity of a body part (i.e., thumb) is reduced due to anesthesia induced via digital nerve block, the perception of its size increases by 60-70% (Gandevia & Phegan, 1999). Similarly, surgical elongation of the limbs can alter body representation by changing the tactile afferent input (Di Russo et al., 2006).

Figure 1.5

Illustration of how the geometry of somatosensory receptive fields (RFs) shapes the Body Model ("Pixel Model"; Longo & Haggard, 2011).



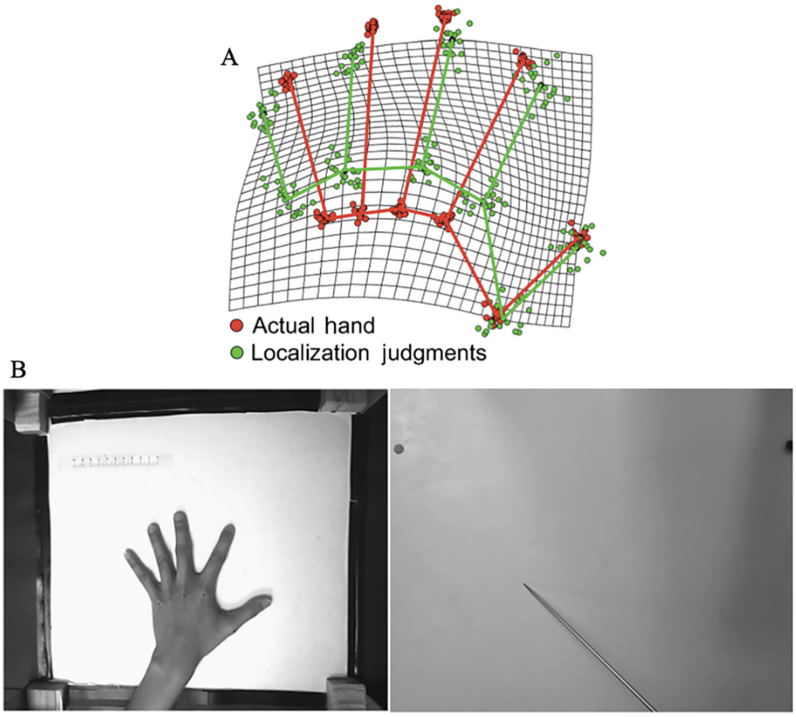
Note. RFs vary in size and shape across body-parts such that RFs are smaller and denser in highly tactile sensitive body parts (i.e., hand) than in less sensitive (e.g., the forehead). Consequently, for the same tactile distance, in the hand the number of RFs in the hand is higher compared to the forearm, resulting in the classic Weber's illusion (i.e., the same tactile distance is perceived larger on the hand than in the forearm). Moreover, considering RFs on the limb (e.g., hand dorsum), they are stretched parallel to the long axis. Thus, the RFs are smaller and more densely along the mediolateral compared to the proximodistal axis. Consequently, the distance orientated across the width of the hand dorsum is stretched compared to the distance presented along its length (Figure from Longo & Haggard, 2011; Redrawn in Longo, 2022)

Proprioception

Proprioception refers to the sense of position and movements of body parts in space. It is mediated by receptors (i.e., proprioceptors) in joints, muscles, tendons, and skin that provide information regarding the position of the body-part in space (Proske & Gandevia. 2012; Sherrington, 1907). As introduced before, this information is crucial in building the sensorimotor representation of one's body-part in space (i.e., Body Schema). Indeed, Body Schema is mainly based on proprioceptive information that allows monitoring of the body's position in space. This representation is continuously updated according to changes in body posture to interact with the environment properly. Moreover, proprioceptive information contributes also to shaping Body Model. Similarly, to touch, features of the Body Model based only on proprioceptive information can emerge investigating how the distance is estimated between two points on the body. Indeed, to compute the distance between two landmarks on the body, the position of body parts in the space (i.e., based on online efferent proprioceptive information) has to be estimated and combined with the information stored in the Body Model (i.e., body metric properties regarding the shape and the size of body parts connecting the joints) (Longo & Haggard, 2010b). Thus, when proprioceptive information is the dominant sensory information available, the Body Model seems to be systematically distorted (Gurfinkel & Levick, 1991; Longo & Haggard, 2010b). Specifically, Gurfinkel and Levick (1991) first described an underestimation of the distance between the perceived location of joints. Crucially, Longo and Haggard (2010b) developed a method to investigate the distortion of the Body Model of the hand through proprioceptive localization of body landmarks. In this experiment, participants had to indicate the perceived location of landmarks (i.e., the knuckle and tip of each finger) on their unseen left hand using a long stick (localization judgment task, Figure 1.6A, B). The authors found a systematic overestimation of hand width and an underestimation of finger length, reflecting the maintenance of distortions characteristic of early somatosensory maps (e.g., the progressively increased magnification of the digits from radial to ulnar; Duncan &, Boynton, 2007; Vega-Bermudez & Johnson, 2001). The fundamental role of proprioceptive information in shaping body representation is also shown in the "Pinocchio illusion" (Lackner, 1988). The vibration of the biceps tendon of a stationary limb leads to a reflex muscle contraction (e.g., Hagbarth & Eklund, 1966), causing the illusory sensation of limb movement (e.g., Goodwin et al., 1972). Then, when the nose is touched with the vibrated arm, subjects feel a contraction of the arm and an illusory extension of the nose. Indeed, in this illusion, by generating incorrect proprioceptive information about the limb position in space, the metric properties of the body are altered. The presence of a conflict between proprioceptive and tactile information (i.e., incongruence between the arm elongation produced by the vibration of the biceps) is resolved by the brain by inducing changes in the perception of body size (i.e., the sensation of a nose elongation) (Gallace & Spence, 2014). Similarly, Ehrsson and colleagues (2005a) vibrated the participants' tendons of wrist extensor muscles while they positioned their hands on their waists. This configuration led to the sensation that the hands were flexing inwards, and participants perceived a reduction of 28% in their waist size.

Figure 1.6

Proprioceptive Body Model (Longo & Haggard, 2010; Longo, 2020)



Note. *A*. Distortion of the proprioceptive body model of the hand (in green) compared to the actual hand (in red) (Figure from Longo, 2020). A strong overestimation of hand width relative to length is found. *B*. Experimental setup of the localization judgment task showing the position of the actual hand under the occluding board and the pointing task of the landmark using a long stick. (Figure from Longo & Haggard, 2010b).

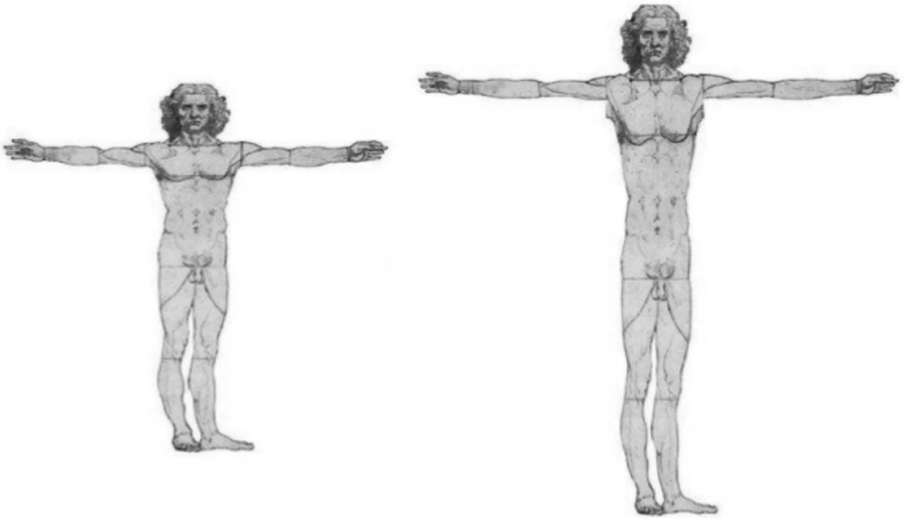
Vision

Vision is the most studied sensory modality in different aspects of cognition since it has been considered the dominant and the most reliable sense. Concerning body representations, vision provides numerous clues about the physical structure in terms of size and shape and the spatial organization of the body in terms of relations between the different body-parts. Thus, visual information is crucial for building and creating the Body Structural Description and Body Image. Indeed, recent studies have proposed that explicit judgments of body size can be highly distorted (D'amour & Harris, 2019; Linkenauger et al., 2009, 2015b; Sadibolova, 2019). For instance, right-handed people estimate that the right arm is longer than the left one (Linkenauger et al., 2009). Moreover, Linkenauger and colleagues (2015b) found systematic distortions in the perception of body size by asking participants to estimate the length of their body parts as multiples of their hand length. Surprisingly, the magnitude of these distortions correlated with the tactile sensitivity of body parts such that the less sensitive body parts (i.e., torso) were strongly overestimated (Figure 1.7). Thus, the perception of the body-part size is inversely proportional to cortical magnification in SI. This result is explained by the authors as a "reverse distortion" process. It could be a compensatory mechanism of the perceptual system to correct the somatotopic maps distortions and provide tactile size constancy across body parts. Thus, according to this mechanism, the representation of one’s own body size seems to differ according to the dominant sensory modality (i.e., touch or vision), leading to different patterns of distortions. Body Image distortion has also been studied within the framework of perceptual adaptation (i.e., perceptual changes due to prolonged exposure to a previous stimulus; Webster, 2011). For instance, prolonged exposure to extreme body size (i.e., distorted pictures in the size of one’s own body or general bodies) can modulate the representation of one’s own body size (e.g., Brooks et al., 2016; Hummel et al., 2012a, b). Crucially, after exposure to a thin picture of one’s own body, a larger picture is perceived as the most realistic and vice versa after the exposure to a fat picture (i.e., perceptual adaptation aftereffect). Thus, mere exposure to extreme body type pictures can induce a distortion of one’s own Body Image. Other examples of Body Image modulations have been demonstrated through bodily illusion (Perera et al., 2017; Schmalzl & Ehrsson, 2011). Accordingly, Perera and colleagues (2017) showed that an illusory stretching or shrinking of the finger can actually alter the perceived one’s own body size in the direction of the illusion. Moreover, visual information is also fundamental for constructing Body Schema (Graziano, 1999), indeed, the position sense depends deeply on the position seen and on the position felt (van Beers et al., 1996). Thus, distorted visual information about one’s own body can also affect body schema by altering grasping parameters (Marino et al., 2010).

Overall, the results of these studies showed the importance of visual signals in building and shaping different body representations; indeed, the type of visual information provided can alter one’s own body representation.

Figure 1.7

Scaled illustrations of the real (left) and perceived (right) body proportions based on the results of the work of Linkenauger et al., 2015b.



1.3.2 Contribution of Body Representations in sensory information processing

So far, I reviewed evidence showing the importance of each sensory modality in building and shaping body representation. In this section, I will focus on how this representation, in turn, is crucial in processing sensory information. Indeed, the way we perceive and represent the body is essential for interpreting the numerous sensory information that constantly reaches the body and thus for perceiving the external world. Accordingly, the body has also been defined as a *perceptual ruler* (Poincaré, 1952). For instance, the same environment and objects would be perceived as bigger from a child's point of view compared to an adult's perception. Here, I will consider the effect of body representation in the modulation of tactile and haptic processing first and then of visual perception.

As emerged previously, touch is always referenced to the body since the skin forms the body's physical surface. Moreover, the somatosensory tactile processing of the stimulus properties has to be combined with incoming sensory bodily information (e.g., proprioceptive signals regarding body posture, visual information about body features) and store body representations (e.g., implicit and explicit representation of body size and shape, structural relation between body parts). Thus, the final percept is strictly body-referenced. Several works have shown that vision of the body influences primary tactile elaboration, accelerating tactile processing (Tipper et al., 1998, 2001) and improving tactile spatial acuity (Kennet et al., 2001; Press et al., 2004; Schaefer et al., 2005; Serino et al., 2009b; Taylor-Clarke et al., 2002, 2004a). This effect has been defined as the visual enhancement of touch (VET). For instance, Press et al. (2004) showed that when two tactile stimuli were delivered on the forearm while looking at it, the tactile discrimination between the two tactile locations was faster compared to the same spatial positions presented on a neutral object. Moreover, various findings suggested that, during VET, the vision of the body influences the activity in the somatosensory cortex (Fiorio & Haggard, 2005; Serino et al., 2009c). Indeed, through vision, the bodily space to which tactile information is referred is better defined; consequently, the size of the tactile receptive field is reduced, and tactile acuity increases (Haggard et al., 2007). Moreover, Taylor-Clarke and colleagues (2004), in line with the Weber's illusion previously described, investigated distance tactile estimations between paired tactile stimuli presented to the finger and the arm. Through a visual distortion procedure, they selectively magnified the visual size of the forearm (i.e., lower tactile spatial sensitivity) and minified the hand (i.e., higher tactile spatial sensitivity). After this exposure, perceived tactile distance on the forearm increased, while it decreased on the hand compared to baseline. Thus, distorted visual feedback impacting body size representation can influence somatosensory spatial representations.

Moreover, aspects related to proprioceptive information about the external posture of one's body in space (i.e., Body Schema) can also affect tactile processing (de Vignemont et al., 2005; Liu & Medina, 2021). For instance, de Vignemont et al. (2005) asked participants to estimate the tactile distance of two points presented on the index finger while inducing the Pinocchio's illusion (see paragraph 1.3.1) and generating the perception of a change in the index finger size (Lackner, 1988). Thus, the illusion biased tactile distance judgments by producing overestimation when the finger was extended. Also, several studies have revealed that changing body-related proprioceptive information by crossing hands can influence tactile localization. Indeed, an impairment in reporting the correct order of two stimuli when arms are crossed and stimuli are applied to each hand was shown (Heed & Azañón, 2014; Shore et al., 2002; Yamamoto & Kitazawa, 2001). The deficit in this performance seems to be due to the conflict that the crossing limb posture generates between the tactile and spatial frame (Röder et al., 2004; Schicke & Röder, 2006; Yamamoto & Kitazawa, 2001a). Then, the order of the two stimuli is correctly processed in the somatotopic frame; however, it is reported imprecisely due to the incorrect remapping of the stimuli in space (Azañón et al., 2016; Badde et al., 2016; Overvliet et al., 2011). These studies suggest that proprioceptive information automatically updates body representation, thereby influencing tactile processing.

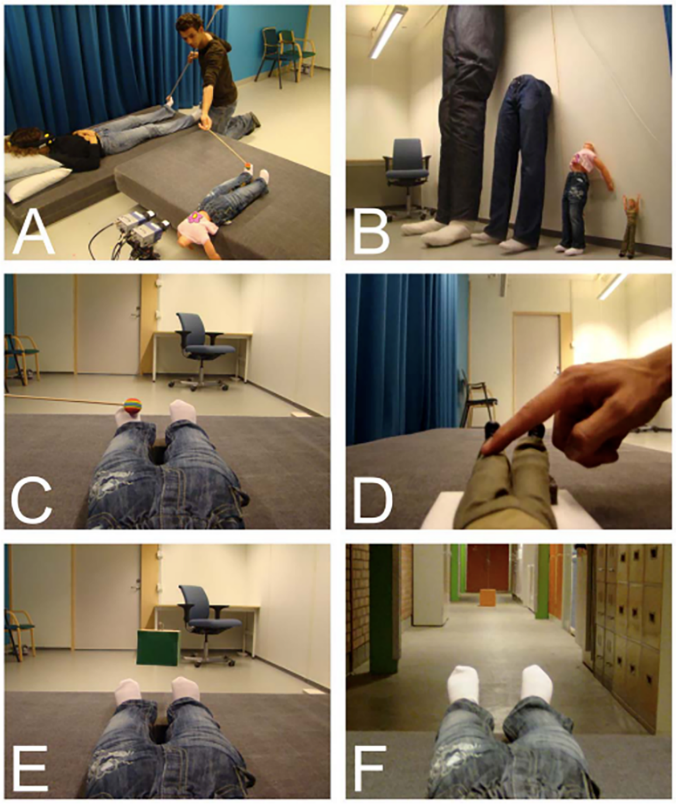
Besides influencing aspects of primary tactile processing, body representation would also mediate haptic manipulation and the construction of object representation (Bruno & Bertamini, 2010; Haggard & Jundi, 2009). Indeed, the tactile object perception could change according to the perceived representation of the body part involved in the interaction with the object (Serino & Haggard, 2010). Crucially, Bruno and Bertamini (2010) used the RHI to induce a change in the hand size representation using bigger or smaller fake hands. Thus, participants perceived the same object as larger after the bodily illusion with the big hand and as smaller after the illusion with the small hand. Also, Haggard and Jundi (2009) induced the RHI illusion with small or large gloves, and participants judged the object's weight after grasping and lifting objects of different weights. They found a change in the object weight estimates according to the size of the view hand. Thus, the evidence presented suggests that the perception of external objects would be biased by one's own body representation, revealing that the body would be a reference for the perception of features of external objects, such as weight and size.

Similar modulations have also been demonstrated in the visual perception of objects. Indeed, previous studies have shown that objects' size and distance are processed in relation to the size of the observer's body (Linkenauger et al., 2013, 2015a; Proffit & Linkenauger, 2013; van der Hoort et al., 2011, 2016). Specifically, van der Hoort and colleagues (2011) altered the perceived size of the participant's body by inducing ownership feelings towards a doll's body (80 cm or 30 cm) and a giant's body (400 cm). Then, they measured object size and distance perception using different tasks (i.e., verbal size and distance estimation, hand aperture, and walking distance) (Figure 1.8). In ten experiments, it has been shown that the perceived size and distance of objects increased when participants experienced a small virtual body as their own, while the distance and the size of the objects were reduced with a large-body illusion. Similarly, Banakou et al. (2013) induced the ownership illusion toward a 4-year-old virtual child and a virtual adult of the same height. They found that feelings of ownership toward the virtual child led to overestimating the object size compared to the virtual scaled adult. However, not only the size of the body can influence visual perception. Indeed, numerous evidence supports that other modifications of the body morphology can affect the perceived size and distances, such as the perceived length of the arm (Linkenauger et al., 2015a; Witt et al., 2005) or the eye-height (Leyrer et al., 2011; Wraga et al., 1999). Crucially, Linkenauger et al. (2015a) demonstrated that modifying the length of a virtual arm of a self-representing avatar affects the perceived distance of nearby objects, as assessed through a visual and action-base matching task. Indeed, participants increased their arm's reach after a minimal reaching experience with the long arm, and a decrease in perceived distance estimations was observed. These results also fit nicely with the previous study that showed that manipulations of reaching ability (such as after the use of a long tool) influence the perception of distance of objects placed in near space (Bourgeois et al., 2014; Witt et al., 2005; Witt & Proffitt, 2008).

In conclusion, the evidence presented in this section would suggest that our perception of the external world is related to the representation of our body; indeed, visual and tactile information would be scaled according to how we perceive our body.

Figure 1.8

Experimental set-up of the work of van der Hoort et al. (2011).



Note. *A*. Main experimental set-up; *B*. the four artificial bodies; *C*. the image seen by participants during visuo-tactile stimulation, *D*. the Barbie doll experiment; *E*. object size estimation, and *F*. distance estimation. (Image from van der Hoort et al., 2011)

1.4 Aims of the research project

The aim of this thesis is to investigate the bidirectional relation between body representation and sensory processing. In particular, incoming sensory information shapes and influences each other, integrating with stored body representations. The purpose of this continuous negotiation between the various sensory inputs and the already formed representations is to create an integrated and updated representation of one's own body. At the same time, the way in which the body is represented can influence how incoming sensory information is perceived. Therefore, in the present doctoral thesis, I further investigate the mechanisms underlying the multisensory integration involved in building a coherent body representation. Also, I examine how, in the opposite direction, body representation shapes the processing of sensory modalities as well as how the single senses influence each other in a complex network of bidirectional relations.

Specifically, I will first present how integrating different incoming sensory information can influence the perception of one's body and the space around the body. Thus, Study 1 (Chapter 2) examines the influence of a conflict between tactile and visual information in the perception of one's own body and of the potential space of action. Whereas Study 2 (Chapter 3) investigates the plasticity of the morphological body representation while holding a tool in the hand, without performing any movement (i.e., online tool incorporation). Thus, the first part of the thesis focuses on how the sensorimotor representation of one's own body in space is constantly updated and modulated based on incoming sensory information (Study 1 and 2). Furthermore, Study 1 examines how changes in body representation can affect the perception of the external space (i.e., space of body-objects interaction).

The second part of the present work explores how body representation can influence the processing of individual sensory modalities. Specifically, I will examine if body representation affects the processing of incoming individual sensory information (i.e., haptic and visual) even when dealing with rather automatic integrative perceptual phenomena. More specifically, Study 3 investigates if the proprioceptive information about arms position in the external space modulates haptic phenomena such as the Uznadze haptic aftereffect. Study 4 aims to understand the role of visual processing of the size of body parts in influencing the visual version of the Uznadze aftereffect. Thus, in this second part, I focus on the influence of the different components of body representation (i.e., a stable visual representation of body parts as perceptual visual stimuli or a more contingent update of the body parts representation in space through proprioception) on the integrative rather automatic perceptual processes.

Overall, the present work highlights the critical bidirectional relation between body representation and sensory information processing: sensory integration can modify body representation, and, at the same time, body representation may influence perceptual phenomena.

Chapter 2.

Study 1:

Multisensory conflict affects Body Schema and Reaching Space*

**This work has been conducted in collaboration with Ivana Frigione and Angelo Maravita.*
The relative paper is now in preparation.

Study 1: Multisensory conflict affects Body Schema and Reaching Space

In this chapter, I will present the first work of this thesis. Two experiments were conducted aimed at investigating how a conflict between touch and vision could induce changes in one's own body representation (i.e., affecting the sensorimotor representation of one's own body in space) and in the representation of the space around the body (i.e., modulating the perception of one's own action potential in space). The results emphasize the reciprocity between body and sensory processing, revealing how multisensory dysregulation can modulate both one's own body representation and the perception of the body-objects interaction space.

2.1 Introduction

The efficient and accurate integration of different sensory information into a coherent representation is a critical mechanism for perceiving the external world (Ernst & Bülthoff, 2004) and one's own body (Graziano & Botvinick, 2002). As we discussed previously, multisensory integration plays a crucial role in building the sense of ownership toward one's own body (Blanke, 2012; Ehrsson, 2012). Thus, perceptual body illusions based on the disruption of the congruency of the bodily signals have been used to alter it. Indeed, feelings of *disownership* can be induced by creating a conflict between visual and tactile or motor signals in real-time (Kannape et al., 2019; Newport & Preston, 2011; Roel Lesur et al., 2019) or with pre-recorded video (Gentile et al., 2013). De Vignemont (2011) defined the experience of *disownership* as the awareness of the disruption of the sense of body ownership and not only as the result of this disruption itself. This experience can be characterized by different feelings such as the feeling of unfamiliarity (i.e., body properties feel as abnormal), the feeling of unreality (i.e., the body part is recognized, but it is not considered living), the feeling of uselessness (i.e., the body part is ignored as useless) and the feeling of disownership (alienation of body parts which could also be combined to delusional beliefs). As presented in Chapter 1, previous works suggest a possible link between Body Ownership, Body Schema, and Peripersonal Space (see section 1.2). Indeed, it has been proposed that body ownership is derived from the localization of bodily information on a multimodal map of the body (i.e., Body Schema), grounding the position of multisensory bodily information in space (de Vignemont, 2007). Thus, multisensory integration within the PPS could be a mechanism underlying Body Ownership (Makin et al., 2008), as shown by the overlapping between the multisensory areas involved in Peripersonal Space and those in Body Ownership (Grivaz et al., 2017) and the possibility of inducing Body Ownership feeling within the PPS (Guterstam et al., 2016). Moreover, previous studies showed how ownership feelings toward the fake hand during the RHI could emerge if a recalibration of Body Schema is possible (Lewis & Lloyd, 2010; Llorens et al., 2017) and if the illusion is induced according to the anatomical constraints of one's body (Ide, 2013; Preston, 2013). In addition, also Body Schema seems to be strictly related to space representation: the representation of a body part in space is crucial to grasp and reach objects within the external environment (e.g., the individual arm's length is related to PPS extension; Longo & Lourenco, 2006). Indeed, different kinds of manipulations altering body representation affect space's coding, e.g., after tool-use (Cardinali et al., 2009) or after varying the perceived body size through bodily illusion (Linkenauger et al., 2015a; Petroni et al., 2015). Although it is now evident that a conflict between touch and vision alters feelings of ownership toward one's own hand, it is still unclear whether this multisensory disintegration may also impact deeper aspects of the sensorimotor representation of one's own body in space (i.e., Body Schema) and of the space around the body in terms of action potentiality (i.e., Reaching Space).

To this purpose, we investigated the influence of a conflict between tactile and visual information and the consequent feeling of the loss of Body Ownership in the relation between body and space. In Experiment 1, we investigated if the visuo-tactile conflict could influence the dynamic sensorimotor representation of the body in space through the Forearm Bisection Task (i.e., a paradigm aimed to assess changes in body metric representation; Sposito et al., 2012; Tosi et al., 2018). In Experiment 2, we verified the effect of the same multisensory conflict on the PPS representation by using the Reachability Judgment Task (i.e., a paradigm used to evaluate the extension of the reaching space; Bartolo et al., 2014; Coello et al., 2008; Wamain et al., 2016). We expected that multisensory conflict would affect body and space representation by leading to less defined borders of our body and our potentiality of action.

2.2 Experiment 1

Experiment 1 investigated the effect of the multisensory conflict on body representation, considering both the sense of Body Ownership and Body Schema. Previous literature showed that a visuo-tactile mismatch alters the sense of bodily self (Gentile et al., 2013; Roel Lesur et al., 2020). However, it is unclear whether the same multisensory conflict can even affect the representation of the body in space. Based on the hypothesis that the sense of ownership would derive from the localization of bodily signals on the multimodal map of the body (de

Vignemont, 2007), we expect that a multisensory conflict may also affect the metric representation of one's own body, making the boundaries less defined.

2.2.1 Methods

Participants

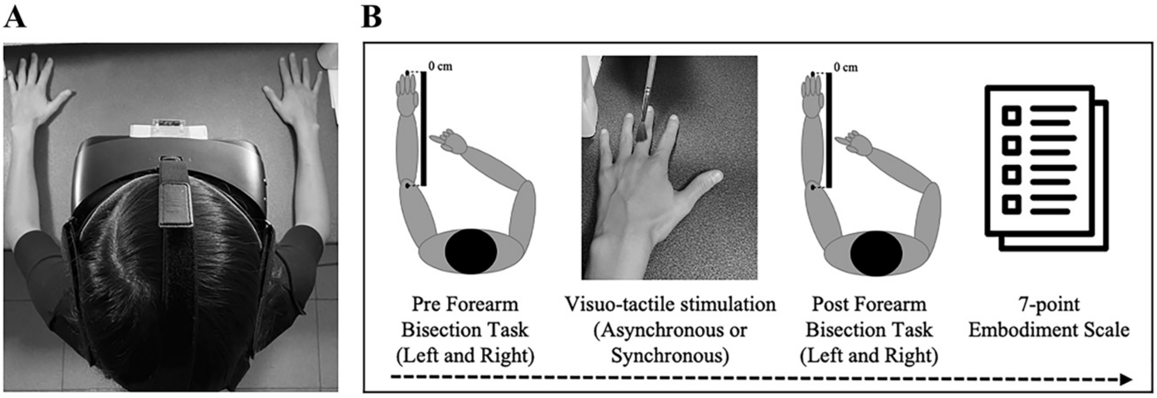
26 participants (16 female, M = 30.11, SD = 9.16) took part in Experiment 1. All subjects were right-handed, as assessed by Edinburgh Handedness Inventory (Oldfield, 1971). Participants were unaware of the experimental aim and self-reported the absence of a history of neurological or psychiatric disease. They gave written informed consent to participate in the study, approved by the Ethical Committee of the University of Milano-Bicocca and conducted in accordance with the standards of the Helsinki Declaration (World Medical Organization, 1996). Our number of participants has been chosen based on the sample size used commonly in similar studies with the Forearm Bisection Task (Sposito et al., 2010, 2012; Romano et al., 2019), because a power analysis for Linear Mixed Models is not yet a standard method. Based on previous studies, a sample size of 26 participants would be appropriately powered to address the study's issue.

Procedure and Experimental Design

Blindfolded participants comfortably sat in front of a table, placing their arms radially (Figure 2.1A). We used a Forearm Bisection Task to measure changes in body metric representation (Sposito et al., 2012; Tosi et al., 2018). They were asked to indicate the perceived midpoint of the forearm, considering the elbow (olecranon) and the middle finger tip as the extremities (Figure 2.1B). Bisections were made for both forearms, in a counterbalanced order across participants, performing ballistic movements with the index finger of the contralateral hand. Corrections of the estimation were not allowed. Each trial started with the contralateral index finger positioned 30 cm from the subject's midsagittal plane. The perceived midpoint was measured with a flexible ruler, placed a few millimeters close to the participant's arm with the starting point (0 cm) at the tip of the middle finger. Participants performed 10 trials for each forearm. The Forearm Bisection Task was performed before and after two visuo-tactile stimulation conditions (80 trials in total). During the visuo-tactile stimulation (adapted from Roel Lesur et al., 2020), participants wore Head-Mounted Displays (HMD, Samsung Gear VR) connected to a 180° webcam (60 frames, 1280x720 resolution; ELP, AilipuTechnology CO., Ltd, 2,7 inches, 1080 pixel), streaming in real-time a video of participants' body. The camera was placed on the HMD to ensure the same first-person perspective (Figure 2.1A). Before starting, participants were exposed to the real-time video feed for a few seconds to promote habituation to the new environment. Participants were asked to avoid any movements with their heads and hands. Then, using a paintbrush, the participant's left hand was stroked at a frequency of 1 Hz in different positions and directions for 60 sec (Figure 2.1B). Each participant was exposed to two conditions, and the order was counterbalanced across participants. In the synchronous condition (i.e., control condition), the tactile stimulation was congruent with the visual feedback seen in the HMD. In contrast, in the asynchronous condition (i.e., experimental condition), the visual stimulation was 850 msec delayed compared to the tactile one; thus, participants felt the touch on their hands before seeing it. After each condition, we assessed changes in feelings of embodiment, disembodiment, and physical sensation through the 7-point Embodiment Scale (adapted from Romano et al., 2021; Figure 2.1B).

Figure 2.1

Procedure of Experiment 1.



Note. A. Posture and position of participants during. *B.* Experimental design: before and after a visuo-tactile stimulation, a Forearm Bisection Task was performed for both forearms (the order was counterbalanced across participants). During the visuo-tactile stimulation, participants observed their left hand, through the HDM, being stroked by a paintbrush during a synchronous or asynchronous condition. In the end, the Embodiment Scale was filled in. The visuo-tactile conditions order was counterbalanced across participants.

Also, we checked if participants explicitly recognized the difference in delay between the two conditions by asking them, at the end of each condition, if the tactile and visual feedback were at the same time ("Was the touch you felt on your hand and the touch you saw through the HDM synchronous?", similar to Roel Lesur et al., 2020). Moreover, at the end of the experiment, we also explored the overall experience perceived by participants through a qualitative interview, and the participants' forearm length was measured (i.e., distance from the middle fingertip to the olecranon).

Analysis

We standardized the questionnaire responses using an ipsatization procedure to control any response bias in the subject's questionnaire ratings. We computed the mean across all the responses to all questions and conditions for each participant. Then, we divided it by the standard deviation across all questions and conditions for that individual. This procedure allows using parametric tests since it transforms questionnaire data in Z-scores with a normal distribution (Cattell, 1944; Fischer & Milfont, 2010; Romano et al., 2014). We computed the scores of the three subscales of the Embodiment Scale by averaging the items of each scale (see Romano et al., 2021). Then, we compared each subscale (i.e., embodiment, disembodiment, and physical sensation) across the two visuo-tactile conditions (synchronous and asynchronous) using Paired Sample t-tests.

Regarding the Forearm Bisection Task, we computed the percentage deviation scores for each trial by dividing each estimation (i.e., subjective midpoint) for the arm length and multiplying it by 100 (% deviation = subjective midpoint/arm length × 100). If the deviation was more than 50%, it indicated a proximal shift (i.e., deviation toward the elbow), while if the deviation was less than 50%, the shift was distal (i.e., deviation toward the finger) (Sposito et al., 2012; Tosi et al., 2018). Then, a difference between the bisection percentage before and after the two visuo-tactile stimulation conditions was calculated (i.e., Bisection Shift = Pre – Post visuo-tactile stimulation): a positive value means a distal shift towards the fingers, while a negative value indicates a proximal shift towards the elbow. We thus tested any influences of the visuo-tactile stimulation on the Bisection Shift using a Linear Mixed Model (Baayen et al., 2008). Mixed-effects modelling offers the advantage of extending the traditional general linear model when its assumptions are not met and taking more specifically into account the interindividual variability. We chose the maximal random-effect structure appropriate for our experimental design to set up the model (Barr et al., 2013). The following fixed factors were considered: Condition (Asynchronous vs. Synchronous), Forearm (Left vs. Right), and their interaction. Random intercepts and slope were estimated for the Condition and Forearm factors within participants. We included participants as a random effect variable to consider inter-subject variability properly. F test with Satterthwaite's method for degrees of freedom was used for statistical significance, and α was set to 0.05. Then, we considered mean values and 95%

Confidence Interval (CI) to explore significant effects and interactions (Cumming, 2014; Masson & Loftus, 2003). We reported marginal R^2 (R^2_m) to express the variance explained by fixed effect and conditional R^2 (R^2_c) to express the variance explained by both fixed and random effects of the overall model. In addition, we performed a correlation analysis to investigate the relationships between subjective ratings in the embodiment scale and the shift in the forearm's metric bisection. Analyses were performed using Jamovi (Version 1.6.23.0) and lme4, lmerTest, MuMIn packages (Bates et al., 2015; Kuznetsova et al., 2017) of R software (R Core Team 2016).

2.2.2 Results and Discussion

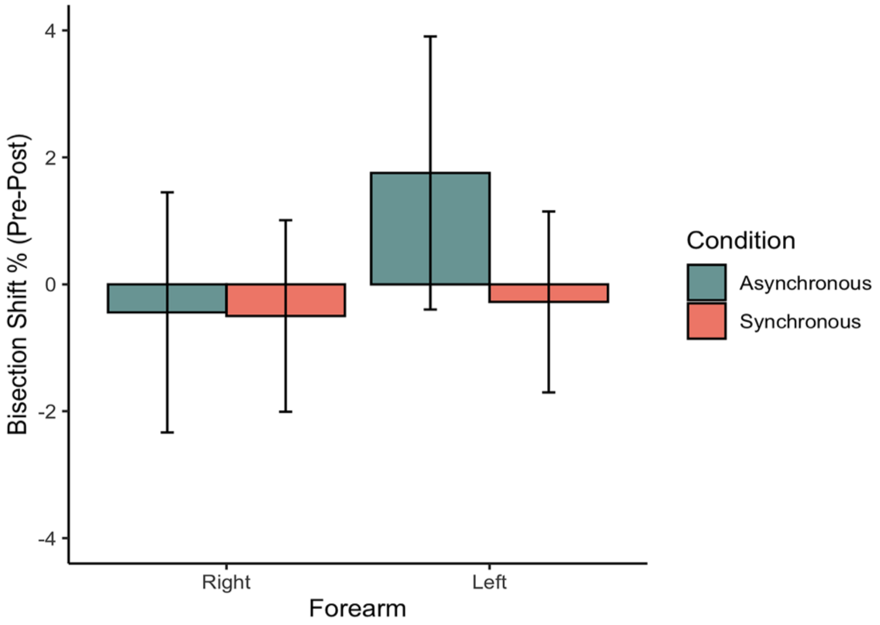
All participants, except four, recognized a difference in synchrony between the two visuo-tactile conditions: the manipulation was effective in inducing the perception of delay. We then removed these 4 participants from further analysis as they reported an absence of any differences between the two experimental conditions. Then, we explored how the current manipulation affects feelings of embodiment, disembodiment, and physical sensation toward one's hand. The values of the 3 subscales of the Embodiment Scale differed across the asynchronous and synchronous condition (Embodiment: $t(21) = 3.10$, $p = .005$, Cohen's $d = 0.66$; Disembodiment: $t(21) = -2.69$, $p = .014$, Cohen's $d = -0.57$; Physical Sensation: $t(21)=-2.30$, $p = .031$, Cohen's $d = -0.49$). Specifically, for the Embodiment subscale, the scores were lower in asynchronous than in the synchronous condition, suggesting a decrease in the feelings of ownership toward one's hand (Asynchronous: M = 0.36, SE = 0.07; Synchronous: M = 0.73, SE = 0.09). While the values were higher in the asynchronous condition for the Disembodiment (Asynchronous: M = -0.82, SE = 0.11; Synchronous: M = -1.06, SE = 0.08) and Physical Sensation scale (Asynchronous: M = -0.53, SE = .10; Synchronous: M = -0.74, SE = 0.10), suggesting that the experimental manipulation was effective in inducing feelings of disembodiment and physical sensations. We further explored the Disembodiment subscales by considering the two subcomponents: Loss-of-own-hand (i.e., loss of control and position sense of the own hand) and Movement (i.e., perception of the movement of one's hand toward the virtual hand and vice versa) (Longo et al., 2008; Romano et al., 2021). Since the questionnaire was previously built for the Rubber Hand Illusion paradigm (Longo et al., 2008; Romano et al., 2021), our experimental paradigm seems not to involve items related to the movement component. In contrast to the Rubber Hand Illusion, the real hand and virtual hand are placed in the same position, thus we did not expect participants to perceive any approaching feelings between the virtual and real hand position. Indeed, by comparing each Disembodiment subcomponent across the two conditions, we found different results. A significant result was present only for the Loss-of-own-hand component ($t(21) = -3.23$, $p = .004$, Cohen's $d = -0.69$): the scores were higher in the asynchronous condition (Asynchronous: M = -0.73, SE = 0.13; Synchronous: M = -1.04, SE = 0.11), revealing stronger feelings of loss of one's own hand. In contrast, the Movement component did not show a significant difference across conditions, confirming our prediction ($p > .53$).

Considering the effect of the visuo-tactile stimulation on the Forearm Bisection Shift, the analysis on the Bisection Shift revealed a significant interaction effect between Condition and Forearm (F(1,813) = 10.94; $p < 0.001$). For the Left Forearm (i.e., stimulated hand during the visuo-tactile stimulation), there is a distal shift only in the Asynchronous condition (M = 1.75; SE = 1.04; CI: -0.40, 3.91), while in the Synchronous condition, bisection estimations seem not to change after the visuo-tactile stimulation (M = -0.28; SE = 0.69; CI: -1.70, 1.15). While, for the Right Forearm (i.e., not manipulated hand), the Bisection Shift is comparable between the Asynchronous (M = -0.44; SE = 0.91; CI: -2.33, 1.45) and Synchronous condition (M = -0.50; SE = 0.73; CI: -2.01, 1.01) with a percentage score around 0, suggesting consistency between estimates before after visuo-tactile stimulation (Figure 2.2). The main effects of the Forearm and Condition were not significant ($p > .17$). Considering the overall model, both random and fixed effects explained 43.26% of the variance, while fixed effects explained 2.56%.

Correlation analysis revealed that the alteration of the subject's feelings of embodiment toward one's own hand were not significantly correlated with the amount of Forearm Bisection Shift (all $p > .23$).

Figure 2.2

*Results of Experiment 1: effects of the visuo-tactile stimulation on Forearm Bisection Shift***.**



Note. The graph shows the comparison of the percentage of the Forearm Bisection Shift (Pre-Post visuo-tactile stimulation) between Condition (Synchronous and Asynchronous) and Forearm (Left and Right). Positive values indicate a distal shift (toward the fingers), negative values indicate a proximal shift (toward the elbow). Lines indicate Confidence Intervals set at 95%.

Short Discussion

Experiment 1 showed that the manipulation was effective in inducing a change in the perception of one’s own body. Questionnaire scores revealed a relative decrease in embodiment feelings and an increase in disembodiment and physical sensations during the asynchronous stroking of the real hand. In particular, comparing to the Rubber Illusion paradigm, the present manipulation affects more the Loss-of-hand component of the disembodiment subscale suggesting a specific modulation in the feelings related to the loss of control and the position sense of one’s own hand more than to the perception of a movement in space (i.e., Movement component). Moreover, data showed that visuo-tactile stimulation modulates the estimation of the forearm midpoint. Indeed, only in the Left Hand and after a conflict between the visual and tactile input there was a shift in the midpoint estimation. While after a visuo-tactile stimulation characterized by synchrony between visual and tactile feedback, we found coherence between the estimates performed before and after stimulation. In this condition, the Body Schema representation would remain consistent over time, supporting the idea that, in general, there is coherence in how we perceive our body parts. However, this coherence could be altered after a multisensory conflict as if the limb is perceived differently from the pre-stimulation condition and participants no longer rely on the same bodily information.

2.3 Experiment 2

Experiment 1 showed a modulation of the visuo-tactile mismatch on the sense of Body Ownership and on Body Schema. In Experiment 2, we investigated the effect of the multisensory conflict on PPS in terms of action space within reach (i.e., reaching space, Delevoye-Turrell et al., 2010; Rizzolatti et al., 1997) as measured with a Reachability Judgment Task (Bartolo et al., 2014; Coello et al., 2008; Wamain et al., 2016). Considering the close link between Body Schema and Reaching Space, we expect a modulation of action space as a consequence of a multisensory conflict. Since in the previous experiment we found a specific modulation on the metric representation of the stimulated arm and PPS is strictly anchored to the body-part considered, in this second experiment, we verified the effect specifically on this arm (i.e., left arm).

2.3.1 Methods

Participants

A new sample of 27 participants (16 females, M = 23.92, SD = 3.43) participated in Experiment 2. All participants were unaware of the experimental aim and none of them had been involved in Experiment 1. One participant was removed from the sample due to a technical problem during the experiment (N = 26). All subjects were right-handed, as assessed by the Edinburgh Handedness Inventory, and nobody self-reported a neurological or psychiatric disease history. They gave written informed consent to participate in the study, which was approved by the Ethical Committee of the University of Milano-Bicocca and conducted in accordance with the standards of the Helsinki Declaration (World Medical Organization, 1996). The number of participants in Experiment 2 was selected based on the sample size commonly used for reaching tasks (Bartolo et al., 2014; Grade et al., 2015; Petroni et al., 2015; Wamain et al., 2016). Therefore, a sample size of 27 participants would be adequately powered to address the experiment's issue.

Procedure and Experimental Design

The experiment was composed of two sessions: the Pre-Experimental Session, in which the individual threshold of the peripersonal space was determined through a Reachability Judgment Task, and the Experimental Session, in which Reachability Judgment Task was performed before and after the two visuo-tactile stimulation conditions (Synchronous and Asynchronous).

Pre-Experimental Session: determination of individual reachability threshold

The Reachability Judgment Task was implemented within a virtual reality scenario created using 360° photos through Unity 2018 software. Photos were taken using a 360° cam (Insta360 ONE X2) within the same room of the experiment, from the perspective of a mannequin sitting in front of a table (distance from the camera lens to the floor of 120 cm; distance between the dummy's body and the top of the table of 35 cm). Participants comfortably sat during the experiment at a fixed distance from a table (i.e., equal to the distance of the mannequin from the table) and observed a 360-degree picture through the HDM (Oculus Quest 2) from the same perspective as the virtual body (Figure 2.3A). To increase the sense of embodiment toward the virtual body, both the mannequin and the participant wore black cloth. These manipulations made it possible to increase the realism of the setting and immersion in the virtual environment. Before starting the experimental task, the participants were allowed to explore and observe the virtual room and virtual body for 60 sec to induce a sense of embodiment over the virtual body and reduce possible discomfort due to the virtual environment.

Then, the experimental task began, and photos were randomly presented through the HDM connected to the computer (OMEN X 900-293nl Desktop, Intel Core i7-7800X, 16GB RAM, NVIDIA GeForce RTX 2080Ti 11 GB). Participants had to evaluate as quickly and accurately as possible whether a virtual object presented at different distances on the table was reachable or not with their left hand (Figure 2.3B). 32 different 360° pictures were presented randomly. In each picture, an object (blue parallelepiped, 3x3x6 cm) placed along the sagittal body-midline axis was displayed in one of the 32 possible positions (from 0 cm, the starting of the table, up to 80 cm; in steps of 2.5 cm). The two-alternative forced choice (reachable-unreachable) was provided by pressing the right and left pedals (counterbalanced across participants) without actually performing any movements with the arm.

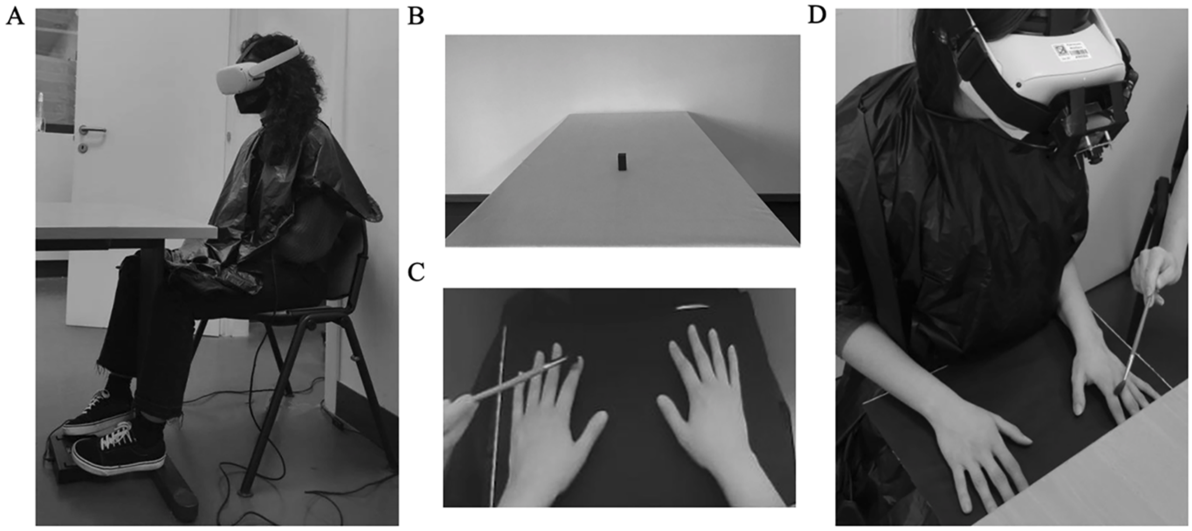
The stimulus disappeared as soon as the response was provided, and a grey screen was presented for a variable time between 1500 msec and 2000 msec between one stimulus and the other one. Two blocks were presented, and each position of the object was repeated five times, resulting in a total of 160 trials for each block. Moreover, before administering the task, the participants were instructed to actually perform ten grasping movements with the left hand toward the same object placed at the individual's actual maximum reachability distance. This procedure allowed reinforcing the movement that has to be imagined during the experimental task (Coello et al., 2008). In the end, we measured the length of the arm (measured from the acromion to the tip of the middle finger) and the maximum reachable distance (measured from the edge of the table to the further point reachable by stretching the arm) of each participant. The pre-session was used to determine the participants reaching space threshold.

Experimental Session

In the Experimental Session, the Reachability Judgment Task was performed again but before and after the two visuo-tactile stimulation conditions. The Reachability Judgment Task was exactly the same as in the previous session, except for the distances at which the object was presented. Indeed, we selected a specific range of distances for each participant according to the individual reachability threshold identified in the Pre-Experimental Session (i.e., reference distance). Therefore, 13 possible positions were proposed, considering the six positions before (i.e., reachable distances) and the six positions after (i.e., unreachable distances) the individual reachability threshold. Each position was repeated 5 times in a randomized order (total of 65 trials). As in Experiment 1, participants were exposed to the visuo-tactile stimulation in two conditions (Synchronous and Asynchronous). After each condition, we assessed again changes in the three subscales of the Embodiment Scale and in the perception of the synchrony between the tactile and visual stimulus. The procedure for the visuo-tactile stimulation was exactly the same except for the position of the hands (Figure 2.3 C, D). Indeed, in order to prevent a conflict between the position of the virtual body during the Reachability Judgment Task and the actual position, we asked participants to place their hands on a support located on their legs and to maintain this fixed position for the overall experiment. Additionally, we assessed the effectiveness of the manipulation in a more quantitative way by asking participants to rate a 10-points statement (i.e., control question) regarding how much they perceived the synchrony between the tactile and visual stimuli after each visuo-tactile condition (i.e., from absolutely synchronous to absolutely NOT synchronous). At the end of the experiment, we explored the experience perceived by participants through a qualitative interview.

Figure 2.3

Procedure of Experiment 2.



Note. *A.* Posture and position of participants during the Reachability Judgement Task: participants judged whether or not a virtual stimulus was reachable with their left hand without performing any actual movement with the arm. *B.* Example of stimulus during the Reachability Judgment Task. *C.* Participant's perspective through the HDM during the visuo-tactile stimulation. *D.* Procedure of visuo-tactile stimulation. Participants placed their hands on a support on their legs and observed their left hand being stroked by a paintbrush during the synchronous and asynchronous conditions.

Analysis

Considering the Pre-experimental Session, we calculated the point of subjective equality (PSE) for each participant, which indicated the individual virtual threshold of reachability. Within each block, the positive responses (i.e., the object is reachable) were summed for each of the 32 distances (from 0 to 80 cm), with a maximum value of 5 (all positive responses). The PSE was extracted from each participant's psychometric functions and computed by plotting the proportion of responses for which the object is perceived as reachable. Data points were fitted with a logistic function using the following equation:

$$P = \frac{1}{1 + e^{-\beta(\chi - \alpha)}}$$

in which P is the proportion of the responses for which the object is considered as reachable, χ is the distances at which the object was presented, α was the intercept, and β was the slope of the psychometric function. These estimated coefficients were used to calculate the PSE ($-\alpha/\beta$, negative ratio of the two parameters), which is the critical value of the transition at which subjects begin to report more than 50% of the times that the object was reachable (i.e., reachability threshold).

Regarding the Experimental Session, we again computed ipzatized scores of the three subscales of the Embodiment Scale and compared them between the Asynchronous and Synchronous visuo-tactile conditions. Moreover, we checked the effective difference in synchrony between the visual and tactile stimulation in the two conditions by comparing the score of the subjects' responses to the control question. Participants who did not perceive the difference in the delay were discarded from the analysis. Considering the Reachability Judgment Task, we performed the same analysis as the Pre-experimental Session but considering 13 distances. Subsequently, we computed the PSE for each participant, Condition (Synchronous and Asynchronous), and Session (Pre and Post visuo-tactile stimulation). We considered the difference between post and pre visuo-tactile stimulation thresholds (i.e., Reachability Shift = Post - Pre visuo-tactile stimulation), and subsequent analyses were performed on this variable. Then, we verified the effect of the visuo-tactile stimulation on the reaching estimation (Reachability Shift). Here, we used the General Linear Model since the use of a Linear Mixed Model did not improve fit to the data. Data were inspected for outliers in each condition: points that were outside ± 2.5 SD from participants' mean of Reachability Shift were discarded from the analysis. Thus, three more participants were excluded. Since the normality of data was confirmed by the Shapiro-Wilk test for both variables ($p > .28$), a Paired Sample t-test on the dependent variable Reachability Shift was performed to compare the two visuo-tactile conditions. At last, to investigate the relationships between subjective ratings in the embodiment scale and the shift in reachability judgments, we performed a correlation analysis.

2.3.2 Results and Discussion

Pre-experimental Session

We calculated the PSE for each participant during the pre-experimental session (M = 454.0, SE = 20.3). These values represent the virtual individual reachability threshold, and we used it as the reference distance to build the Reachability Judgment Task in the experimental session. We compared the virtual maximum reachability with the real one, and we found a significant difference (*t*(22) = 3.83, *p* <.001, Cohen's *d* = 0.80). Indeed, participants tend to overestimate their action possibility (Mean difference = 90.0, SE difference = 23.5). This result is consistent with the previous literature that showed that participants tend to overestimate their reaching ability both in real-world and virtual settings (Weat & Proffitt, 2018; Gagnon et al., 2021).

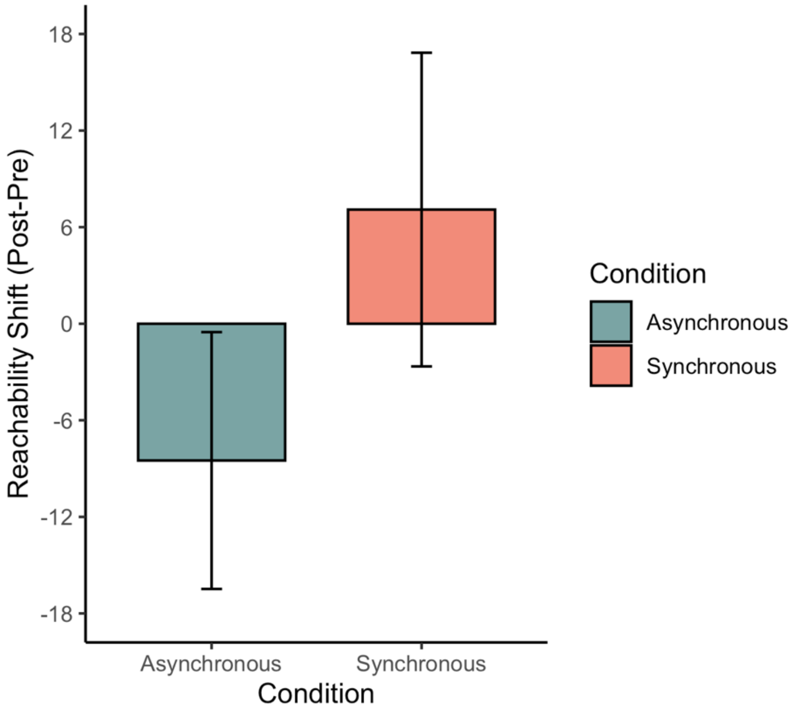
Experimental session

Regarding the experimental session, the delay manipulation was effective in producing two conditions differing in the synchrony between the tactile and video feed (Wilcoxon non-parametric tests for non-normally distributed data: Z = 350, *p* < .001, rank biserial correlation = 0.994). Thus, participants, on average, actually perceived the presence of the delay only in the asynchronous condition (Asynchronous: M = 7.78, SE = .51; Synchronous: M = 1.07, SE = 0.44). We removed from the further analysis only one participant who didn't perceive any difference between the two conditions. Moreover, we found a difference between the two visuo-tactile conditions in the Embodiment subscale (*t*(25)= -3.22, *p* = .004, Cohen's *d* = -0.63), revealing lower feelings of embodiment during the asynchronous condition (Asynchronous: M = 0.46, SE = 0.08; Synchronous: M = .79, SE = 0.04). However, in this experiment the Disembodiment (*t*(25) = 1.89, *p* = 0.070, Cohen's *d* = 0.07) and Physical Sensation (*t*(25) = 0.99 , *p* = 0.331, Cohen's *d* = 0.11) subscales were not significant. As in Experiment 1, we further explored the Disembodiment subscale by considering its two subcomponents separately. Indeed, we found a significant difference between the two conditions only in the Loss-of-own-hand component (*t*(25)= 2.37, *p* = .03, Cohen's *d* = -0.46): the scores were higher in the asynchronous condition (Asynchronous: M = -1.04, SE = 0.07; Synchronous: M = -1.25, SE = .07), revealing a stronger feeling of loss of one's own hand (i.e., loss of control and position sense of the own hand). While the Movement component (i.e., perception of a movement of one's own hand toward the virtual hand and vice versa) did not show a significant difference (*p* > .99). This lack of difference could be due to the fact that during the visuo-tactile stimulation, the position of the participant's hand matches the position of the hand observed through the viewer. Thus, Loss-of-own-hand component seems to be more sensitive to the difference between synchronous and asynchronous stimulations following this experimental task.

Considering the effect of the visuo-tactile stimulation on the reachability judgments, we found a significant difference in the Reachability Shift between the Asynchronous and Synchronous condition (*t*(21) = -2.27, *p* = .034, Cohen's *d* = -0.48). As shown in the Figure 2.4, values are positive considering the Synchronous stimulation, suggesting an extension of the reaching space after simultaneous stroking (M = 7.09; SE = 4.69; CI: -2.65, 16.83). In contrast, the asynchrony between the visual and tactile feedback would lead to a reduction of the reaching space: values are indeed negative (M = -8.50; SE = 3.84; CI: -16.48, -0.52). Again, correlation analysis revealed that the alteration of subject feelings of embodiment toward one's hand were not significantly correlated with the amount of Reachability Shift (all *p* >.10).

Figure 2.4.

Results of Experiment 2: effects of the visuo-tactile stimulation on Reachability Shift..



*Note***.** The graph shows the comparison of the Reachability Shift between the two conditions (Synchronous and Asynchronous). Positive values indicate an extension of the reaching space after the visuo-tactile stimulation, while negative values indicate a reduction. Lines indicate Confidence Intervals set at 95%.

Short Discussion

Experiment 2 confirmed that the asynchronous stroking induced changes in bodily-self perception by specifically decreasing feelings of embodiment and increasing the perception of loss of one's hand. However, we did not find an overall significant effect in the disembodiment and in physical sensations subscales. Compared to the previous experiment, these differences could be due to the experimental setting modifications during the visuo-tactile stimulation. In Experiment 1, hands were placed on a table in a position separated from the rest of the body. In Experiment 2, to allow a better continuity between the visuo-tactile setting and virtual reachability task with 360° pictures, we modified participants' position by placing their hands on a support positioned on their legs. It is possible that placing the hands on a support more adjacent to one's body may have reinforced cues coming from one's body, reducing disembodiment feelings and physical sensations. This result indicates that the illusion could be highly susceptible to contextual modification and that minimal changes in setting could modulate its effect. However, Romano and colleagues (2021) also did not find changes in the Physical Sensation subscale after their experimental manipulation. So, it is possible that this factor would be less sensitive and more variable to experiment manipulation as compared to the Embodiment and the Disembodiment subscales. In addition, results showed that visual-tactile stimulation, inducing changes related to body ownership, also affects the perception of one's potential for action. Indeed, the presence of multisensory conflict due to asynchronous stimulation between touch and vision would lead to perceive a reduction of one's reachability space, as if one's action potential toward objects were limited to a narrower space.

In contrast, the synchronous stimulation would instead increase the reachability space, indicating an extension of the space of interaction with objects. It is possible that the presence of continuous stroking in which tactile and visual feedbacks are consistent and coherent would reinforce one's own body representation and, consequently, also the perception of one's ability to reach objects in space.

2.4 General Discussion

In this study, through a multisensory conflict, we induced changes in the perception of one’s own body in space and the space around it. In Experiment 1, we found that a multisensory conflict can affect, at the same time, the feelings of ownership towards one’s body part and the metric representation of the body. This result suggests that the alteration of a coherent multisensory integration due to the discrepancy of incoming tactile and visual information may decrease feelings of ownership toward the one’s own body part and, at the same time, make the dynamic sensorimotor representation of the hand in space (i.e., Body Schema) less defined. In Experiment 2, we found that the same mismatch between tactile and visual information can also influence the Peripersonal Space, decreasing the perception of the potentiality of actions towards objects (i.e., Reaching Space). The results of Experiment 2 confirmed a reduction of the sense of ownership towards one's own hand due to a multisensory conflict and extended this influence also to the perception of the action space around one's own body.

Multisensory Conflict and Body Representation

This work confirmed that a temporal mismatch between visual and tactile stimuli affects the subjective sense of the bodily self by decreasing the sense of ownership and enhancing feelings of loss toward one's own hand (as also shown in Gentile et al., 2013; Kannape et al., 2019; Otsuru et al., 2014; Roel Lesur et al., 2020). We even found that a conflict between two modalities seems to affect body metric representation, inducing a change in the forearm midpoint estimation. This result suggests that the Body Schema, as the sense of Body Ownership, would also be ruled by principles of temporal and spatial congruence between multisensory signals (see paragraph 1.2.1), essential to build a proprioceptive skeleton on which multisensory information about the body is centred. Previous studies showed a close link between the sense of Body Ownership and Body Schema (de Vignemont, 2011; Lewis & Lloyd, 2010; Llorens et al., 2017; Romano & Maravita, 2019). Crucially, Romano and Maravita (2019) propose that the feeling of *disownership* could be related to a failed updating of the coherent representation of one's body in space in the presence of a noisy signal due to degraded information. Thus, Body Ownership can be considered a property of the multisensory integration space and, therefore, could emerge only as a result of a correct updating of the body position in space, i.e., the centring of such multisensory neurons. So, in this study, we disrupted the congruency principles of multisensory integration, interfering with the correct updating of the Body Schema and generating an uncertainty (i.e., prediction error) about the position of the hand in space, which in turn may have caused a reduction in the sense of Body Ownership. Thus, the mismatch between visual and tactile stimuli would not allow the body schema to be updated coherently, leading to a more labile and weak body representation. For this reason, in the presence of a multisensory conflict, the dynamic sensorimotor representation of the hand would not remain consistent over time. At the same time, Body Schema also represents the expectation of how the senses should integrate over time (Lewis & Llyod, 2010). Thus, in the absence of visuo-tactile mismatch, information would be integrated in the expected way according to previous experience and a coherent body representation, and Body Schema would not undergo any changes, remaining consistent over time.

This result confirms the extreme dynamism and plasticity of some aspects of our body representation and how it is continuously updated based on the type of incoming information. The present work showed that a visuo-tactile conflict induces both an increase in *disownership* feelings and a change in the body metric representation, confirming the link between the sense of Body Ownership and the internal representation of the metric of the body.

Multisensory Conflict and Peripersonal Space

The perceptual mismatch also seems to affect the representation of the space around the body: reachability judgments differ depending on the coherence of incoming sensory information. PPS is a multisensory space anchored to a body part and could be considered the space of body-object interactions. By compromising the congruency of sensory signals coming from the body through a mismatch between touch and vision, it is possible that also the perception of the space around our body and the perception of the possibility of interacting with objects would change. Thus, in the presence of multisensory conflict, in which one's own body representation is not correctly updated, the probability of the body getting in contact with the objects would be likely reduced. In this way, the object’s distance would be judged as if they was placed at longer distances and the reaching space is reduced. In contrast, in the synchronous condition, tactile and visual signals are spatially and temporally synchronous and multisensory integration principles are observed. Therefore, the feeling of ownership toward the seen hand is reinforced, since the continuous and consistent stroking would imply much more cues and information regarding one's own arm. Consequently, it is possible that the reinforced body representation would have increased the probability of contact between the object and the body, enhancing the perception of one's potential to reach objects in space.

This result fits nicely with previous works that showed that change in body representation due to multisensory stimulations affect PPS depending on the perceived body location and not the real one (Noel et al., 2015; Salomon et al., 2017). This study further reveals that a change in PPS is also possible without a direct modulation of the perceived location but only by disrupting the coherence of incoming sensory information, confirming the close relationship between multisensory conflict, Body Ownership and Peripersonal Space.

Body Ownership, Body Schema and Peripersonal Space

This study showed that Body Ownership, Body Schema, and Peripersonal Space share a common mechanism, as a multisensory conflict induces not only a reduced sense of Body

Ownership, but also affects the perception of one's body and the surrounding space. Thus, a less defined body representation with a reduced sense of ownership would also affect the space of hand-object interactions. However, we did not find an explicit association between the sense of disownership, Body Schema and Peripersonal Space, respectively. Thus, an implicit and automatic influence more linked to the multisensory integration of online sensory cues would mainly explain the effect on the Body Schema and PPS, while subjective feelings regarding body disownership may reflect more cognitive aspects (Gallagher et al., 2021). Another hypothesis is that the current modulation in healthy patients may not be sufficient to reproduce the disownership feelings present in patients fully. So, it could be interesting to look at the same experimental question but in patients suffering from Body Ownership disorders (i.e., somatoparaphrenia) in which the sense of disownership is stronger.

Thus, although Body Schema and PPS are closely related and are based on partly common mechanisms, they can be considered partially independent (Cardinali et al., 2009) and dissociable from each other (Bassolino et al., 2015). Indeed, some apparent discrepancies in the two concepts emerged also in the present work. If multisensory mismatch influences both Body Schema and Peripersonal Space, with the synchronous stimulation only PPS is affected. In the condition of synchrony between tactile and visual cues, the metric perception of one's body would not be modulated explicitly, probably because Body Schema also relies on the expectation of how different sensory signals should be integrated with each other (Lewis & Llyod, 2010). Thus, in the absence of discrepancies, it tends to be consistent over time without any explicit changes. While the influence of this synchronous and continuous sensory stimulation would instead emerge during estimates of reachability: the more enriched and coherently integrated representation of one's body would induce an increase in the perception of one's potential for action. Thus, Body Schema is the necessary “skeleton” to support PPS representation, but it is not enough to explain other additional signals integrated in this representation (Cardinali et al., 2009; Brozzoli et al., 2012). However, future studies are needed to further explain the synchronous stimulation effect found in PPS.

In conclusion, results suggest that a multisensory conflict would not only influence the subjective sense of the bodily self but also alter the relation between body and space, affecting the representation of one’s own body in space and of the surrounding space in terms of action potentials. Thus, this works underling a close relationship between Body Ownership, Body Schema and, the Peripersonal Space.

Chapter 3.

Study 2:

Holding a tool updates Body Schema without active movements*

This work has been conducted in collaboration with Angelo Maravita, Claudio Brozzoli, Alice C. Roy, and Alessandro Farnè. The relative paper is now in preparation.

Study 2: Holding a tool updates Body Schema without active movements

Study 1 showed how an incongruence between different incoming sensory signals affects both the sensorimotor representation of the body in space and the perception of one's action potential. Previous studies revealed that the use of a tool can also modulate one's action potential since it effectively extends the possibilities of acting in space (Bourgeois et al., 2014; Cardinali et al., 2009; Sposito et al., 2012). In accordance, Study 2 aimed to investigate the effect on Body Schema of a mere tool holding in the hand without performing any action. We hypothesized that the Body Schema already updates to incorporate the tool length as a result of the integration of all incoming sensory information while holding the tool in the hand. Findings are critically discussed in comparison to previous evidence.

3.1 Introduction

Given the limits of our effectors in terms of physical extension in the far space and functionality to perform given tasks, we constantly interact with the surrounding environment through the use of tools that allow us to extend our body both physically and functionally, amplifying our sensorimotor abilities. Indeed, several studies have shown that using a tool to interact with objects placed outside one's reaching space increases the perceived length of the sensorimotor arm representation (see section 1.2.5). The prominent idea is that, after active training to reach far objects, the tool is included in the Body Schema, i.e., tool embodiment, causing an increased length of the arm representation. Therefore, tool would not be treated as an external object but as body-part (Iriki et al., 1996; Maravita & Iriki, 2004; Martel et al., 2016). From the pivotal work of Iriki et al. (1996), in which the neural basis of the tool use-dependent assimilation into the Body Schema was assessed (section 1.2.5), the effects of active tool-use have also been investigated in humans using different tasks. A modulation in different components of body representation has been shown, such as in motor (Cardinali et al., 2009, 2016; Martel et al., 2019), proprioceptive (Bahmad et al., 2020), and somatosensory ones (Cardinali et al., 2009, 2011; Sposito et al., 2012; Miller et al., 2014).

More recently, it has been proposed that just holding the tool without performing any movements influences somatosensory cortex processing (Miller et al., 2019a, 2019b). Indeed, a new perspective emerged from the work of Miller and colleagues (2018), according to which tools are considered sensory extensions of the body and holding a tool would involve the repurposing of the same body's somatosensory processing mechanisms to control and sense the tool. Indeed, not only humans accurately localize where an object contacts the surface of a tool, but also an overlapping emerges between the neural mechanisms related to touch localization on the body and the tool (i.e., primary somatosensory and posterior parietal cortex) (Miller et al., 2018, 2019b). Such somatosensory recalibrations seem to happen as soon as the tool is held in the hand, without performing any actions with the tool, i.e., an online modulation.

Evidence of online modulation with the hand-held tool was also described in some studies with neuropsychological patients (Berti & Frassinetti, 2000; Pegna et al., 2001; Maravita et al., 2001; 2002). For instance, in a pioneering work, Berti and Frassinetti (2000) showed a patient with a rightward error in line bisection task present only within near and not far space. Crucially, the rightward bias also emerged in far space when line bisection is performed with a long stick, showing an online remapping of space so that, in the authors' words, "far becomes near". Also, Maravita et al. (2001) showed similar modulation in patients with visual-tactile cross-modal extinction (i.e., touch on the left hand is not perceived when associated with a visual stimulus near the right hand). However, if the right visual stimulus is presented at the end of a stick held by the patient with the right hand, cross-modal extinction also emerges in far space. Thus, both the somatosensory recalibration described by Miller and colleagues (2018, 2019a, 2019b) and the remapping of space described in neuropsychological studies seem to occur as soon as the participants hold the tool in their hand. However, it has yet to be determined whether wielding the tool in hand without performing any movement causes a parallel modulation of the body representation.

Here, we investigated the effect of online tool incorporation into the Body Schema, testing the hypothesis that Body Schema modulations already occur during the holding of the tool in hand, without active tool training. We assessed Body Schema while holding a short or a long tool using the tactile localization task. In this task, participants pointed to a touch screen to indicate where they had felt tactile stimulation on their forearm. This paradigm has been shown to be able to capture changes in body representation after active tool training (i.e., distalization of perceived positions; Cardinali et al., 2009; 2011). If the tool incorporation is online, we expect a distalization of the felt location of touches on the forearm by simply holding the long tool in hand, revealing online somatosensory Body Schema plasticity.

3.2 Experiment 1

3.2.1 Methods

Participants

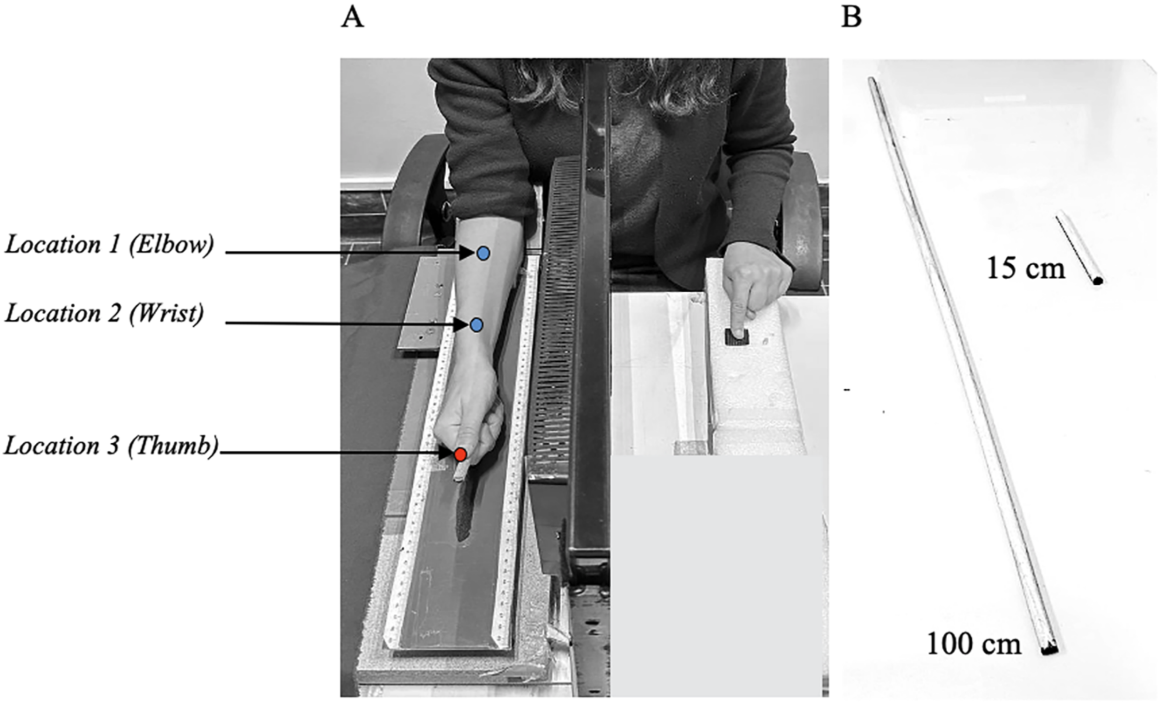
40 volunteers (28 females, M = 29.27, SD = 6.13), participated in Experiment 1. All participants were right-handed, as assessed by the Edinburgh Inventory (Oldfield, 1971). Participants were randomly assigned to one of two groups, which differed in the possibility of seeing or not the tools (Vision vs. No vision group). All participants reported normal or corrected-to-normal vision, normal tactile sensitivity and no history of psychiatric disorders. Before taking part in the study, the experimental protocol was explained in detail and all participants gave written informed consent to participation. The experiment was approved by the local ethics committee (Comité d'Evaluation de l'Ethique de l'Inserm) in accordance with the Declaration of Helsinki (World Medical Organization, 1996). A power analysis was performed for sample size estimation using the software G*Power 3.1 (Faul et al., 2007), setting the within-between interaction for a mixed ANOVA with a medium effect size of 0.25, a power level of 0.85 and a correlation of 0.5 between the measures. The analysis indicated the necessary sample size of at least 38 participants.

Procedure

Participants sat at a table with a touch screen positioned perpendicular to the table and aligned with their sagittal axis. They placed their right arm behind the monitor on a horizontal support and their left arm on the left side of the touch screen with their index finger on a black marker located on a foam support (Figure 3.1A). The experimenter drew two dots on the participants' right arm (i.e., tactile stimulation locations), out of the participants' sight, close to the elbow (Location 1, 5 cm distal from the forearm-arm boundary line) and the wrist (Location 2, 5 cm proximal from the forearm-wrist boundary line). Participants held in their right hand two possible tools (i.e., wooden rods): a Short (15 cm length) or a Long (100 cm length) tool (Figure 3.1B). Then, blindfolded participants performed a tactile localization task: they were touched (single stimulation of 1 s) with a von Frey monofilament on one of two possible locations on their right forearm while holding the tool. After each tactile stimulus, participants had to point on the touch screen with their left index finger toward the position corresponding to the perceived tactile stimulus, and then always return to the starting position. Each *Condition* (Short and Long tool) consisted of two blocks of 20 trials, i.e., 10 trials for each location.

Figure 3.1.

Experimental setting of Study 2.



Note. *A.* The experimental setting for Experiment 1 (two stimulation locations: Location 1 and 2, in blue) and for Experiment 2 (three stimulation locations: Location 1, 2, and 3): an example with the short tool in the hand. *B.* Tools used in Experiments 1 and 2.

Experimental Design

Participants were randomly assigned to two *Groups*: one group performed the entire experiment blindfolded without ever looking at the two tools (i.e., No Vision group), while the other group looked at the tools before starting the tactile localization task (i.e., Vision group). Both groups performed the tactile localization task blindfolded while holding one of the two tools in the two different conditions (i.e., Short and Long). Participants took a 5-min break between the two conditions. During the break, movements of the right forearm were not allowed: participants of the No Vision group kept the mask on their eyes, while those of the Vision group took it off to look at the second tool. The order of Short/Long tool was counterbalanced across participants. After participants completed the two conditions, we asked them to estimate the length of both tools by sliding their index finger on a meter until they reached the perceived length of the tool.

3.2.2 Data Analysis and Results

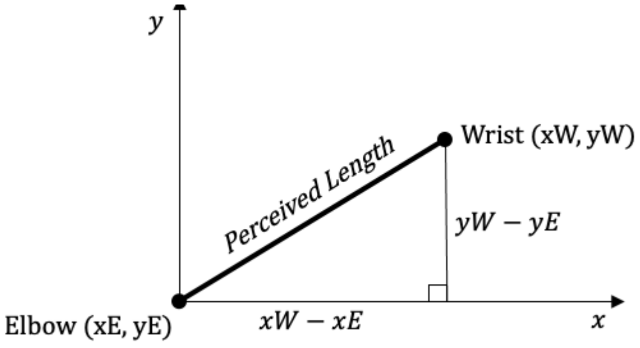
To indirectly calculate the estimation of the forearm's length of participants in the two conditions, we computed the distance between the two pointed locations (Location 1 and 2), considering the average of the trials at each location. In this way, participants never explicitly estimated the length of their forearms. Each pointing on the touch screen was collected in terms of pixel coordinates (x,y) and converted in cm. Thus, we calculated the vector *Perceived Length* (PL) for each participant (i.e., the distance between the mean of the two pointed locations):

$$PL = \sqrt{(xW - xE)^2 + (yW - yE)^2}$$

with xE, yE representing the coordinates of the point near the elbow (Location 1) and xW, yW representing the coordinates near the wrist (Location 2) (Figure 3.2). All data were inspected for outliers in each condition and group: points that were outside ± 2.5 standard deviations from the participants' mean of *Perceived Length* were discarded. Thus, two participants were removed from the analysis.

Figure 3.2

Perceived Length calculation.



Note. Coordinates to calculate the distance between the two pointed locations (i.e., Perceived Length): Elbow (xE, yE) and Wrist (xW,yW). The *Perceived Length* vector is computed in each subject and in each condition.

First, we assessed whether holding a long tool could affect the participants' body representation based on whether they could see the tool or not. Thus, since data were normally distributed (Shapiro Wilk test: all $p > .09$), we performed a 2x2 mixed ANOVA on *Perceived Length* with Condition (Short, Long tool) as within-subjects factor and Group (Vision, No Vision) as between-subjects factor. Neither the main effects nor the interaction were significant (all $p > .16$). Indeed, the means length estimation are comparable between the two tools in both groups (Vision Baseline: M = 13.94, SE = 0.97; Vision Long: M = 14.45, SE = 1.10; No Vision Baseline: M = 15.05, SE = 1.21; No Vision Long: M = 14.34, SE = 1.36).

We thus explored the trend of the two groups, inspecting performances on a single-subject basis. Therefore, we computed the Long-Short difference in the Perceived Length for each subject (PL Long – PL Short = Long tool effect) to examine the proportion of participants for whom performance was similarly affected by the tool. In the Vision group the majority of the participants (13 out of 19, 68.42%) showed an increase in the estimated arm length while holding the Long tool. Whereas, in the No Vision group, we found the opposite trend: 12 out of 19 (63,16%) displayed the increase in the perceived length holding the Short tool.

Finally, we focused on the estimation of the length of the two tools. Participants perceived the two tools as different in both Vision (Short: M = 16.57; SE = 1.39; Long: M = 63.87; SE = 5.35) and No Vision (Short: M = 17.47; SE = .95; Long: M = 23.38; SE = 2.37) group, as shown by the significant Paired Sample t-tests (Vision: $t(18) = -9.65$, $p < .001$, Cohen's $d = -2.21$); No Vision: $t(17) = -2.36$, $p < .030$, Cohen's $d = -0.56$). However, if the estimation of the Short tool was comparable between the groups ($p > .60$), the perception of the Long tool was significantly different ($t(36) = -6.69$, $p < .001$, Cohen's $d = -2.17$). Indeed, the Long tool in the Vision group was estimated to be significantly longer than in the No Vision group, thus, more in line with the actual tool length.

3.2.3 Discussion

Experiment 1 showed that holding a tool in the hand does not affect the perceived distance between the two chosen points on the arm. Indeed, wielding a 100-cm tool does not appear to significantly extend the perceived forearm distance as compared to a short 15-cm tool, contrary to the plasticity observed following active tool-use described in the previous studies (Cardinali et al., 2009; Romano et al., 2019). Also, visual feedback related to the tool in hand would not significantly modulate body representation. Although there is no significant difference between the Long and Short tool, looking at the single-subject data a trend for such modulation seems to emerge: the majority of the participants in the Vision group perceived their arm as longer while holding the long tool. Previous studies have shown that the tool incorporation can differ according to the specific sensorimotor constraints imposed for its control, leading to changes in the representation of a specific body-part (Cardinali et al., 2016; Miller et al., 2014). Thus, these data may indicate the absence of effective online modulation of the tool or it is possible that the locations chosen in the task are not effective in capturing a significant change, as they are too proximal. Indeed, during tool holding, the hand and the most distal part of the forearm (i.e., wrist joint) would be the body parts more involved in supporting the tool weight. In addition, factors related to the time course of the effect may have limited the occurrence of the effect on body representation. Previous studies showed that changes in body representation would emerge following training of around 10-15 min (Cardinali et al., 2009; Martel et al., 2016; Sposito et al., 2012). Therefore, given the shorter duration of the present paradigm while holding the tool (around 5 min for each condition), it is possible that the time duration of the task is not long enough for the online effect to emerge. Finally, it is necessary to ensure that the tool used (i.e., wooden stick of 100 cm) actually induces an effect on body metric representation following active training, as observed in previous works with other types of tools (Cardinali et al., 2009; 2011). We, thus, controlled for these potential factors in Experiment 2. First, we considered an additional stimulation point to account for the distal segment mostly involved in the tool holding (3 locations in total, Figure 3.1A) and we added two more blocks to test the temporal aspects of online tool incorporation (4 blocks in total). We also considered an active tool-use session to test for embodiment effects by comparing the body morphological representation before and after the tool training, as in the classical paradigm. Finally, in Experiment 2, we considered only the Vision condition since a trend was found in this group for an increase in perceived arm length while holding a long tool. Moreover, the estimations of the long tool length of participants in this group were closer to the real length than in the No Vision group.

3.3 Experiment 2

3.3.1 Methods

Participants

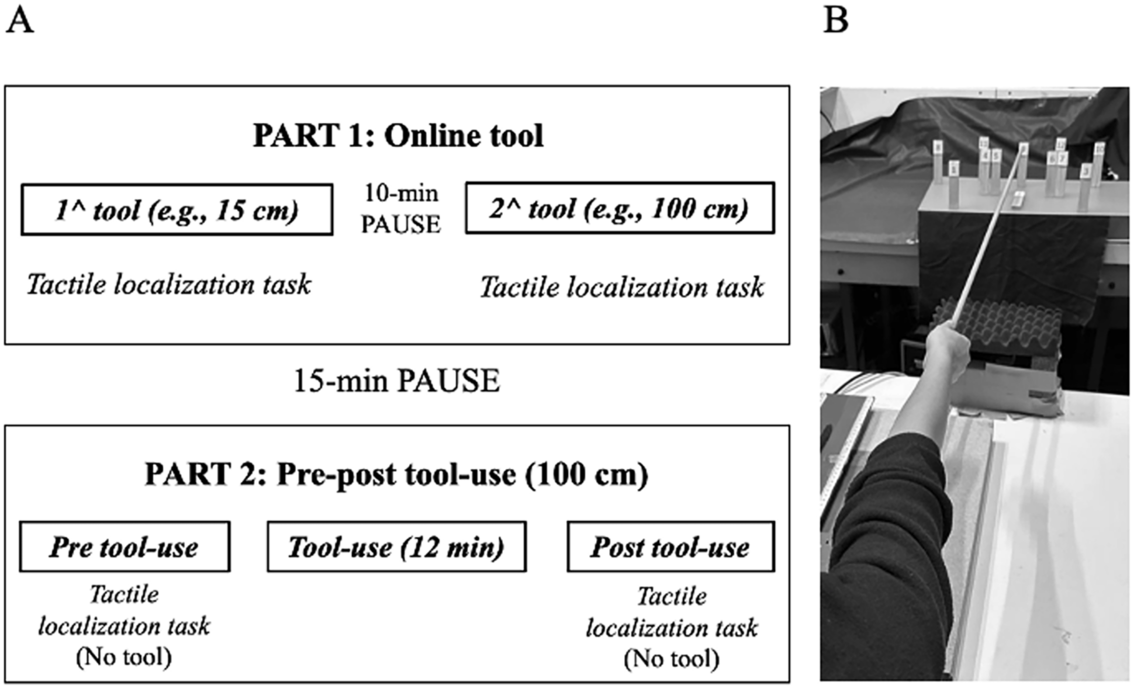
Participants included in Experiment 2 were 28 new volunteers (22 females, M = 27.04, SD = 5.84). All participants were right-handed as assessed by the Edinburgh Inventory (Oldfield, 1971) and none of them participated in Experiment 1. All participants reported normal or corrected-to-normal vision, normal tactile sensitivity and no history of psychiatric disorders. Before taking part in the study, the experimental protocol was explained and all participants gave written informed consent to participation. The experiment was approved by the local ethics committee (Comité d'Evaluation de l'Ethique de l'Inserm) in accordance with the Declaration of Helsinki (World Medical Organization, 1996). A power analysis was performed setting the within interaction for a RM ANOVA with a medium effect size of 0.25, a power level of 0.85 and a correlation of 0.5 between the measures. The analysis indicated the necessary sample size of at least 21 participants. Therefore, a sample size of 28 participants would be appropriately powered to address the experiment's issue.

Procedure and Experimental Design

Experiment 2 consisted of two parts, separated by a 15 min break (Figure 3.3A). In Part 1 (i.e., Online tool), the experimental procedure was exactly the same as in Experiment 1, except for the following changes. First, a new stimulation location placed on the tip of the thumb was added (i.e., Location 3, Thumb) (Figure 3.1A). In this way, each block was characterized by a total of 30 trials, 10 for each location. In addition, participants performed a total of 4 blocks for each condition (i.e., Short and Long tool) and all participants were able to see the tools before starting the tactile localization task. In contrast to Experiment 1, participants performed 10-minute break between conditions and they were allowed to move their arm. This modification was intended to allow the effect of the first condition to wear off. In Part 2 (i.e., Pre and Post tool-use), participants performed three phases: pre tool-use session, tool-use training, and post tool-use session. In the tool-use phase (Figure 3.3B), participants had to use the tip of the long tool (100 cm) to hit and drop objects (11.7 x 2.34 x 0.78 wood planks) located between 120-145 cm away from the participant's body. We asked participants to move only their right arm to touch the objects without any shoulder movement. Each movement began according to the sound of a metronome (0.17 Hz) with the tool on a starting position on a support and at the end of each movement participants returned to the starting position. 12 numbered objects were presented, and participants had to follow a specific sequence of numbers to drop the objects, for a total of 8 randomized sequences. Tool-use training lasted about 12 minutes for a total of 96 movements. In the pre-and post-tool-use phases, subjects were asked to perform two blocks of the tactile localization task again by placing their arm and hand in the same posture as Part 1 but without holding any tool. Tactile stimulations were delivered in the same 3 possible locations on the right forearm as in Part 1.

Figure 3.3

Experimental Design and Procedure of Experiment 2



Note. A. Experimental Design of Experiment 2: the experiment consisted of the Online task with both the Short and the Long tool (i.e., Part 1) and the Pre-post tool-use task with the Long tool only (i.e., Part 2). Participants performed a tactile localization task in both parts, including three possible tactile locations. *B.* Procedure of tool-use training in Part 2**:** the tip of the long tool was used to drop the numbered object (wooden blocks) according to specific sequences.

3.3.2 Data Analysis and Results

We calculated two *Perceived Length (PL)* vectors related to two different segments for each participant and each condition using the same formula as in Experiment 1. The first one (i.e., *PL Proximal)* measured the proximal segment which is the distance between the Location 1 (i.e., close to the Elbow) and Location 2 (i.e., close to the Wrist), the same vector as in Experiment 1. The second vector (i.e., *PL Distal)* was related to the distal segment that measured the distance between the Location 2 and Location 3 (i.e., thumb tip). These vectors were computed for each Condition (Long and Short) in Part 1 and for each Session (Pre and Post tool-use) in Part 2.

Pre and Post tool-use

First, we controlled the presence of a Body Schema modulation after tool-use (Part 2). Each variable was inspected for outliers: points that fell outside ± 2.5 standard deviations from the *Perceived Length* participants' mean were discarded. Thus, two participants were removed from the analysis. Since data were normally distributed (Shapiro Wilk test: all p > .28), we performed two Paired Sample t-tests between the Pre *PL* and Post *PL,* one for each vector (*PL Proximal* and *PL Distal*) to verify whether tool-use plasticity actually affects body representation. Considering *PL Distal*, the analysis showed a significant result (t(25) = -2.22, p = .036, Cohen's d = -0.44). After tool-use, we observed a significant increase in the perceived distance (Pre: M = 11.94; SE = 0.64; CI = 10.6, 13.3; Post: M = 12.56; SE = 0.71; CI = 11.1, 14.0), revealing that participants pointed according to an extended body representation when stimulated on the Location 2 and 3 (Figure 3.4A). In contrast, the analysis on *PL Proximal* did not show a significant difference (p > .85), indeed the means are comparable between the two conditions (Pre: M = 14.17; SE = 0.71; CI = 12.7, 15.6; Post: M = 14.25; SE = 0.88, CI = 12.4, 16.1).

Online tool

Secondly, we investigated the presence of a somatosensory Body Schema plasticity also during the holding of the tool (Part 1), by comparing the mean perceived length while holding the two tools (Short, Long) in both vectors *(PL Proximal, PL Distal)*. As before, we removed outliers that were more than 2.5 SD above or below the participants' mean for each condition and vector. Since data were normally distributed (Shapiro Wilk test: all p >.12), two Paired Sample t-tests between the Short *PL* and Long *PL* were performed*,* one for each distance (*Proximal, Distal*). Similarly, only the analysis on *PL Distal* showed a significant result (t(24) = -3.02, p = .006, Cohen's d = -0.60), while the result of the analysis on *PL Proximal* was not significant (p > .43). Considering *PL Distal*, the perceived distance was significantly longer while holding a long (Long: M = 11.80; SE = .54) than a small tool (Small: M = 11.04; SE = 0.55). Thus, participants estimated the position of the Location 2 and 3 as farther apart while holding the long tool than the small (Figure 3.4B). While considering *PL Proximal,* the means are comparable between the two conditions (Small: M = 14.68; SE = 0.75; CI = 13.1, 16.2; Long: M = 15.08; SE = 0.73; CI = 13.6, 16.6).

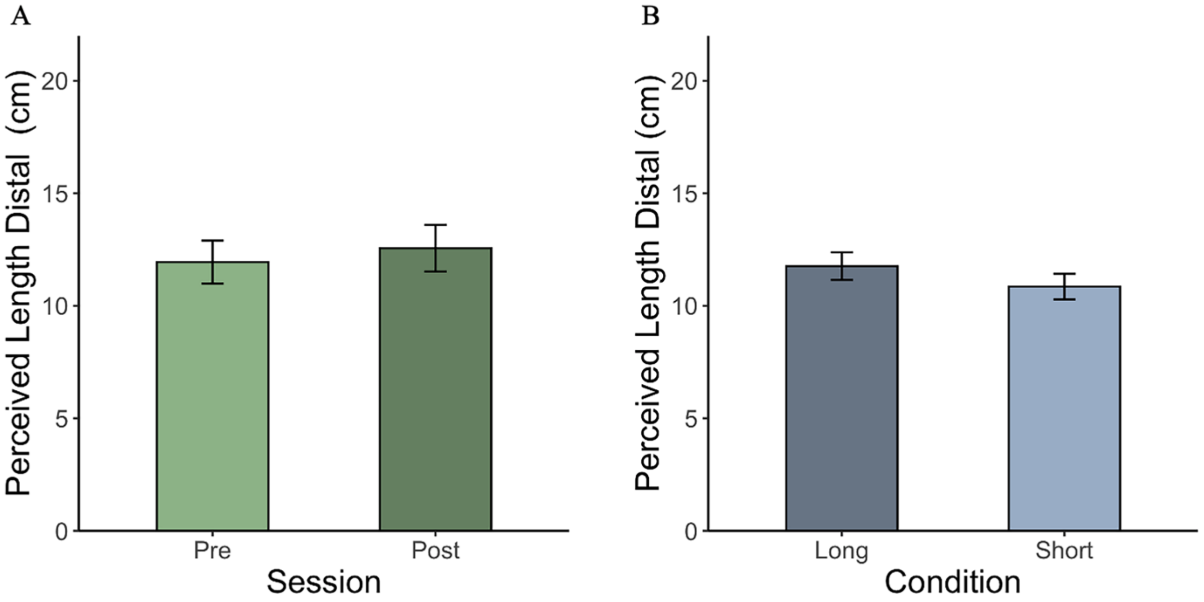
Then, to investigate the temporal aspects of the effect we performed two 2x4 RM ANOVAs on *Perceived Length* again for both vectors (*PL Proximal* and *PL Distal*) with

Condition (Short, Long) and Block (Block 1, Block 2, Block 3, Block 4) as with-in factors. The analysis on *PL Distal* confirmed the presence of a significant main effect of the condition (F(1,24) = 9.12, *p* = .006, $\eta^2_p = .27$), while no other effects were significant (all *p* > .48). This result suggests that the effect would emerge immediately from the first block and persist equally throughout the duration of the task. As in Experiment 1, the analysis on PL Proximal did not show any significant effect (all *p* > .35).

At last, we compared the strength of the two effects on *PL Distal*: "offline" (i.e., after a tool-use training) and "online" (i.e., during the holding of the tool) effect. We subtracted the Perceived Length of one condition (Pre or Baseline) from the other (Post or Long) in each participant to compute the strength of both the "online" and "offline" effect. Thus, we performed a Paired Sample t-test between Δ Offline (Post-Pre) and Δ Online (Long-Short). The analysis did not show any significant difference (*p* > .57), suggesting that the two effects are comparable (Δ Offline: M = 0.59, SE = 0.29; Δ Online: M = 0.77; SE = 0.25).

Figure 3.4

Results of Experiment 2.



Note. *A.* Pre and post tool-use task. *Perceived Length* for the *Distal Segment* segments before (Pre) and after (Post) tool-use. *B.* Online tool-use task**.** Perceived Length for the *Distal Segment* while holding a Long or Short tool.

3.3.3 Discussion

Consistently with the previous literature, active training with a 100-cm tool was effective in increasing the perceived arm representation. Specifically, only the points located on the thumb and near the wrist (i.e., distal segment) are located farther apart after tool-use training, probably because the distal segment would be more involved in maintaining the tool. Most importantly, we found a similar modulation during the online tool task. Thus, simply holding the tool and without previous training, participants tend to localize the tactile positions as farther apart but only for the distal segment. Moreover, the effect emerges very quickly and seems to be constant over time. Indeed, it would arise from the very first block (i.e., within about 2-3 min) and would remain persistent for the entire duration of the task (about 10-12 min). Analogous to Experiment 1, the estimation of the length of the proximal segment (i.e., from the location near the elbow to the one near the wrist) did not appear to change. Therefore, in line with previous studies (Cardinali et al., 2016; Miller et al., 2014), the tool plasticity effect present only on the distal segment may be due to the structural and functional features of the tool (Cardinali et al., 2016; Miller et al., 2014). Moreover, the online and the offline effects go in parallel: not only is the same part of the arm being changed, but there is not a significant difference in the two effects. Overall, these findings suggest that the simply passive holding of a tool in hand can alter the morphological representation per se. Thus, active tool-use would not be necessary to induce Body Schema plasticity.

3.4 General discussion

In this work, we investigated if holding a tool in the hand update the Body Schema, suggesting rapid and online incorporation of the tool into body representation. For this purpose, participants held a long or a short tool in their right hand while performing a tactile localization task in which they pointed towards the location where they felt a tactile stimulation on their arm. We observed that simply holding a tool modulates the morphological representation of the body. Indeed, participants tend to perceive the distance between the wrist and the thumb locations as larger while holding the long tool than the short one, suggesting an update of the Body Schema. Previous studies found modulations of Body Schema mainly due to active movements (Bassolino et al., 2015; D’Angelo et al., 2018; Romano et al., 2019; Tajadura-Jiménez et al., 2012). For instance, in the classical tool-use paradigms, modulations of Body Schema have always been induced only after an active use of the tool (i.e., action-dependent tool plasticity) (Cardinali et al., 2009; Sposito et al., 2012; for a review see Martel et al., 2016). In contrast, here, for the first time, we have demonstrated that modulation of Body Schema occurs online simply by wielding a tool in the hand. Interestingly, in the present study, the effects of online tool incorporation are comparable to those shown after active tool-use training. This online modulation would emerge very quickly within the first few minutes that participants hold the tool in their hands. Moreover, the effect is maintained stable as long as the tool is kept in the hand. This result is in line with the work of Miller and colleagues (2019a, 2019b), in which it has been shown that the hand-held tool would be treated as sensory body extension: when participants located stimuli on the tool, they used the same neural processes involved in localizing tactile stimuli on the body. Thus, sensing with the tool would be sufficient to integrate the tool into the somatosensory system without motor training (Fabio et al., 2022). Indeed, in Fabio et al. (2022) participants simply held and sensed the tool to localize tactile stimuli on the tool's surface properly. In contrast to Miller et al. (2018), we applied the touches directly to the body surface to detect changes in Body Schema. It is possible that tool-dependent sensory remapping described in Miller (2018, 2019a, 2019b) may, in turn, cause an embodiment of the tool into the Body Schema, also updating body representation. However, we did not test this hypothesis directly, and future studies are necessary to further investigate the relationship between tool sensory remapping and tool embodiment in the Body Schema.

It is important to note that we are not claiming that actions do not play a key role in modulating Body Schema, as previous studies have shown (Bassolino et al., 2015; D'Angelo et al., 2018; Romano et al., 2019). Holding a tool can immediately update our action potentials in space. Thus, the sensory system and Body Schema would update to achieve better control of possible body movements with the tool and its sensory consequences. This idea is supported by the fact that we found the same effect of the extension of the body length always in the distal segment both in the online (i.e., during the holding of the tool) and offline (i.e., after active tool training) task, suggesting the presence of common mechanisms. Therefore, the difference we found between short and long tools would be related to the fact that only the long tool can really extend the possibility to act in space. Thus, Body Schema plasticity could emerge from the potentiality of the tool to extend one's own capabilities, driven by the possible actions allowed by the tool features. This interpretation is in line with previous work that showed modulation of Reaching Space and Body Schema even after participants had only imagined acting with the tool, without any movements (Baccarini et al., 2014; Davoli et al., 2012; Witt & Proffitt, 2008).

A key aspect of this study is that the tool incorporation effect emerges only in the distal part of the arm. Indeed, in both the online and the tool-use training paradigm, the distal segment (i.e., the distance between the tip of the thumb and the point near the wrist) is modified as a consequence of tool embodiment. Crucially, as shown in Experiment 2, the two tactile locations are perceived farther apart both while holding the long tool and following active tool training. At the same time, the perception of the length of the proximal segment (i.e., the distance from the point near the wrist to the one near the elbow) does not seem to be affected (Experiment 1 and 2), probably because this part of the arm would be less implicated in the tool holding. Indeed, during tool-wielding, the hand and the most distal part of the arm (i.e., wrist joint) would be the most involved body parts in supporting the tool's weight. Thus, in line with previous work, the effect on the distal segment could be mainly due to the structural and functional features of the tool to control it with a specific motor pattern (Cardinali et al., 2016; Miller et al., 2014; Romano et al., 2019).

At last, previous studies have used the hand-holding of the tool as a control condition compared to active tool-use, claiming the presence of an effect only after active training (Iriki et al., 1996; Miller et al., 2017). However, in these studies, the effect was always studied offline, i.e., after active training or simple holding in the hand. In contrast, we verified the effect during the wielding of the tool. Thus, the effect while holding the tool may emerge primarily online during the actual presence of the tool in hand. However, it remains to be determined whether and how long the online effect might persist once the tool is removed from the hand. This additional aspect could further clarify the role of the action in the tool embodiment effect by directly comparing the "offline" effects both after the tool-holding and those following active tool-use training.

In conclusion, these findings suggest that simply holding a tool is sufficient to elicit change in the morphological representation of the body. Thus, active movement with a tool would not be crucial for tool embodiment. Here, we provide the first evidence of the online tool embodiment effect on Body Schema, but further works are necessary to deepen and clarify the specificity of this effect.

Chapter 4.

Study 3:

The influence of arm posture on the Uznadze haptic aftereffect*

**This work has been submitted to the Journal of Experimental Psychology: Human Perception and Performance in collaboration with Olga Daneyko, Angelo Maravita, and Daniele Zavagno.*

Study 3: The influence of arm posture on the Uznadze haptic aftereffect

The studies presented in the previous chapters confirmed the importance of integrating incoming information in building and shaping the body representation. Not only that: Study 1 also explicitly emphasized the bidirectionality of the relation between body and senses, showing that the way body is perceived influences the perception of surrounding stimuli and objects. Accordingly, Study 3 considers how changes in one's body posture during haptic object size processing can influence the final percept. The results reveal that crossing the arms affects the haptic processing of the object, increasing the size-contrast adaptation aftereffect.

4.1 Introduction

Haptic feedback is critical to properly interact with objects: by grasping an object we acquire information about its three-dimensional structure such as its shape, size and texture. A coherent representation of an object is created by combining different kinds of somatosensory sensations and information (i.e., input from receptors in the skin are integrated with proprioceptive afferent signals) (Berryman et al., 2006; Van Doorn et al., 2010; Yau et al., 2016). Like most perceptual experiences, haptic perception is also susceptible to perceptual adaptation. Adaptation aftereffects refer to perceptual changes due to prolonged exposure to a previous stimulus (Webster, 2011). Crucially, a repeated and prolonged exposure to a stimulus distorted in size (i.e., adaptation stimulus) leads to perceive the dimension of the subsequent medium-sized stimulus (i.e., test stimuli) distorted in the opposite direction to the size of the adaptation stimulus (i.e., the size-contrast aftereffect). An established paradigm to study the size-contrast aftereffect is the Uznadze Illusion. During this illusion, after simultaneous and prolonged exposure to two objects different in size, two new objects of the same size are perceived as different. Indeed, the test stimulus after the larger adapter is perceived as smaller, and the test after the smaller adapter is perceived as bigger (Uznadze, 1930, 1966). Thus, the difference between the two test stimuli is reinforced due to this double stimulation (Homskaya et al., 1995). All experiments previously conducted on the Uznadze haptic aftereffect focused on measuring the direction and sometimes also the magnitude of the illusion without manipulating arms positions, that is with uncrossed arms (Daneyko et al., 2020; Kappers & Bergmann Tiest, 2014; Uznadze, 1966). As presented in section 1.3.2, the postural manipulation of crossing arms allows to induce a strong conflict between somatotopic and external reference frames, and it implies a re-weighting of tactile and proprioceptive signals

(Eimer et al., 2003; Holmes et al., 2006; Matsumoto et al., 2004; Yamamoto & Kitazawa, 2001). For instance, not only the accuracy of judging the temporal order of touches on the two hands decreases when the arms are crossed (Yamamoto & Kitazawa, 2001), but this posture seems to also reduce the perceived intensity of nociceptive stimuli (Sambo et al., 2013).

Relatively recent studies that explore the relationship between body and tactile processing (Longo et al., 2010; Medina & Coslett, 2010) suggest two similar models based on three types of body representation that are crucial for interactions between the tactile representation, the body, external space, and action (see section 1.1.1). The first representation is related to the skin surface that links to somatotopic coordinates (i.e., "primary somatosensory representations" or "superficial schema"); the second is concerned with body size and shape representation (i.e., "body form representation" or "body model"); the third is a dynamic representation of the position of the body in space (i.e., "postural representations of the body" or "postural schema"). According to Medina & Coslett (2010), the processing of the position of tactile stimuli relies on the somatotopic representation related to the stimulus position on the skin. Subsequently, the processing moves further to a high-order representation where the tactile information is combined with the information about the hand's position in external space. With respect to the Uznadze haptic illusion, this hypothesis suggests that crossed arms might create a conflict between the somatotopic and the high-level representations that should result in different perceptual experiences with respect to the situation when the arms are kept uncrossed, i.e., parallel in front of the body (Shore et al., 2002). However, the role of body posture on haptic processing has been less investigated, although proprioception information is fundamental in haptic perception and seems to influence object processing (see section 1.3.2). For instance, during the Aristotle illusion, when a small sphere is touched with crossed fingers it is perceived as being two objects rather than only one (Benedetti, 1985), probably because the sensations that derive from the touched object are elaborated as if the fingers were in the usual uncrossed posture.

The aim of the present study is to investigate the role of arm posture (i.e., proprioceptive cues regarding the position of the arms in space) in the occurrence of the Uznadze haptic aftereffect. Specifically, we aimed to verify whether Uznadze's classic haptic aftereffect is the "product" of a relatively earlier (i.e., somatosensory processing based on somatotopic coordinates) rather than later (i.e., egocentric coding of hand position in external space) stage of information processing. To this purpose, two experiments are described in which the direction and the magnitude of the illusion were measured by employing the "See what you feel" method (SWYF; Daneyko et al., 2020). This method makes use of an actual 3D scale visually presented to participants whose task is to find on it the objects that match in size those they are clenching out of sight. The two experiments are similar except for the position of the arms, which were either uncrossed (standard posture) or crossed throughout Experiment 1, or which switched continuously from uncrossed to crossed during the adaptation phase in Experiment 2. A modulation of the magnitude of the haptic size aftereffect due to different arms positions (or even a modification of the direction of the illusion) would suggest that the aftereffect critically relies on the representation of hands in egocentric external space and not only on somatotopic mapping of somatosensory stimuli. A lack of significant differences in the occurrence of the illusion with respect to arms positions would instead support the hypothesis that the aftereffect is driven by an early stage of processing, mainly relying on somatotopic representations. In both cases, we would be able to provide further understanding of the construction of haptic experiences through bimanual processing and the role of egocentric spatial location of significant body parts.

4.2 Experiment 1

In Experiment 1, we investigated whether inducing the illusion with arms crossed would modulate the haptic aftereffect compared to the standard uncrossed position. If the proprioceptive information relative to the crossed arm posture influences the haptic illusion, we expect to find a difference in the magnitude of the haptic effect between the two types of arm postures. This result would mean that higher-order representations of body and space may also affect the haptic aftereffect. Alternatively, if the strength of the effect is independent of the arms localization in external space, then we should not find a difference in the illusion’s magnitude, thus suggesting that the haptic illusion would basically result from low-level somatosensory processing.

4.2.1 Methods

Participants

Participants were 40 Italian healthy volunteers (30 females, mean age = 23), enrolled from the University of Milano-Bicocca and were compensated with course credits. Participants were randomly assigned to one of two groups, which were differentiated for how arms were positioned throughout the experiment (uncrossed or crossed). All participants were right-handed, as assessed by the Edinburgh Inventory (Oldfield, 1971) before the start of the experiment. None of the participants were familiar with the Uznadze haptic size aftereffect and were unaware of the experiment's purpose. Before taking part in the study, the experimental protocol was explained in detail and all participants gave written informed consent to participation. The experiment was approved by the Ethics Committee of the Department of Psychology of the University of Milano-Bicocca and conducted in accordance with the Declaration of Helsinki (World Medical Organization, 1996). A power analysis was performed for sample size estimation using the software G*Power 3.1 (Faul et al., 2007), with a medium effect size of 0.25 and a power level of 0.85. The analysis indicated the necessary sample size of 38 participants.

Materials

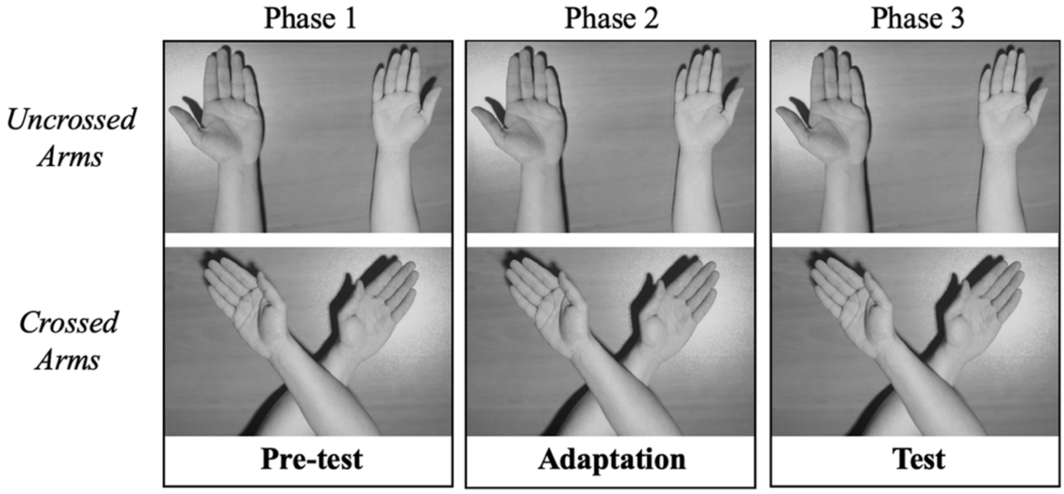
To assess the Uznadze haptic illusion, we employed a crossmodal matching method dubbed 'See what you feel' (SWYF): the method entails that participants are to find the best match of the spheres they are clenching out of sight on a visual scale made of actual spheres that differ from each other in diameter (for a detailed description, see Daneyko et al., 2020). The visual scale consisted of 12 spheres mounted on a wooden base (80 cm in length) at regular spatial intervals. The spheres were organized in growing size order from left to right (diameter from 2.2 cm to 4.7 cm) and each sphere was denoted below by a letter (from N to A). The test stimulus (TS) corresponded to sphere E on the visual scale (3.9 cm in diameter); the small adapting stimulus (AS) corresponded to sphere I on the scale (2.9 cm); the big AS corresponded to sphere C on the scale (4.3 cm).

Experimental Design and Procedure

Participants were randomly assigned to two groups: one group performed all phases with crossed arms, the other with uncrossed arms (Figure 4.1). For all participants, the illusion was induced for the two hands simultaneously. Moreover, the hand with which a participant was asked to start all matching tasks and the position of the small adapting sphere were pseudo-randomized across participants. In line with a previous study (Daneyko et al., 2020), the experiment consisted of three phases: a Pre-Test (Phase 1), an Adaptation (Phase 2) and a Test Phase (Phase 3) (Figure 4.1). Participants sat in front of a table and with palms facing upward placed their arms under the tabletop in an empty compartment open on both sides. In this way, hands were out of sight during the experiment. The visual scale was placed on the table at a distance of 30 cm from the participant’s torso, at a comfortable height that allowed for a top and frontal view. In Phase 1, participants were requested to indicate on the visual scale placed in front of them which sphere matched in size the one they were grasping: a test sphere was therefore placed in one of the hands, and the participant sought for its match on the visual scale. Pre-Test matching was carried out two times for TS and for both AS, switching from one hand to the other after matches for the three spheres were made (but always starting with TS). In Phase 2, an adapting sphere was placed in each of the participant's palms. Participants were asked to clench their hands tightly and then to open them again; the spheres were thus removed and immediately re-positioned in the participant's palms, who had to clench again. This sequence was repeated 15 times, with the small and big adapting spheres always placed respectively in the same hand. On the 16th episode, the two AS were substituted by the two TS without any warning (i.e., Phase 3). Participants were thus requested to find on the visual scale a match for the size of each TS they were clenching in their hands. The hand with which Phase 3 started was counterbalanced across all participants. The total duration of the experimental session was approximately 30 minutes.

Figure 4.1

Experimental procedure for Experiment 1.



Note. Based on the group they were assigned to (uncrossed arms vs. crossed arms), participants maintained the same arm posture during all phases of the experiment.

4.2.2 Data Analysis and Results

To measure the effect of adaptation on the test spheres (Phase 3), we subtracted Pre-Test from Test estimations, deriving the value ΔT (ΔT = Test minus Pre-Test). ΔT is a measure of the visually perceived distance between Test (i.e., perceptual evaluation of the size of TS after adaptation) and Pre-Test (i.e., perceptual evaluation of TS before adaptation) estimations. For each participant, there were two ΔT values, one corresponding to the size impression after adaptation to the small sphere (ΔT_{small}) and the other corresponding to the size impression after adaptation to the big sphere (ΔT_{big}). Data were inspected for outliers: points that were outside ± 2.5 SD from the participants' mean were discarded, considering the ΔT means for each type of adaptation and arm posture. Thus, two participants were removed from the sample. We tested for normality distribution, examining skewness and kurtosis and using the Shapiro–Wilk test. The variables' distributions were essentially symmetric and ascribable to a normal distribution, as shown by a normal range of skewness and kurtosis (all values $< |1|$, except for ΔT_{small} Crossed group kurtosis = -1.29). While according to the Shapiro-Wilk test, only the left-hand Pre-Test data and ΔT_{big} for the Uncrossed group were not normally distributed ($p < .05$). Thus, we decided to use parametric tests, also considering the general robustness of parametric tests to normality violations (Knief & Forstmeier, 2021).

First, to verify the presence of any difference in the Pre-Test estimations (Phase 1), we compared the actual size of the TS (3.9 cm) and its visually evaluated size using One Sample t-tests for each hand. The analysis showed significant differences for both hands (Left Hand: $t(37) = -5.90$, $p < .001$, Cohen's $d = -.96$; Right Hand: $t(37) = -6.77$, $p < .001$, Cohen's $d = -1.10$). Mean matching values are significantly underestimated compared to the actual size (Left Hand: $M = 3.60$ cm; $SE = 0.05$ cm; Right Hand: $M = 3.60$ cm; $SE = 0.04$cm). Moreover, a Paired Sample t-test did not show significant differences between the two arm postures in the visually estimations during Phase 1 ($p > .9$). Finally, an Independent t-test conducted to compare the size estimations between the two hands showed no statistical difference ($p > .8$). All results are in line with those reported by Daneyko et al. (2020).

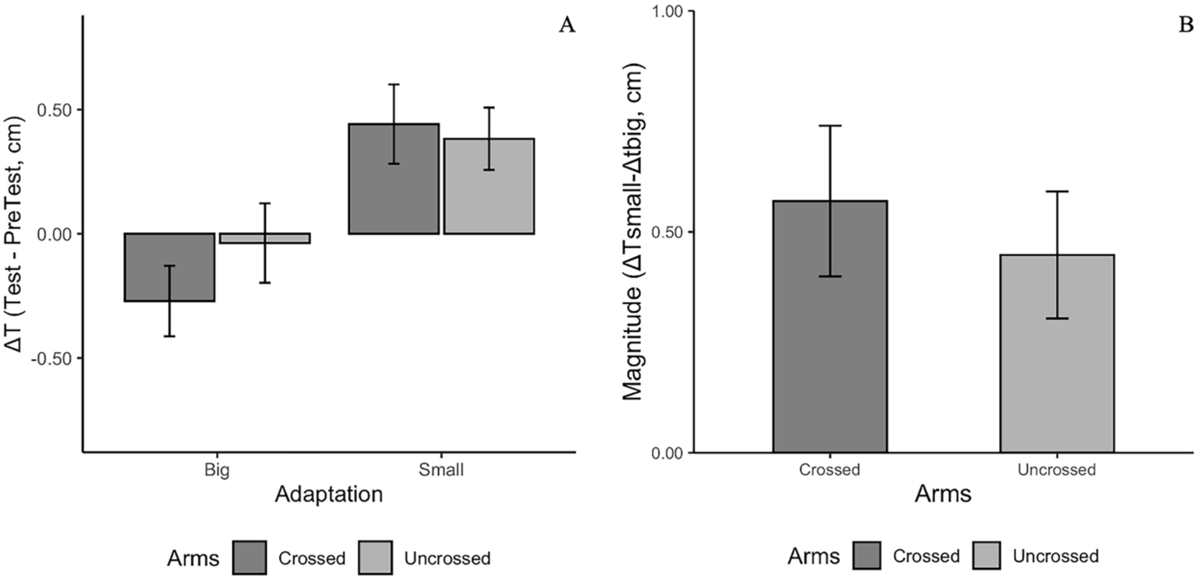
Then, an ANOVA for repeated measures was carried out on the new variable ΔT data with adaptation (AS_{small}, AS_{big}) as the within subject variable, and arms (crossed, uncrossed) as between subjects variable. Adaptation determined a significant main effect: $F(1, 36) = 90.47$, $p < .001$, $\eta^2_p = .71$, Cohen's $d = 1.83$. The effect of arms was not significant ($p > .2$); instead, the interaction adaptation×arms produced a significant effect: $F(1, 36) = 6.04$, $p < .05$, $\eta^2_p = .14$, Cohen's $d = 0.35$. Regardless of arm posture, TS was perceived bigger after adaptation to AS_{small} ($M = 0.41$ cm, $SE = 0.05$ cm, CI: .31, .51) and smaller after adaptation to AS_{big} ($M = -0.15$ cm, $SE = 0.05$ cm, CI: -.26, -.05) . However, arm posture affected the evaluations of TS differently in relation to the different adaptation spheres: adaptation to AS_{big} with arms crossed leads to a stronger effect, while the difference in size estimation for

TS with arms crossed or uncrossed is only mildly affected by arm posture after adaptation to AS_{small} (Figure 4.2A).

The aforementioned differences should also lead to a difference in the overall magnitude of the illusion, expressed for each participant as the absolute difference between ΔT_{small} and ΔT_{big} (Magnitude). On such data an Independent t-test was conducted with arms as between factor. A significant main effect on the overall size of the illusion emerged: $t(36) = 2.34$, $p < .005$, Cohen's $d = 0.76$. Figure 4.2B shows that the perceived difference between the two TS was greater with arms crossed ($M = 0.71$ cm, $SE = 0.09$ cm) than with arms uncrossed ($M = 0.45$ cm, $SE = 0.07$ cm). Analyses were performed using Jamovi (Version 1.6.23.0) and R software (R Core Team 2016).

Figure 4.2

Results of Experiment 1



Note. *A.* Size of the Uznadze illusion express as ΔT (Test-PreTest, cm) distinguished by adaptation (Big, Small) and arm posture. Positive values indicate size overestimation, negative values size underestimation. *B.* Size of the illusion calculated as the absolute difference between ΔT_{small} and ΔT_{big}, (Magnitude, cm) distinguished by arm posture. Error bars indicate Confidence Intervals (CIs) set at 95% level.

4.2.3 Discussion

During the visual evaluation of the test spheres before adaptation (Phase 1), we found a general underestimation of the visual size of the stimuli compared to their actual dimension. This visual estimation bias was also reported in an earlier study that made use of the same crossmodal method to assess the magnitude of the illusion (Daneyko et al., 2020). Crucially, with reference to Phase 3, in both groups of participants, the direction of the aftereffect illusion was not affected by arm posture: the test sphere appeared always bigger in the hand previously adapted to a small sphere and smaller in the hand adapted to a big sphere (Daneyko et al., 2020; Kappers & Bergmann Tiest, 2014; Uznadze, 1966). These results suggest a main role of somatotopic rather than spatial egocentric mapping of hands, in determining the adaptation aftereffect. However, we even found that the magnitude of the illusion is enhanced by maintaining the arms crossed throughout the entire experiment; this hints at the possibility that proprioceptive information (i.e., high-level factor) may also play a role.

A discussion of these findings would be too speculative at this stage, but we can hypothesize that sensorimotor control of bimanual grasping in the opposite hemispace may require more effortful control during the task as the crossed arms position is an uncommon posture for grasping and object manipulation. Overall, it could be hypothesized that two concurrent factors determine the *fixed-set* that, according to Uznadze (1996), would induce the adaptation aftereffect. On one side, the somatotopic coding, which is anatomically determined and, therefore, unchangeable. On the other hand, there is the spatial mapping of the hand which depends on the current position of the hands in the extrapersonal space. When both are kept constant during the adaptation phase, the aftereffect occurs regardless of whether they spatially coincide (uncrossed hands) or not (crossed hands). In Experiment 2, this hypothesis is tested by systematically interfering with the spatial location of the hands in external space (i.e., with the spatial component of the *fixed-set*) by crossing and uncrossing hands on each trial during adaptation.

4.3 Experiment 2

In Experiment 2, a mixed adaptation procedure was used in which participants repeatedly switched arms position from crossed to uncrossed and vice versa. Once the adaptation phase was completed, participants judged the size of the test sphere in the crossed or uncrossed posture, depending on their group settings. We hypothesized that such manipulation during the adaptation phase might disrupt the stability between the spatial and the somatotopic component of the fixed-set during adaptation, thus affecting the overall magnitude of the aftereffect.

4.3.1 Methods

Participants

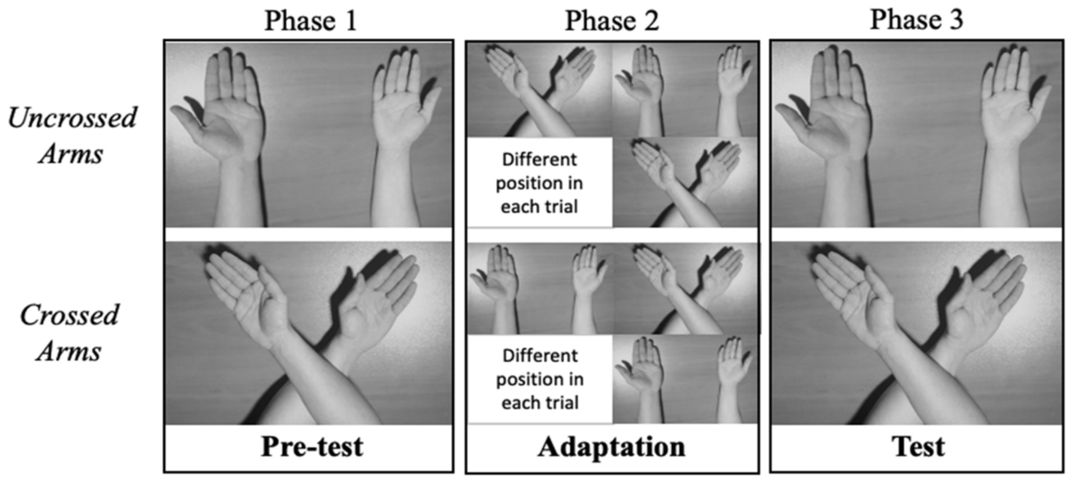
Participants included in Experiment 2 were 40 Italian healthy volunteers (28 females, mean age= 23), enrolled from University of Milano-Bicocca and compensated with course credits. As in the previous experiment, participants were tested to be right-handed and performed the same protocol.

Materials, Experimental Design and Procedure

Experimental stimuli and procedures were the same as in Experiment 1, except for the following main difference: the position of the arms varied continuously during adaptation, from crossed to uncrossed and vice versa (see Figure 4.3). For instance, in the uncrossed arms group, participants carried out Pre-Test and Test matching with uncrossed arms (i.e., Phases 1 and 3), they however started the adaptation sequence (i.e., Phase 2) with crossed arms and switched back and forth from crossed to uncrossed during the 15 steps adaptation sequence, ending the sequence with crossed arms to then carry out test matching (i.e., Phase 3) with uncrossed arms (Figure 4.3, top row). The other group of participants conducted the experiment in the exact opposite way.

Figure 4.3.

Procedure of Experiment 2.



Note. During adaptation (i.e., Phase 2), arm posture changed continuously from crossed to uncrossed and vice versa. The position of the arms during Pre-Test (i.e., Phase 1) and test matching (i.e., Phase 3) were instead kept constant.

4.3.2 Data Analysis and Results

As in Experiment 1, the dependent variables ΔT_{small} and ΔT_{big} were calculated and inspected for outliers: three participants were discarded from the analysis (N = 37). Data were essentially normally distributed as assessed by the Shapiro-Wilk test (all $p > .05$) and the normal range of skewness and kurtosis (all values < |1|, except for the kurtosis of ΔT_{small} Crossed group = 1.82 and ΔT_{big} Uncrossed group = 1.38).

Thus, we first considered the TS Pre-Test matching values (Phase 1). One Sample t-tests conducted for the two hands separately revealed a significant difference between the actual size of the TS (3.9 cm) and its visually evaluated size (Left Hand: $t(36) = -6.89$, $p < .001$, Cohen's $d = -1.13$; Right Hand: $t(36) = -5.09$, $p < .001$, Cohen's $d = -0.837$). As in Experiment 1, mean matching values are significantly underestimated compared to the actual size (Left Hand: $M = 3.55$ cm, $SE = .05$ cm; Right Hand: $M = 3.61$ cm, $SE = .06$ cm). An Independent t-test was conducted on TS's Pre-Test values for each hand, comparing the two arms (crossed, uncrossed), but no significant difference emerged ($p > .7$). Finally, we also compared the Pre-Test matching values between the two hands using a Paired Sample t-test: results confirmed that means are statistically undistinguishable ($p > .1$).

An ANOVA for repeated measures was conducted with adaptation (AS_{small}, AS_{big}) as within subjects variable, and test matching arms (crossed, uncrossed) as between subject variable. Only adaptation determined a significant main effect: $F(1, 35) = 75.54$, $p < .001$, $\eta^2_p = .68$, Cohen's $d = 1.92$. As in Experiment 1, TS is perceived bigger ($M = .27$ cm, $SE = .05$ cm, CI: 0.16, 0.37) in the hand adapted to AS_{small} and smaller in the hand adapted to AS_{big} ($M = -.38$ cm, $SE = 0.06$ cm, CI: -0.51; -0.25), regardless of arm posture during test matching. Factor arms and its interaction with adaptation did not determine significant effects ($p > .9$).

As for Experiment 1, we calculated the absolute difference between ΔT_{small} and ΔT_{big} (Magnitude) for each participant to test the overall size of the illusion. We performed an Independent t-test on such data with arms during test matching as between variable: mean magnitudes are not statistically distinguishable ($t(35) = -0.02$, $p =.985$, Cohen's $d = 0.006$). To test the absence of a difference in the effect between the two arm postures, we also performed a Bayesian Independent t-test. The Bayesian analysis showed a Bayes factor (BF_{01}) of 3.134 ± 0.004% in favor of the null hypothesis of no differences in the aftereffect magnitude between the crossed and uncrossed postures. This analysis indicates that the null hypothesis is 3.134 times moderately better at explaining the data than the alternative hypothesis of a difference between the two arm postures.

4.3.3 Discussion

Results for Pre-Test matching show an underestimation of the spheres size prior to adaptation, which is in line with results from Experiment 1 and those reported by Daneyko et al. (2020). Given the consistency of such finding, the visual size underestimation of a haptic sensation appears to be a general feature of the SWYF method (Daneyko, Maravita, & Zavagno, in preparation). The mixed adaptation, in which arms position changed back and forth from crossed to uncrossed, did not affect the outcome of the illusion; nor was this affected by test matching arm posture. This result allows us to speculate that the instability of the spatial component of the *fixed-set* is efficiently compensated by the fast recoding of sensory representation of the body in egocentric space (Lloyd et al., 2003), thus, not affecting the illusion.

4.4 General Discussion

In this study, we aimed to investigate whether proprioceptive information about the position of one's hands in space could modulate the Uznadze haptic aftereffect. To this purpose, we conducted an experiment in which Pre-Test matching, adaptation, and Test matching were always carried out either with arms uncrossed (i.e., parallel) or crossed (Experiment 1). Results from this experiment showed that the direction of the illusion was not affected by arm posture, with a TS clenched in the hand adapted to a small AS haptically perceived as bigger than a TS clenched in the hand adapted to a big AS. However, we found an effect of arms posture on the magnitude of the illusion, which resulted statistically bigger for crossed arms. It has been shown that crossing arms induces a conflict between the somatotopic and body-centered frames of reference (Shore et al., 2002; Yamamoto & Kitazawa, 2001). Consequently, a re-mapping of coordinates is necessary to process and compare the objects' features properly. We thus hypothesize that the sensorimotor control of bimanual grasping in the opposite hemispace would require more effortful control, which may enhance the adaptation and/or size-matching processes underlying the illusion.

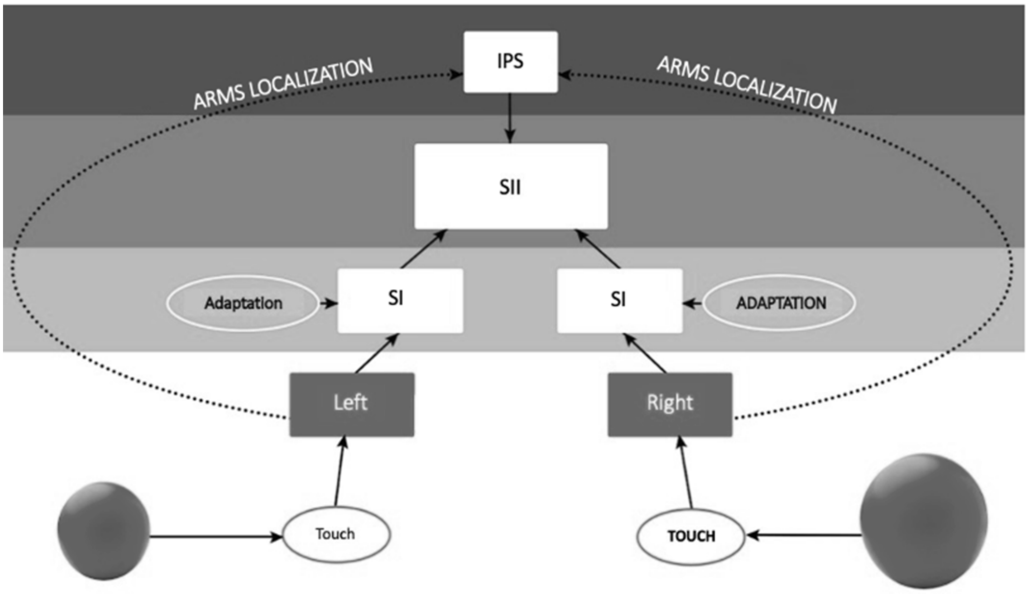
Is the stability of different aspects of the set-fixing condition, somatotopic or spatial mapping of hands in external egocentric space, critical for the aftereffect? Experiment 2 was designed to answer such question by employing mixed arm postures during the adaptation phase. One group of participants carried out Pre-Test and Test matching with uncrossed arms, the other with crossed arms. Crucially, both groups were requested to continuously switch their arm posture between the crossed to the uncrossed arms position throughout the adaptation phase. Such manipulations did not affect the direction nor the magnitude of the illusion. Therefore, even interfering with the stability of the spatial component, the aftereffect still occurs. This result indicates that, in the adaptation phase, the brain can quickly recode the location of arms in space, thus relying on the critical somatotopic coding to match the bimanual stimulation. Moreover, such results allow to speculate about the role played by arm posture. In our view, the continuous change of the arm posture can reduce the effect of adaptation with arms crossed found in Experiment 1, thus reducing the difference in the strength of the effect between the two groups. Thus, the adaptation with the crossed arms would have an impact on the magnitude of the illusion only if the stability of the spatial component during adaptation is preserved. The findings of this experiment also suggest that posture during the Test Phase has a minor effect on the magnitude of the illusion. In other words, it is possible that test size estimations would be driven mainly by the characteristics and size of the stimuli manipulated in the hands during adaptation and not by the posture of the arms during the testing phase.

Given the results that emerged from the two experiments, we hypothesized that the illusion is mainly related to low-level somatosensory processing linked to somatotopical representations of the skin surface ("primary somatosensory representations" or "superficial schema"). Indeed, the brain would be able to quickly remap the position of the hand in space, suggesting the main role of somatosensory inputs and the characteristics of the manipulated stimuli in the occurrence of the illusion, as shown also by Kappers and Bergmann Tiest (2014). However, also the representation of the location of the body in the external space ("postural representations of the body" or "postural schema") seems to subsequently modulate the effect. It is possible that size coding with crossed arms would require additional cognitive processing, thus, increasing the haptic aftereffect. These findings appear in line with several works that showed how hand laterality and hand position in external egocentric space could alter tactile processing (Eimer et al., 2003; Holmes et al., 2006; Kennett et al., 2001; Matsumoto et al., 2004; Yamamoto & Kitazawa, 2001). It seems that both somatotopic and postural representations could be involved in processing passive and active touch (Medina & Coslett, 2010).

Following the overall results of the present work, we hypothesized a General Model of Induction (Figure 4.4) to explain the possible neural mechanisms underlying the Uznadze aftereffect. The neural coding of the stimulus depends on the sensitivity of the cortical neurons to specific stimulus properties. In particular, the haptic perception of objects involves the integration of different information derived from cutaneous mechanoreceptors, proprioceptive and kinesthetic receptors located in muscles, tendons, and joints to extract information about the objects' surface, shape, temperature, and weight. Then, the information is somatotopically transmitted to the primary somatosensory cortex (SI), secondary somatosensory cortex (SII) necessary for haptic integration and intraparietal sulcus (IPS), integrating the position of limbs in external space. In the Test Phase, when participants grasped two identical spheres, they felt the two spheres different in size: the test sphere appears larger to the hand subject to less adaptation (i.e., small adapting sphere), while it seems smaller to the hand with greater adaptation (i.e., big adapting sphere). This process calls for a critical integration of bimanual information in the cortex. The comparison between the sensory information coming from each hand likely starts in SI, where some neurons holding bimanual receptive fields are found (Iwamura et al., 1994). Such comparison continues in SII, which receives information processed by SI of both sides of the brain and holds neurons with larger and bilateral receptive fields (Disbrow et al., 2003; Friedman et al., 1980; Iwamura, 2000; Pons et al., 1987). This area is not only related to sensory processing, but it also seems involved in multimodal integration and object manipulation and recognition (Binkofski et al., 1999; Fitzgerald et al., 2004). The crucial role of SII would be to compare sensory information from each hand (i.e., processed in SI) and the information relating to the arms location in space (i.e., processed in IPS). Ishida and colleagues (2013) showed the role of SII in processing active touch: they found a population of neurons in SII that are selectively activated during active manipulation of objects, compared to passive touch in the absence of voluntary movement. The posterior parietal cortex (IPS) then plays a crucial role in monitoring tactile afference in reference to the external egocentric space (Bolognini & Maravita, 2007). The posterior parietal cortex (IPS) then plays a crucial role in monitoring tactile afference in reference to the external egocentric space (Bolognini & Maravita, 2007). Thus, since the illusion aftereffect occurs with both postures and even when interfering with the spatial component of the fixed-set of the illusion during adaptation, our results support the role of a similar mechanism, possibly located in SI/SII, in generating the aftereffect. Nevertheless, the influence of body posture on the magnitude of the haptic perception would involve a processing that extends to the IPS for the ongoing remapping of body parts in space. However, further investigations are required to verify the causal role of different brain areas in the occurrence of the illusion and the modulation of its magnitude, as anatomical data were not collected in the present work.

Figure 4.4

General Model of Induction.



Note. In the adaptation phase, two spheres of different sizes are grasped simultaneously with the two hands. Due to the different dimensions of the AS, each hand is subject to a different amount of adaptation. Sensory information coming from the hands is transmitted somatotopically to SI (responsible for the haptic processing) and IPS (responsible for coding the arms position in space). Finally, SII works as a comparator between the sensory information coming from SI and arms position information from IPS.

In conclusion, we investigated the role of arm posture (i.e., proprioceptive cues regarding the position of the arms in space) on haptic perception by using the established Uznadze haptic aftereffect. The present work allows to confirm and extend evidence on the illusion, showing that the aftereffect occurs both when a person maintains stably arms crossed or when the stability between the spatial and somatotopic components is compromised during the adaptation phase. Thus, somatotopic mapping would be the crucial component in the occurrence of the illusion. Moreover, the present study suggests that the position of the arms in space also affects the magnitude of the illusion if the crossed posture is maintained stably during the adaptation. Therefore, the effect seems to be determined primarily by low-level somatotopic mapping (i.e., size of the manipulated stimuli); yet also high-level factors (i.e., proprioceptive information regarding the arms position in space) could modulate the haptic perception.

Chapter 5.

Study 4:

Bodily stimuli increase size-contrast aftereffect*

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*This work has been conducted in collaboration with Daniele Zavagno and Angelo Maravita
The relative paper is now in preparation.

Study 4: Bodily stimuli increase size-contrast aftereffect

Study 3 considered the influence of body representation in haptic processing, supporting the role of the body as a reference in perceiving the external environment. Accordingly, also Study 4 examines the importance of the body in perception but in the visual domain. Specifically, the present study aims to investigate how visual body stimuli are differently susceptible to size adaptation. In contrast to the works described in the previous chapters in which manipulations of one's own body representation were discussed, Study 4 considers the representation of the body in general and how this representation can influence visual stimuli processing. Results reveal that visual perception of body stimuli is more susceptible to size adaptation.

5.1 Introduction

As in the previous chapter, the Uznadze Illusion (Uznadze, 1930;1966) is considered but in the visual domain. Indeed, the Uznadze aftereffect seems to be consistent across different sensory modalities, e.g., tactile (Maravita, 1997) and visual (Bruno et al., 2018). However, previous studies induced the illusion only with geometrical 3D shapes such as cubes, spheres, and tetrahedra without comparing the strength of the adaptation effect across stimuli (Kappers & Bergmann Tiest, 2014; Bruno et al., 2018). In fact, it is still unclear if different kinds of stimuli are similarly susceptible to this illusion since size perception is particularly important for certain types of stimuli relative to others. Classically, the perception of the object size has been explained by considering the combination of visual clues such as the object's size on the retina, the perceived distance from the observer, and the principle of size constancy (Goldstein & Bruce, 1999; Schwartz, 2010). One stimulus for which size perception is definitely important is the body. Indeed, body size could influence the external world's perception, suggesting a causal link between body representations and the external space (Proffitt & Linkenauger, 2013).

As emerged in section 1.3.2, the size of the body could be considered a fundamental reference to perceive the size and the distances of objects, and it would allow measuring the external environment as a *perceptual ruler* (Poincaré, 1952). Previous studies have shown that the size of objects is processed in relation to the size of the observer's body (van der Hoort et al., 2011; 2016). Size processing is also crucial for elaborating individual body parts, such as the hands. Hands, indeed, are the principal means to communicate and interact with others. Furthermore, hands are extremely crucial for motor planning, interaction with objects, and tactile exploration. The alteration of the visual feedback regarding the hand size seemed to modulate the perception and the interaction with the external environment, influencing motor planning (Marino et al., 2010) and size estimation (Linkenauger et al., 2010). Specifically, the work of Marino and colleagues (2010) revealed how a distorted apparent size of the hand could affect hand-object interactions: by simply observing an enlarged hand, the grasping parameter changed as the movement was performed by a bigger hand. Thus, the body and its parts are special and unique objects of great biological and social valence. For this reason, the human brain is endowed with a specific neural system dedicated to the visual processing of the body and its parts (Peelen & Downing, 2005; Taylor et al., 2007). Moreover, hands have a further cortical specialization: the visual representation of the human hand seemed to elicit stronger responses, specifically in the occipitotemporal areas (Bracci et al., 2010; Bracci et al., 2012; Espírito Santo et al., 2017).

Here, given the importance of size in body perception, we investigate if body stimuli are differently susceptible to size adaptation as compared to abstract shapes. In particular, we hypothesized that the magnitude of the size-contrast aftereffect would change according to the type of stimulus presented. To this aim, we induced the Uznadze illusion, comparing the strength of the effect between stimuli depicting hands and abstract objects resembling hands in their perceptual features, such as color and shape. Thus, if the Uznadze Illusion is influenced by the identity and complexity of the inducing stimulus, we expect to find an increase in the magnitude of the effect in the presence of bodily stimuli compared to non-bodily stimuli.

5.2 Experiment 1

The aim of Experiment 1 is to test whether the identity of the stimulus could modulate the Uznadze Illusion. To date, the illusion has always been induced with simple geometric shapes (Kappers et al., 2013; Bruno et al., 2018), and how the effect can be modulated in the presence of complex stimuli has never been tested. For this purpose, we compared the aftereffect magnitude between bodily stimuli (i.e., hands), which activate a dedicated neural representation in the brain and for which the size processing is crucial to properly interact in the external environment, and abstract stimuli with low-level features similar to hands (i.e., color and shape) and without any adaptive or biological meaning. If the Uznadze effect is mediated by high-level categorical processing, we expect differences in the magnitude of the illusion between the presentation of hands and abstract stimuli.

5.2.1 Methods

Participants

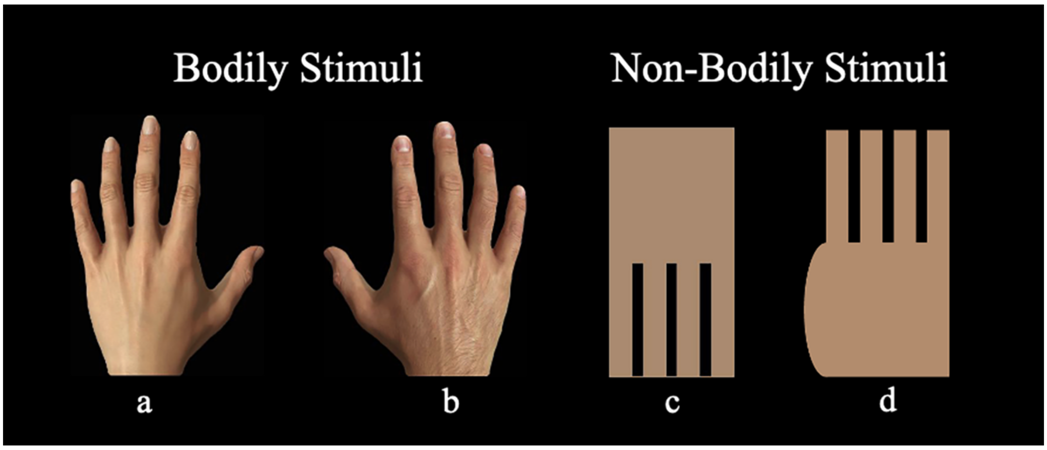
34 healthy volunteers (20 female, M = 21.38, DS = 2.34) took part in the experiment. All participants had normal or corrected-to-normal vision and were right-handed as assessed by the Edinburgh Inventory (Oldfield, 1971). None of the participants were familiar with the Uznadze aftereffect and were unaware of the experiment's purpose. Before taking part in the study, the experimental protocol was explained in detail, and all participants gave written informed consent to participation. The study was approved by the Ethics Committee of the Department of Psychology of the University of Milano- Bicocca and it was in accordance with the Declaration of Helsinki (World Medical Organization, 1996). A power analysis was performed for sample size estimation using the software G*Power 3.1 (Faul et al., 2007), with a medium effect size of 0.25 and a power level of 0.80. The analysis indicated a critical sample size of 34 participants.

Stimuli

Two types of stimuli were presented: Bodily Stimuli (BS, Figures 5.1a and b) and Non-Bodily Stimuli (N-BS, Figure 5.1c). The BS were pictures depicting the left and right hands of males or females. While the N-BS were abstract stimuli created from the hands' picture with Adobe Illustrator (Adobe illustrator 2020 v24.3) and designed to have the same shape and color features as the hands. In particular, the N-BS of Experiment 1 consists of a rectangle with the same width as the dorsum of the hand (i.e., from the beginning of the knuckle of the index finger to that of the little finger). Above this rectangle, four smaller rectangular shapes, recalling the actual fingers, were added, defined in width by the measure of the index finger and in length by the distance from the knuckle to the point of the index finger. Then, this shape was turned 180° to reduce the congruency with the hand's posture. The total height of the figure corresponds to the distance from the base of the hand to the tip of the index finger. Stimuli (BS and N-BS) were distorted in width and length starting from the standard stimulus (100%) to create the adaptation and test stimuli using the Adobe Illustrator software. Each stimulus was distorted by 70% to create the small adaptation stimulus (i.e., 30% reduction of the standard stimulus) and by 130% to create the large adaptation stimulus (i.e., 30% increase over the standard). While, for the test stimuli, the standard stimulus was distorted from 90% to 160%, in steps of 5%, for a total of 15 different levels.

Figure 5.1

Example of stimuli used.



Note. Body Stimuli depicting female (a) and male (b) hands and Non-Bodily stimuli of Experiments 1 and 2 (c) and Experiment 3 (d).

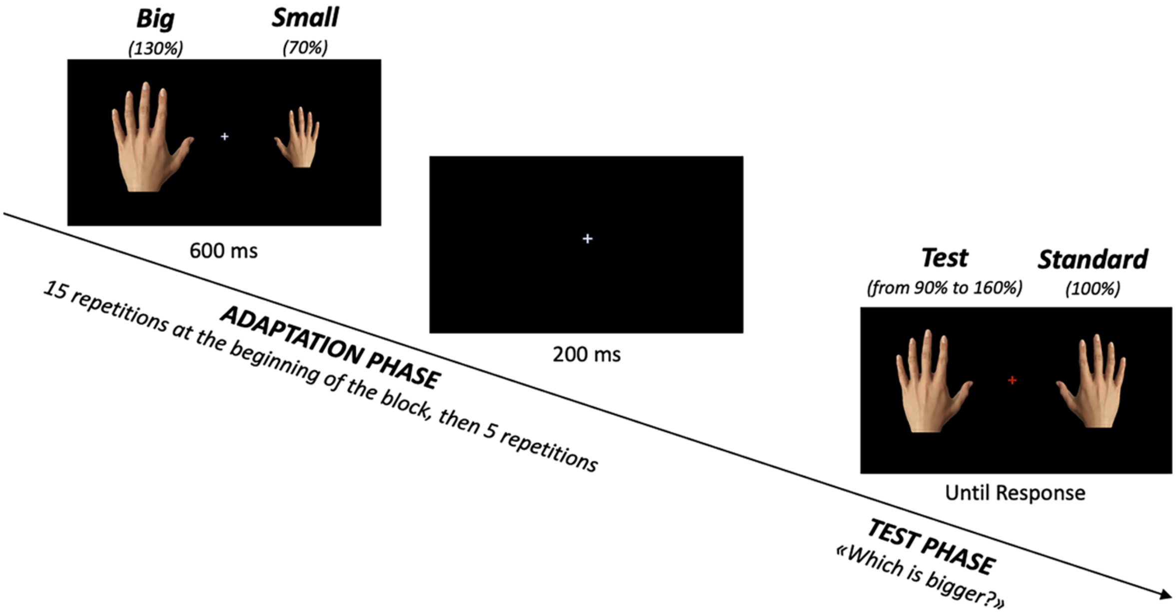
Procedure

Participants were seated at a distance of 57 cm from the screen, and the head position was stabilized using a chin rest. The luminance of the room was maintained constant. The stimuli were presented using the software Inquisit 6 (2021) and displayed on an Acer 22’’ monitor (1680 x 1050 resolution). The Uznadze Illusion consists of an adaptation and a test phase (adapted from Bruno et al., 2018; see Figure 5.2). In each trial, during the adaptation phase, a large (130%) and a small stimulus (70%) are repeatedly presented at the side of a central white fixation cross. Each stimulus was placed at 7 cm from the fixation cross. Stimuli were presented for 600 ms and were followed by a blank presented for 200 ms. This sequence was repeated fifteen times in the first trial of each block, while in subsequent trials, it was repeated five times. Participants were asked to observe the stimuli during the adaptation phase, constantly fixating on the central cross. In the test phase, a new set of stimuli is presented to the sides of a red central fixation point: a standard stimulus of a constant dimension (100%) and a test stimulus variable in size among fifteen possible distortion levels. In the test phase, participants were asked to indicate which stimulus seemed bigger while keeping their gaze on the fixation cross. Participants responded as quickly and accurately as possible by pressing the

"V" key with the left index if the bigger stimulus was on the left or the "M" key with the right if the bigger stimulus was on the right. The test stimuli lasted until the participant's response. The position of the large and small inducers was fixed in each block and varied across blocks in a counterbalanced order. The test stimulus was always presented at the same position as the large adapting stimulus. To ensure that participants kept their gaze on the fixation cross, one of ten possible numbers (from 0 to 9) appeared inside the fixation cross in five trials per block. At the end of each block, participants reported if the number "0" had previously appeared during the block.

Figure 5.2.

Experimental Procedure.



Note. Each trial was characterized by an adaptation phase in which a Big (130%) and a Small (70%) stimulus were repeatedly presented and a test phase with a new set of stimuli (the Standard stimulus with a costant size and the Test stimulus with a variable size distortion). The participant's task is to judge which stimulus seems bigger between the standard and the test.

Experimental Design

Participants performed two experimental sessions on different days with a specific type of stimulus (e.g., BS or N-BS), counterbalanced between the participants. Each session was composed of two blocks, differing in the position in which the adaptation stimuli (i.e., large and small stimulus) were presented. In each block, the position of the adaptation stimuli was kept fixed, and a total of 75 trials were presented in a randomized order, defined by the fifteen possible distortion levels of the test stimulus repeated five times.

Analysis

As an index of the magnitude of the illusion, we calculated for each participant and type of Stimulus (BS or N-BS) the point of subjective equality (PSE). PSE represents the subjective point in which participants perceived the standard and the test stimuli as equal in size. This value was extracted from each participant's psychometric functions and computed by plotting the proportion of responses for which the test is larger than the standard. Within a block, the responses "the test stimulus is larger than the standard" were summed for each of the 15 levels of distortion (from 90% to 160%), with a maximum value of 5 and a minimum of 0.
Data points were fitted with a logistic function using the following equation:

$$P = \frac{1}{1 + e^{-\beta(\chi-\alpha)}}$$

in which P is the proportion of responses for which the test stimulus is perceived to be larger than the standard, χ was the level of the distortion of the stimulus, α was the intercept, and β was the slope of the psychometric function. These estimated coefficients were used to calculate the PSE ($-\alpha/\beta$, negative ratio of the two parameters), which is the critical value of the transition at which subjects begin to report more than 50% of the times that the test stimulus is bigger than the standard. Specifically, the PSE indicates how much the test stimulus must be distorted in size to be perceived as the same size as the standard due to the illusion effect. Indeed, in the presence of the illusion, the test stimulus should appear smaller than its actual size due to the adaptation effect to the bigger adapting stimulus. Data in each condition were inspected for outliers, and points that fell outside ± 2.5 standard deviations from the participants' mean were discarded. Thus, three participants were removed from the analysis. The normal distribution of the data was assessed with Shapiro-Wilk Test.

To verify the presence of the illusion, we compared with a One-Sample t-test the PSE with the point of objective equality (POE), i.e., the point at which the standard and the test stimulus were physically equal in size. Therefore, in absence of illusion, the PSE should not significantly differ from the POE. Thus, we compared the computed PSE for each type of stimulus (BS or N-BS) against the null hypothesis PSE=POE=100%. Then, we tested if the illusion was stronger for BS than N-BS. To this aim, we compared the PSE of both stimuli with a Paired Sample t-test. And finally, we performed a mixed ANOVA with Stimulus as with-in factor and Order of Session as between factor (BS First vs. N-BS First) to verify if the order of stimuli presentation could modulate the difference between BS and N-BS. We explored interaction reliably considering 95% Confidence Interval (CI) without further post hoc tests analysis (Cumming, 2014). Statistical analysis was performed using R (Version 1.4.1103, R Core Team, 2013) and Jamovi software (Version 1.6.23.0 the Jamovi project, www.jamovi.org).

5.2.2 Results and Discussion

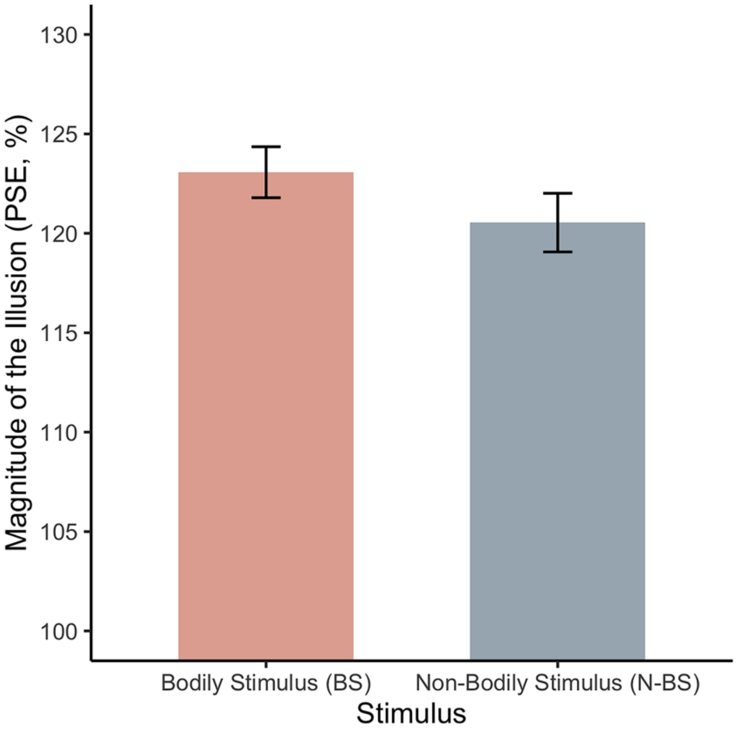
We considered the PSE for each type of Stimulus (N-BS and BS). Since data were normally distributed, One Sample t-test was conducted separately on the data for both BS and N-BS. We found a significant difference between the PSE means of each type of stimulus and the POE (BS: $t(30) = 36.8$, $p < .001$, Cohen's $d = 6.61$; N-BS: $t(30) = 28.4$, $p < .001$, Cohen's $d = 5.11$), demonstrating that the task was effective in inducing a size-contrast effect. This result shows that after a period of adaptation, the perception of the size of the test stimuli is altered in both stimuli such that the test stimulus is perceived as equal to the standard stimulus when its dimension is increased by more than 20% (BS: M = 122.51%, SE = 0.63; N-BS: M = 120.24%, SE = 0.72). Furthermore, PSE in BS was significantly larger than PSE in N-BS ($t(30) = -4.22$, $p < .001$, Cohen's $d = 5.99$), showing that the illusion was stronger for stimuli depicting body parts as compared to abstract shapes (Figure 5.3). At the same time, the order of the session seems not to affect the difference between the two stimuli. Indeed, the Mixed ANOVA confirmed a significant main effect of Stimulus ($F(1,29) = 16.98$, $p < .001$, $\eta^2_p = .37$), but neither the main effect of Order of Sessions nor the interaction Stimulus×Order of Sessions reached the significance ($p > .2$).

The results of Experiment 1 are consistent with the previous works on the Uznadze Illusion, which show that after a period of adaptation, the perception of the size of the two test stimuli is altered: after the small adapting stimulus, the standard stimulus is perceived as bigger, and after the big adapting stimulus the test stimulus is perceived as smaller (Maravita, 1997; Kappers et al., 2014; Bruno et al., 2018). This double stimulation leads to the effect of perceiving the test and standard stimulus as equal in size when the test stimulus has a large size distortion for both bodily and non-bodily stimuli.

Moreover, results show that Bodily Stimuli could influence the effect of the Uznadze Illusion. Indeed, by inducing the effect with stimuli depicting body parts, the aftereffect is stronger than Non-Bodily abstract stimuli, regardless of the order of the sessions. Therefore, considering the importance of body size processing, Bodily Stimuli in the visual field may be specially encoded, thus increasing susceptibility to size adaptation. Indeed, due to a greater social and biological relevance, hands are specifically represented in specialized brain areas (Bracci et al., 2010) and induce an attentional bias (Salvato et al., 2017). Therefore, the greater adaptive valence that the processing of the hand size has compared to a neutral shape could lead to perceiving the Bodily Stimulus as more salient, increasing the effects of size adaptation on the perception of subsequent test stimuli. So, it is possible that the processing of a Bodily Stimulus is more susceptible and adaptable to contextual modifications regarding size perception. These first results would suggest that the effect is not driven only by the stimulus configuration but that the identity of the stimulus and its cognitive features would influence the aftereffect.

Figure 5.3

Results of Experiment 1.



Note. Comparison of mean PSEs (% of distortion) between the two types of stimulus: stronger effect for Bodily Stimuli compared to Non-Bodily Stimuli. Bars indicate Confidence Intervals (CIs) set at 95% level.

5.3 Experiment 2

Experiment 1 showed that Bodily Stimuli are more susceptible to the size-contrast effect than Non-Bodily Stimuli. The aim of Experiment 2 is to investigate further whether this illusion is driven by the distortion of a specific dimension (in width or length). Indeed, systematic bias and anisotropic effects have been reported in the estimation of the size or shape of geometrical figures and objects (Hamburger & Hansen, 2010; Künnapas, 1955; Robinson, 1972) as in the vertical-horizontal illusion in which the vertical line is generally overestimated than a horizontal line of equal length (Oppel, 1855; Fink, 1851). Also, systematic distortions of the hand representation have been found in different previous works (Coelho & Gonzalez, 2018; D'Amour & Harris, 2020; Linkenauger et al., 2015b; Peviani et al., 2019; for a review, see Longo, 2022). Therefore, we wondered if these biases in the size processing of Bodily and Non-Bodily stimuli could modulate the effects of Uznadze. For this reason, in Experiment 2, we specifically investigated the role of each dimension in the illusion by distorting the stimulus in a single dimension (in width or length) and keeping the other dimension constant.

5.3.1 Methods

Participants

26 healthy volunteers (16 females, M = 23.85, SD = 3.46) participated in the experiment. All subjects were unaware of the purpose of the research and gave informed consent to participate in the experiment. All participants were right-handed and reported having a normal or corrected-to-normal vision. The study was approved by the Ethics Committee of the Department of Psychology of the University of Milano-Bicocca and was in accordance with the Declaration of Helsinki (World Medical Organization, 1996). A power analysis was performed for sample size estimation using the software G* Power 3.1 (Faul et al., 2007), with a medium effect size of 0.25 and a power level of 0.80. The analysis indicated a critical sample size of 24 participants.

Procedure and Stimuli

The stimuli and procedure are the same as in Experiment 2, except for the following changes. The stimuli were distorted specifically in length or width such that the distortion could be in width, by keeping the length of the stimulus fixed, or in length, by keeping the width fixed. As before, participants performed two experimental sessions on different days with a specific type of stimulus (i.e., BS or N-BS). The order of sessions was counterbalanced across participants. In each session, four blocks were presented, defined by the combination of the type of distortion (in width or length) and the respective position of the adapting stimuli.

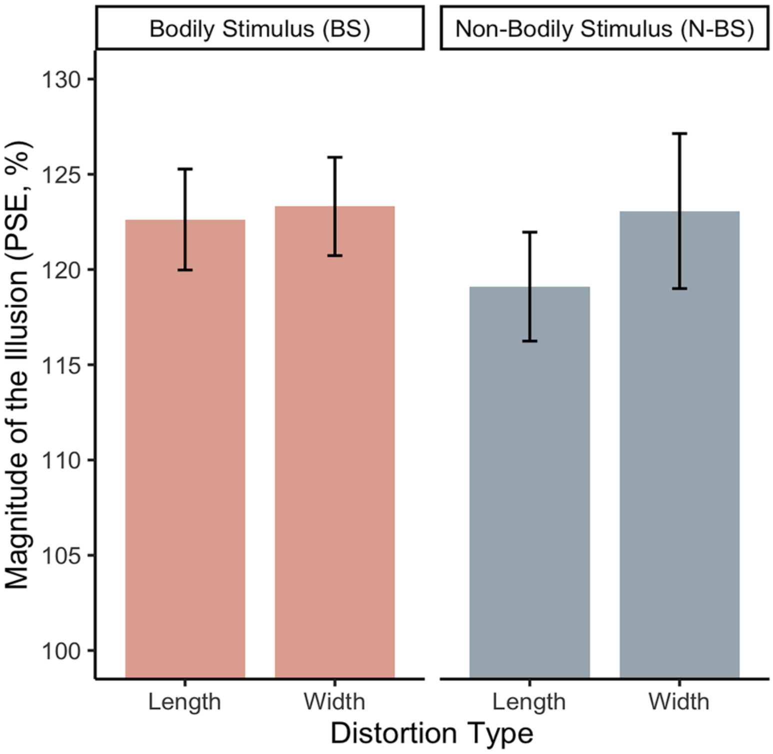
5.3.2 Results and Discussion

As before, we computed the point of subjective equality (PSE) for the test stimulus relative to the standard for each participant and type of Stimulus (BS or N-BS), but also for the type of distortion (Width or Length). We first performed a One-Sample t-test by comparing the strength of the illusion (PSE) in each condition with the condition of the absence of the illusion (POE). We confirmed the efficacy of the task in inducing the effect: a significant difference between the PSE means of each type of stimulus and the POE was found (BS: $t(25) = 20.1$, $p < .001$, Cohen's $d = 3.93$; N-BS: $t(25) = 13.0$, $p <.001$, Cohen's $d = 2.55$). Then, we performed a MR ANOVA with Stimulus and Distortion Type as within factors. Consistently with Experiment 1, the ANOVA showed a significant main effect of Stimulus ($F(1,25) = 4.63$, $p = .041$, $\eta^2_p = .16$). The effect appears to be stronger in the presence of BS (M = 123.14%; SE = 1.15; CI = 121, 125) than N-BS (M = 121.68%; SE = 1.62; CI = 118, 124). Moreover, also the main effect of Distortion Type ($F(1,25) = 7.91$, $p = .01$, $\eta^2_p = .24$) and the interaction Stimulus×Distortion Type ($F(1,25) = 5.40$, $p = .03$, $\eta^2_p = .18$) were significant. In particular, the difference between the two types of distortion is present only with N-BS: there is a stronger effect when stimuli are distorted in width (M = 123.07%; SE = 1.98; CI = 119, 127) than in length (M = 119.10%; SE = 1.39; CI = 116, 122). While for BS, the strength of the effect between the two types of distortion seemed to be comparable (Width: M = 123.31%; SE = 1.25; CI = 121, 126; Length: M = 122.62%; SE = 1.29; CI = 120, 125) (Figure 5.4). Lastly, as before, we checked for any influences due to the order of the sessions by adding the between factor Order Of Sessions in the model. The order of presentation of the two stimuli does not seem to influence the effect, as the main effect of Stimulus is significant ($F(1,24) = 4.76$, $p = .04$, $\eta^2_p = .16$) and neither the main effect of Order of Sessions nor the interactions were significant ($p > .2$). At the same time, the analysis confirmed the significant main effect of Distortion Type ($F(1,24) = 7.64$, $p = .01$, $\eta^2_p = .24$) and the interaction Stimulus × Distortion Type ($F(1,24) = 5.34$, $p = .03$, $\eta^2_p = .18$).

In Experiment 2, we replicated the result of a stronger size-contrast effect in the presence of BS compared to N-BS. When the illusion is induced with a figure depicting body parts, the magnitude of the effect is larger regardless of the order of sessions, indicating that the stimulus identity can modify the effect. Crucially, in addition to Experiment 1, Experiment 2 showed that the effect also seems modulated by the type of distortion (in width or length) but only for N-BS. Indeed, we observed a difference between the two types of distortion for Non-Bodily Stimuli, suggesting that the elaboration of a simpler geometric figure could rely more on local processing (i.e., the elaboration of the single feature of the stimulus). An unpredicted finding was that we found a stronger illusion effect when the abstract shape is distorted in width. When BS are presented, we did not find any difference in the strength of the effect according to the type of distortion. It is possible that hand stimuli could be processed more as a global configuration, so the two distortions would influence the effect in the same way. Therefore, this result suggests that a complex stimulus with a specific meaning, such as the bodily one, would be processed globally, regardless of the specific distorted dimension.

Figure 5.4.

Results of Experiment 2.



Note. Mean PSEs as a function of Stimulus and Distortion Type: only with Non-Bodily Stimuli the two types of distortion modulated the strength of the illusion. Bars indicate Confidence Intervals (CIs) set at 95% level.

5.4 Experiment 3

Experiments 1 and 2 showed that stimuli depicting body parts induce a greater size-contrast effect than neutral shapes. In Experiment 3, we investigated if increasing the perceptual similarity between BS and N-BS would reduce the difference in the illusion between the two stimulus types. Therefore, if the Uznadze illusion is modulated by stimulus identity, increasing the visual similarity between N-BS and BS should induce participants to link N-BS with BS, thus abolishing the difference between them. Indeed, previous studies showed that activity in the lateral-occipital cortex is enhanced by increasing the similarity of a stimulus to a hand (Bracci et al., 2010; Desimone et al., 1984). This result would reinforce the idea that the effect is not based only on low-level factors but that cognitive aspects related to the meaning of the stimulus can modulate the illusion.

5.4.1 Methods

Participants

26 healthy volunteers (14 females, M = 25.71, DS = 4.45), all right-handed and with normal vision or corrected-to-normal vision, participated in the experiment. Data from 2 participants were removed from the analysis as they did not complete both sessions. All subjects were unaware of the purpose of the research and gave informed consent to participate in the experiment. The study was approved by the Ethics Committee of the Department of Psychology of the University of Milano-Bicocca, and it was in accordance with the Declaration of Helsinki (World Medical Organization, 1996).

Procedure and Stimuli

The stimuli and procedure are the same as in Experiment 2, except that we enhanced the similarity between N-BS and BS. To this aim, we added in N-BS an oval with the same width as the index finger in the space occupied by the thumb in the hands, and stimuli were not rotated anymore (Figure 5.1d).

5.4.2 Results and Discussion

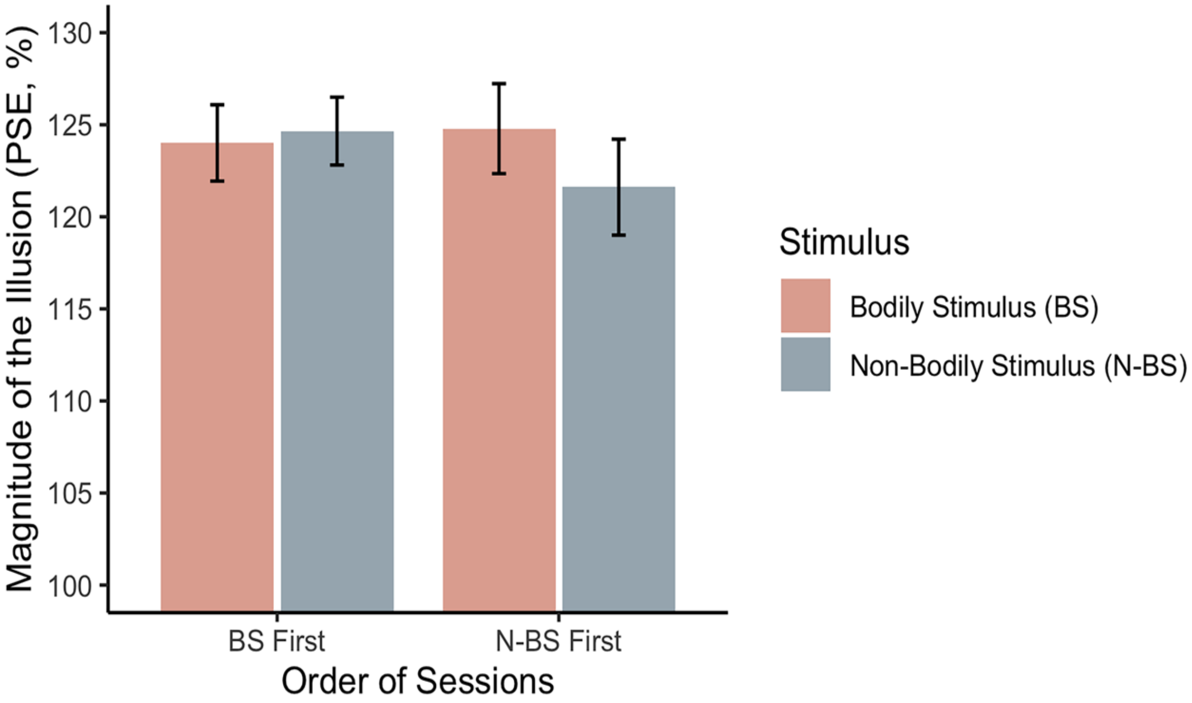
We computed the PSE for each type of stimulus and distortion type. As previously, a check for outliers was conducted for each variable, which led to removing one participant from the analysis. First, we tested the presence of the illusion with two One-Sample t-tests, which showed a significant difference between the PSE means of each type of stimulus and the POE (BS: $t(22) = 28.0$, $p < .001$, Cohen's $d = 5.83$; N-BS: $t(22) = 30.04$, $p < .001$, Cohen's $d = 6.35$). Indeed, due to the illusion effect, a distortion of more than 20% of the test stimulus is necessary to perceive the test and the standard equal in size (BS: M = 124,38%, SE = .87; N-BS: M = 123,20%, SE = .76). Crucially, the RM ANOVA with Stimulus and Distortion Type as within factors revealed a non-significant main effect of Stimulus ($p > .1$). While, as before, the main effect of Distortion Type (F(1,22) = 7.57, p = .01, η^2_p = 0.26) and the interaction Stimulus×Distortion Type (F (1,22) = 5.46, p = .03, η^2_p = .20) were significant. We confirmed the previous results for which the difference between the two types of distortion is present only with N-BS with a stronger effect when stimuli are distorted in width (M = 125.52%; SE = 1.02; CI = 123, 128) than in length (M = 120.87%; SE = .98; CI = 119, 123). In contrast, for BS the effect for the two types of distortion is comparable (Width: M = 124.94%; SE = 1.16; CI = 123, 127; Length: M = 123.81%; SE = 1.00; CI = 122, 126).

As previously, we verified the possible influence of the order in which participants were exposed to the two stimuli by adding the between-subject variable Order of Sessions to the model. Here, we found a non-significant main effect of Stimulus (p > .1) and of Order of Sessions (p > .4) again. However, the interaction Stimulus×Order of Sessions was significant (F(1,21) = 6.15, p = .02, η^2_p = .23), suggesting a role of the order of presentation of the two stimuli in modulating the effect when the similarity of the abstract shape to hand is enhanced. Specifically, we found a stronger aftereffect for BS than for N-BS, but only in participants who first performed the N-BS session (Figure 5.5). The participants who were exposed to BS in the first session showed a similar illusion effect between the two stimuli (BS: M = 124.01%, SE = 1.23, CI = 121, 127; N-BS: M = 124.65%, SE = .97, CI = 123, 127). While, when participants were exposed first to the N-BS, we found again a difference between the two stimuli (M = 124.79%; SE = 1.28; CI = 122, 127) than with N-BS (M = 121.61%; SE = 1.02; CI = 119, 124). Again, the main effect of Distortion Type (F(1,21) = 7.53, p = .01, η^2_p = .26) and the interaction Stimulus×Distortion Type (F(1,21) = 5.39, p = .03, η^2_p = .20) were significant. In contrast, neither the interaction Distortion Type × Order of Sessions nor Stimulus × Distortion Type × Order of Sessions were significant (p > .5).

The non-significant main effect of stimuli suggests that by increasing the similarity between the BS and the N-BS, the difference in the effect between the two types of stimuli disappeared. Indeed, by taking into account the effect of the order of the presentation of the sessions, we found a stronger aftereffect for BS than for N-BS, but only in participants who first performed the N-BS session. This effect would suggest that pre-exposure to hand stimuli would lead to associating the N-BS to BS and, thus, interpreting the next abstract stimulus as if it were a hand. When the illusion is induced first with the N-BS, the abstract stimulus would not be automatically perceived as a hand but would be encoded according to its physical neutral shape. So, in this way is possible that the same figure would be perceived and encoded differently depending on the meaning attributed to it (i.e., as a neutral shape or a body part), leading to a different aftereffect. Moreover, we confirmed the result of Experiment 2: the effect is stronger when stimuli are distorted in width compared to length, but only when the illusion is induced with N-BS.

Figure 5.5

Results of Experiment 3.



Note. Comparison of mean PSEs (% of distortion) between the two types of stimuli and the order of presentation of sessions: the difference in the strength of the illusion between the two stimuli (BS vs. N-BS) is present only when Non-Bodily Stimuli are presented first (N-BS First).

5.5 General Discussion

In the present study, we aimed to clarify if bodily stimuli are more susceptible to size-contrast adaptation effect as compared to non-bodily objects. To this aim, we induced the Uznadze size-contrast illusion with stimuli both depicting body parts and abstract shapes resembling the body only for their perceptual features. The key finding of the present study is that size adaptation aftereffect is modulated by stimulus identity, and it is not a mere perceptual low-level phenomenon occurring at earlier stages of visual processing. Indeed, the aftereffect was stronger by inducing the illusion with stimuli depicting body parts compared to non-bodily stimuli (Experiments 1 and 2), suggesting that visual perception of bodily stimuli is more susceptible to size adaptation. Thus, size perception would be more relevant for bodily stimuli than objects. Indeed, the correct perception of the shape, size, and space position of bodily stimuli is critical in interacting with the environment and is involved in many aspects of social perception. Accordingly, bodily stimuli are “special objects” with specific neural specialization in occipitotemporal areas (Bracci et al., 2010; Bracci et al., 2012; Espírito Santo et al., 2017) and with prioritized processing in the human visual cortex (Downing et al., 2004). It has been shown that there is an attentional bias towards body parts such that the reaction times of visual processing of bodily stimuli are faster compared to non-bodily stimuli (Ro et al., 2007; Salvato et al., 2017). Consequently, it is possible that the attentional bias toward bodily stimuli perceived as more salient and important would enhance the effect of the adaptation on the size perception of the subsequent stimuli. Indeed, a recent theory has considered the role of high-order processes, such as attentional processes, in modulating perceptual adaptation (Kreutzer et al., 2015; Pooresmaeili et al., 2013; Spivey et al., 2000;). Therefore, given the importance of body size, bodily stimuli in the visual field may be specially encoded in terms of size, thus increasing susceptibility to size adaptation.

The results are also in line with recent studies showing that body size is a critical component of body perception, and it serves as a reference in the visual perception of the size and distance of objects in the external world (Proffitt & Linkenauger, 2013). Body representation is extremely susceptible to perceptual changes in the size of bodily stimuli and can adapt rapidly to them. Indeed, previous studies have shown that exposure to body size modulations influences the perception of the size of stimuli and the interaction with them (Banakou et al., 2013; Marino and al., 2010; Linkenauger et al., 2015a; van der Hoort & Ehrsson, 2016; van der Hoort et al., 2011). Crucially, another possible explanation is that the stronger illusion effect in the presence of bodily stimuli could also be related to the flexibility to easily adapt to bodily stimuli's perceptual changes and incorporate them into one's body representation. In the presence of bodily stimuli, changes in hand size could be more easily accepted by unconsciously increasing the effects of the illusion. In line with this hypothesis and since the adaptive valence of the perception of the size of body parts, the adaptation phase would have a stronger impact on the subsequent processing of the hand size than the abstract stimulus. Indeed, these results suggest that the processing of the size of a hand would be more context-dependent such that it would be more susceptible to modifications in the external environment.

The findings of this work support that the illusion is not only perceptual (i.e., based only on low-level features related to the mere perception of the stimulus size), but it would also be influenced by high-level cognitive perception, such as identity and the meaning of the stimulus. Indeed, Experiment 3 further strengthened this idea: when the abstract figure was more visually like a hand and after the pre-exposure to bodily stimuli, there were no longer any differences in the effect between the two types of stimuli. In contrast, when the same abstract stimulus was presented first, without any pre-exposure to a hand, the difference in the effect between the two stimuli emerged again. It is possible that the pre-exposure to the hand would lead to an activation of the semantic and cognitive networks relative to body parts, and it would influence the processing of the following abstract stimulus, perceiving it as a bodily stimulus. Therefore, when the abstract figure is perceived similar to a hand, high-level areas specialized in the visual coding of hands may modulate the aftereffect. In contrast, when it is perceived as a neutral object, there is no more association between the two stimuli, and the abstract stimulus may be processed only based on its actual shape without any high-order modulations. Thus, the salience attributed to the stimulus is not related only to the type of stimulus itself and its shape but also to the meaning attributed to it and the possibility of interpreting it as a hand. Consequently, the crucial aspect would be how the figure is interpreted: when the similarity of the abstract shape to the hand is reduced (Experiment 1 and 2) or when the non-bodily stimuli are presented first (Experiment 3), the two stimuli are not associated, and the size-contrast effect for the abstract stimulus is reduced. Data are in line with the hierarchical theory of Conson and colleagues (2020), according to which the specific neural representation of body parts would lead to an automatic processing to perceive the subcategories of bodily stimuli (i.e., robotic hands) similar to human hands. When these subcategories are presented first, the automatic association is no longer present. Moreover, we even found that this hierarchical representation could also transfer from hand to abstract stimuli that maintain visual configurational features similar to a hand. However, if the subcategory is not perceived as belonging to the hand category (i.e., paw), the pre-exposure did not lead to this automatic processing. This is the case of Experiments 1 and 2, in which the non-bodily stimulus is less similar to a hand.

In the present study, we used abstract figures to control low-level features such as color and shape. However, one alternative interpretation of the results could be that the difference between BS and N-BS would emerge because abstract stimuli do not have a specific meaning, as opposed to bodily stimuli, which are meaningful objects. A further experiment with meaningful non-bodily stimuli as a control could rule out this alternative interpretation, demonstrating a greater susceptibility to adaptation for bodily stimuli.

At last, the effect also seems to be modulated by the type of distortion performed (in width or length) but only for non-bodily stimuli. Indeed, for bodily stimuli, the two distortions lead to the same magnitude of the effect, suggesting a more global elaboration of the stimuli. Indeed, as shown by studies on face processing (Farah et al., 1998; Tanaka & Farah, 1993), the familiarity and the expertise acquired for body parts would have induced more holistic stimulus processing. So, hand size elaboration would be processed according to a prototypical representation of the hand in terms of a unique configuration. This body representation would lead to perceiving the hand stimulus in global terms, beyond possible differences in single dimensions, and would allow more flexibility to accept possible distortions of body dimensions. When the illusion is induced with abstract shapes, there are differences in the effect between the two types of distortions, with a stronger illusion effect when the non-bodily stimuli are distorted in width. These results could suggest that the elaboration of a simpler geometric figure could rely more on local processing (i.e., the elaboration of the single feature of the stimulus). Thus, the stimulus elaboration would change depending on which element was altered. Indeed, non-bodily stimuli are abstract forms that are not familiar and not linked to a specific representation. Therefore, the processing of the stimulus and its features would be related to low-level mechanisms based on the processing of individual elements. For this reason, the two types of distortion would induce different effects. However, the strongest effect found in the presence of a width distortion is an unexpected result, and further studies are necessary to investigate this phenomenon deeper.

In conclusion, bodily stimuli appear to be differently susceptible to size-contrast adaptation than non-bodily neutral stimuli. Indeed, the results of this study show that inducing the illusion with stimuli depicting hands would lead to a stronger effect. It is possible that the adaptive role of size perception of the bodily stimuli would affect the perceptual processes through which the stimuli features are processed, also modulating perceptual illusions (i.e., Uznadze illusion). This result also suggests that the Uznadze illusion would be modulated by high-level cognitive processes concerning the stimulus meaning and identity, and it would not be just a mere perceptual aftereffect.

Chapter 6.

General Conclusion

General Conclusions

"We do not see things as they are,
we see them as we are"
Anaïs Nin (1961)

Which is the contribution of sensory information to build and shape Body Representation, and how does Body Representation, in turn, influence sensory processing? The present doctoral thesis aims to answer these questions. As emerged in the previous chapters, various incoming sensory information shapes and builds how we perceive our body, creating different kinds of body representations. Moreover, sensory information is integrated with the previously formed and stored bodily representations, allowing us to perceive and interact successfully with the external environment. However, the exchange between senses and body representation seems to be bidirectional. Indeed, body representation would also play a role in influencing information processing from different sensory modalities. Therefore, representations of different body features, such as shape, size, proportions, and posture, can result from integrating various sensory information. At the same time, the body representation can be the reference in the processing of sensory signals, thus influencing the perception of the external world. The results of the experiments in the present thesis strongly support the idea of a bidirectional relation between body representation and sensory processing. In the first part of this work, I demonstrated how incoming sensory information is integrated into stored representations of the body, shaping and updating them continuously (Chapters 2 and 3). In addition, Chapter 2 suggests how a change in body representation also influences the perception of the external world. This last aspect is specifically addressed in the second part of the thesis, in which I showed how aspects of body representation, both of one's own body and of the body in general, can influence the processing of individual sensory modalities and more automatic perceptual processes (Chapter 3 and 4). Thus, the present work aims to highlight the critical bidirectional relation between body representation and sensory information processing: sensory integration can modify body representation, and, at the same time, body representation may influence perceptual phenomena.

Specifically, in Chapter 2 (Study 1), it is shown that a conflict between incoming sensory signals induces a change in the representation of the hand in space (i.e., Body Schema) and of the space around the body in terms of potential actions (i.e., Reaching Space). The incongruence between touch and vision reduced the inferred probability of a common cause between the visual and tactile signals, leading to a reduced sense of ownership toward one's own body part. This visuo-tactile conflict, in turn, would update the dynamic sensorimotor representation of the hand in space and the perceived reaching space. This study, consistent with previous literature, showed that the bodily self is a collection of perceptions, an interweave of sensory signals geared towards understanding "what is me" (Apps & Tsakiris, 2013; Gentile et al., 2013; Limanowski & Friston, 2020). As discussed previously, the bodily self can be considered a property of the multisensory integration in the near space, and body ownership would emerge from the expectation that visual stimuli near the body cause tactile sensations. Therefore, the disruption of the statistical regularities between touch and vision provides enough sensory evidence for the brain to reach a perceptual inference that the hand does not belong to one's body, generating uncertainty about the position of one's body in space, i.e., the Body Schema. Although Body Schema is a representation mainly based on proprioceptive information, a modulation in the Body Schema with a merely visuo-tactile conflict was induced without any manipulation of proprioceptive (i.e., change in the perceived position of one's arm in space; Lackner, 1988), metric (change in perceived arm size; Marino et al., 2010) or action-related (arm movement; Tajadura-Jimènez et al., 2012; and tool-use; Cardinali et al., 2009) information. This result confirmed that the construction of body representation is driven by a continuous exchange and interaction between different sensory information. Consequently, by altering certain incoming information, the representation is also modified.

Furthermore, Study 1 suggests that the same visuo-tactile mismatch can also influence the Peripersonal Space, decreasing the perception of potential actions toward objects. Thus, a multisensory conflict would affect both the representation of one's own limb in space and how the space around that arm is encoded. This result is also in line with the work of Romano and colleagues (2014), in which the authors suggest that somatoparaphrenia would not only be a disruption of body representation but also correspond to an alteration of the relation between body and space. Therefore, since the arm is perceived as being less owned by one's body and less defined in space, the probability of the body getting in contact with objects is likely to decrease, thus, reducing the reaching space. Study 1 confirms the extreme dynamism and plasticity of body and space representation and how they are continuously updated based on the type of information received from one's own body. This result also sheds light on the close relationship between aspects relating to the perception of one's own body and the external world. Crucially, alterations in one's body representation would also modify the perception of action capabilities in terms of the possibility of reaching objects. Indeed, according to the body-based scaling hypothesis (Proffitt & Linkenauger, 2013), the external world perception is scaled by one’s own body features and action purposes. The peculiarity of the results in this study is that there is no specific modulation of one's own action capabilities (Linkenauger et al., 2015a; Proffitt et al., 2003; Witt et al., 2005), but they are indirectly affected by how a multisensory conflict in the space near the body is resolved. Thus, the bidirectionality of the relation between body representation and sensory information processing already emerges from the first study presented.

The dynamism and plasticity of the body sensorimotor representation to rapidly adapt to incoming sensory information are also supported by the results of Study 2 (Chapter 3). Specifically, Study 2 demonstrated for the first time that the mere holding of a tool in the hand is sufficient to elicit change in the morphological representation of the body. This result suggests a rapid and online incorporation of the tool into the Body Schema without necessarily performing an action. Crucially, this Body Schema recalibration is extremely rapid: it occurs during the first few minutes in which the tool is held in the hand. When wielding the tool, various sensory signals are integrated with each other to form a coherent perception of the tool in the hand. For example, objects visual features, such as length, shape, size, and color, are combined with tactile and haptic information related to the feedback of the object's contact with the hand and its manipulation, as well as with proprioceptive signals from the muscles, informing about the holding posture of the tool in the hand. All this information is integrated with the different stored representations of one's own body and rapidly updates the metric properties and sensorimotor aspects of the body to act properly in space. Although participants in Study 2 did not perform any actions, I cannot rule out that body schema recalibration is also due to the role of the tool in extending the potentiality to act in space (Cardinali et al., 2009; Sposito et al., 2012). Indeed, an increase in perceived arm length was found when holding a 100 cm tool compared to a 15 cm tool. Therefore, the modification of the body schema may not simply depend on the holding of the object in the hand, but on the affordance of the tool, i.e., the possibility that the use of the tool may increase one's action potential in space (Gibson, 1979; Heft, 2003). Overall, Study 2 also supports the idea that body representation is constantly updated and shaped based on incoming signals and how these are integrated into existing representations. Specifically, body schema would update to achieve better control of possible body movements with the tool and its sensory consequences. This study did not specifically test the possible consequences of wielding the tool in perceiving the external environment and incoming sensory stimuli. However, previous studies have shown that the mere holding of a tool can also alter the perception of the space around the body (e.g., Berti & Frassinetti, 2000;

Maravita et al., 2002; Witt, 2021), supporting the idea of a bidirectional relation between body and sensory elaboration.

In the second part of the thesis, I focused on the influence of different aspects of body representation on the processing of incoming sensory information (i.e., haptic and visual), even when dealing with rather automatic integrative perceptual phenomena, such as the adaptation aftereffects. Specifically, Study 3 (Chapter 4) showed that proprioceptive information regarding the arms position in space affects the haptic size-contrast adaptation aftereffect (i.e., Uznadze Illusion). Indeed, the results showed the occurrence of the aftereffect regardless of the type of posture (crossed or uncrossed arms); however, keeping the arms crossed for the entire duration of the experiment induced an increase in the effect. As discussed previously, the somatotopic mapping would be the crucial component in the occurrence of the illusion, and the effect would be mainly driven by the dimensions of the manipulated stimuli. However, given that the magnitude of the illusion was enhanced with the arms crossed, it suggests that higher-order representations of the body in space may also play a role. Thus, the haptic aftereffect seems to emerge from the interaction between sensory processing and different levels of body representations. Crucially, the illusion, mainly due to a somatotopic mapping (i.e., low-level processing driven by the superficial schema) where limb mapping in space is not explicitly required, can nevertheless be influenced in magnitude by proprioceptive information related to arms position in space (i.e., Body Schema updated). This result is in line with previous studies on spatial remapping (see Section 1.3.2), showing that the accuracy of judging the temporal order of touches on the two hands (Yamamoto & Kitazawa, 2001) decreased when the arms were crossed. During the crossed posture, the externally body-centered frame is activated in parallel with the somatotopic one, thus creating a conflict between the two frames of reference (Shore et al., 2002; Yamamoto & Kitazawa, 2001). Therefore, remapping coordinates is necessary to align different sensory information and create a congruence between the body and the external space. However, such remapping occurs even in purely tactile tasks where recoding the tactile position in the external space coordinates would not be necessary. Consequently, the proprioceptive information regarding the posture in space would be automatically integrated into the body representation during the tactile processing (Heed & Röder, 2012). These results extended the previous findings showing that arm posture would influence not only the primary tactile processing but it would also mediate haptic manipulation and the construction of object representation. Therefore, Study 3 supports the centrality of the body in processing not only primary sensory stimuli but also more complex ones, as in the case of object size processing. Indeed, changes in body features, such as those related to postural modifications, are automatically integrated into the more dynamic body representation and would influence the processing of low-level perceptual phenomena. Interestingly, the location of parts in space would play a role in influencing sensory processing, even if not primarily implicated in the task, as a consequence of the higher cognitive effort required by the automatic remapping. Thus, how body representation is updated to take into account the position in space would affect the construction of haptic experiences, shaping the perception of the object features.

The importance of body representation in sensory processing was also demonstrated in Study 4 (Chapter 5) by investigating how visual processing of the size of body parts can differ compared to non-bodily stimuli. The results revealed that bodily stimuli presentation led to a stronger size-contrast aftereffect (i.e., Uznadze visual Illusion) than non-bodily stimuli, suggesting an increased susceptibility to size adaptation of visual perception of bodily stimuli. The critical finding of Study 4 is that size adaptation aftereffect is modulated by stimulus identity. Indeed, the results support the idea that the body is a special stimulus characterized by unique elaboration processes. Firstly, the body and its parts have a specific neural representation in the occipitotemporal areas (Bracci et al., 2010; Bracci et al., 2012; Espírito Santo et al., 2017). Secondly, it has been shown that there is an attentional bias towards body parts such that visual processing of bodily stimuli in the human visual cortex is prioritized (Ro et al., 2007; Salvato et al., 2017). Thus, the presentation of a bodily stimulus rather than an abstract non-bodily stimulus induces changes in the visual size aftereffect, probably because the salience of the stimulus may reinforce the effects of adaptation. Therefore, not only does the representation of one’s own body shape sensory processes, as seen previously, but also the recall of the representation of bodily stimuli through the visual presentation of a hand modifies the processing of the stimulus features (i.e., size). This interpretation is also supported by the fact that when the similarity between the bodily and non-bodily stimulus has been increased and after a pre-exposure to the hand stimulus (see Experiment 3, Chapter 5), the abstract shape becomes equally susceptible to the illusion as the bodily stimulus. The pre-exposure to the hand may lead to an activation of the semantic and cognitive networks related to body parts and to processing the following abstract stimulus as a body part. Thus, this new meaning attributed to the abstract stimulus (i.e., hand-like) would enhance the strength of the illusion. Previous results also support that the specific neural representation of body parts would lead to automatically processing the subcategories of hands (e.g., robotic hands) as hands (Conson et al., 2020). The presence of this automatism is further evidence of how body representation influences the perceptual interpretation of stimuli. Together, these findings suggest that the adaptive role of the perception of bodily stimuli would affect the sensory elaboration through which the features of stimuli are processed, also modulating perceptual phenomena. Thus, the findings of this last study extend the previous results supporting the idea that not only the representation of one's own body but also the representation of the body in general (here, in terms of conceptual and semantic knowledge about the metric body properties, i.e., Body Image and Body Semantics) plays a crucial role in the processing of sensory stimuli. In this case, the relevance of the body induces different perceptual processing for bodily stimuli than non-bodily stimuli.

In summary, the findings discussed in this thesis corroborate the idea of a continuous and constant interaction between sensory processing and body representations. On the one hand, sensory signals are not processed in isolation, but they are always referred to the body: the elaboration of sensory signals is always conditioned by the way the body is perceived. This concept is reinforced by the fact that visual stimuli referring to the body are processed differently from other stimuli, demonstrating that the body influences the perception of the external world. On the other hand, body representation is influenced by the multiple sensory inputs that form and shape it, defining the different types of body representations. In this way, body representations are constantly shaped by the weights attributed to individual sensory cues. However, how these representations interact and integrate with each other to form a unified and coherent representation is still not fully understood, and future studies are needed to clarify these mutual influences.

Another line of future research could be to further investigate the bidirectional influences between sensory processing and body representation in patients with sensory deprivation (e.g., blind or deafferented patients). For example, studying body representation in deafferented patients (i.e., with somatosensory and proprioceptive deprivation) could be useful to investigate how other preserved sensory modalities would interact to form and maintain body representation in the absence of specific sensory inputs. At the same time, it would provide insight into how this body representation, in turn, influences the perception and the interactions with the surrounding environment.

Overall, the contribution of the present work is to highlight the reciprocal influence between the perception of the body and the external world: body representation is critical in interpreting all sensory signals, and, at the same time, it is determined by the coherent integration of different sensory information. Several models have been proposed to describe the intricate relation between sensory processing and the construction of one's own body representation. However, these models have focused on a specific sensory modality and/or a single directionality of influence. For example, Proffitt & Linkenauger (2013) hypothesize that the body acts as a perceptual metric reference for the visual processing of stimuli according to which the external environment is scaled to perceive size and extent (i.e., body-based scaling hypothesis). Despite the importance of this perspective, this model only considers one directionality of influence and only regarding visual-spatial elaboration (i.e., from body perception to visual processing). On the other hand, Longo et al. (2010) describe the processes to form different body representations (in terms of both online representation built from multisensory integration and abstract knowledge of the body) and their role in different perceptual processes. Although the model accounts for both directions of influence (i.e., from senses to body and vice versa), it only focuses on the role of the body representation in somatic perception (e.g., spatial localization of touch, metric properties of touch, tactile object recognition). Also, the model of Tsakiris (2010a) suggests a bidirectional approach, considering how the feeling of the body as belonging to oneself emerges from the interaction between incoming multisensory information and internal body models in a continuous loop. It proposes a constant and dynamic integration between current sensory information, body postural and dynamic aspects, and body anatomical and structural properties. However, this model focuses on the relation between multisensory processing and body representations only related to the perception of the body as one's own.

In conclusion, results from this thesis indicate that it is necessary to integrate the different models to consider a broader perspective to explain the bidirectional relations between the processing of different sensory information and body representations. Indeed, how different body representations are created and shaped derives largely from the senses, and at the same time, body representation influences current sensory processing. Thus, a significant challenge for future studies is to consider an integrated model that takes into account the mutual interactions between body representation and senses in a continuous exchange. This research project may be just one of the first steps in addressing this challenge.

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