

THE DISTORTED SELF

**The multidimensionality of size representation of the hands
and face in typical, atypical and clinical populations**

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STATEMENT OF ORIGINAL AUTHORSHIP

I, Laura Mora García, hereby declare that this thesis and the work presented in it is entirely my own. To the best of my knowledge and belief, the thesis contains no material previously published or written by another person except where due reference is made.

Signature: _____

Date: _____ 6th May 2020 _____

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ABSTRACT

Knowing the size of our body is essential in order to use it effectively. Therefore, a model of the size and shape of the body needs to be stored. This model is characterised by typical distortions and is subject to active modulation due to constant interaction amongst stored representations, multisensory information and experience. The aim of this thesis was to understand the representation of the size of the body, by focusing on two particularly meaningful body parts: the hands and the face. Different paradigms (localisation task and size estimation task) were used to measure their perceived size, both in healthy adult population (typical and atypical) and in clinical population. Patterns of distortions for the size representation of the hands and face were found to be primarily linked to influences from functionality, usage and experience. Modulation of the representation of the size of these body parts due to long-term practice was explored in groups of experts (magicians and sign language interpreters), in which distortions were specifically altered in line with the type of expertise. A study of clinical populations (a tumour patient and a group of patients with Personal Neglect) shed more light on how damage to different cortical structures (sensorimotor cortex and parietal areas) can influence size representation. Lastly, the neuroplasticity of size representation was explored by investigating bottom-up and top-down modulation. In detail, tDCS over visual areas modulated the representation of the face; whereas passive sensory stimulation modulated the size of the hands, confirming the cross-modality specificity in body part representation. Collectively, this thesis has broadened the understanding of the size representation of hands and face, demonstrating the multidimensional nature of body representation.

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LIST OF PUBLICATIONS

Some of the work presented in this Thesis and part of the PhD programme has been published in different journals, whereas others are in preparation. I include here a list of publications and articles in preparation.

Published articles

Mora, L., Cowie, D, Banissy, M. J., & Cocchini, G. 2018. My true face: unmasking one's own face representation. *Acta Psychologica*, 191, pp. 63-68.

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Mora, L., Gonzalez, C., & Cocchini, C. The flubbed body: malleability of the representation of hands and face in personal neglect.

Mora, L., Sedda, A., Esteban, T., & Cocchini, C. The signing body: a study on the representation of hands and face in sign language practitioners

Caggiano, P., **Mora, L.**, Veronelli, L., Arduino, L. S., Maritato, A., & Cocchini, G. The downsized hand in Personal Neglect

Chapter 1: Introduction



Josephine Cardin Photography

1.1 Introduction

Literature on body representation is broad and prolific and multiple attempts have been made to understand its different components. One way to illustrate the difficult task of representing the body is by understanding that “[f]or a brain to effectively regulate its body in the world, it runs an internal model of that body in the world” (Barrett, 2017, p. 5). Indeed, the brain stores a model of the body which integrates knowledge about configuration, structure, position and spatial relationships amongst its parts (Berlucchi & Aglioti, 2010; Maravita & Iriki, 2004; Sposito, Bolognini, Vallar, & Maravita, 2012), which is integrated with multisensory inputs (Berti, 2013). Without this mental model, we would not be able to use our body effectively (Graziano & Botvinick, 2002). Body representation has been defined as “the immediate prediction, construction and evaluation of one’s own corporal structure and space and those of other bodies” (Pazzaglia & Zantedeschi, 2016, p. 1). Given that the body is not only perceiving, but it is also an object of perception itself (Bermúdez, Marcel, & Eilan, 1995), its physical attributes can be judged, including its size and shape (Di Vita, Palermo, Boccia, & Guariglia, 2019; Longo, 2016).

In the early stages body awareness was seen as a compound of bodily sensations, whereas currently there is an agreement that there are a variety of mental representations which account for the body (De Vignemont, 2010). This means that there are numerous aspects in the representation of the body that can be explored, such as ownership, agency, emotional aspects, structural components, shape and size. These representations ought to include perceptions, organization of one’s own body and other bodies, and information from the senses, in order to build a coherent mental construct (Berlucchi & Aglioti, 1997). Despite the interest in studying this part of human experience, there is currently no final agreement on how the body is represented in the

brain, and more so, how many representations there are. Hence, multiple ‘bodies in the brain’ or representations have been proposed (Berlucchi & Aglioti, 2010).

The goal of this chapter was to provide a general overview on literature considering the different types of body related information, and the different representations that have been postulated. For this, the various models were categorized in two groups: traditional models and contemporary models.

1.2 Theories of body representation

1.2.1 Traditional models

The first classification system on body representations by Head & Holmes (1911), postulated the existence of two separable representations: one relating to the posture of the body, or ‘body schema’; and the other to the localisation of body parts which was consequently called ‘body image’ (Critchley, 1979). Specifically, the body schema is a representation formed by afferent and efferent sensory and motor information that guides actions, whereas body image is a pictorial depiction of the body (Gallagher, 1986, 2005; Paillard, 1999; Rossetti, Rode, & Boisson, 1995). Theories that support this dual division of body representation are part of the *dyadic taxonomy*. In reality, body image in this taxonomy will group all other representations that are not used for action, such as body affect, concept or percept (Gallagher, 2005). Hence, body image will have a size estimation component (perceptual distortion, linked to body percept), and a cognitive-evaluative component (affective/emotional, linked to body concept) (Skrzypek, Wehmeier, & Remschmidt, 2001; Slade & Brodie, 1994). Moreover, the body schema is considered unconscious, whilst the body image is conscious (Head & Holmes, 1911), and they influence each other (Gallagher, 2005; Paillard, 1999).

Double dissociations were investigated in order to warrant this taxonomy, in particular between deafferented patients (altered body schema with preserved body image), and patients with numbness (altered body image with preserved body schema) (Paillard, 1983). In detail, Paillard and colleagues (1983) presented a patient with ‘blind touch’. The patient had full paralysis of her right hand after left parietal infarct, but when blindfolded, she could locate the points where she had been touched, without conscious awareness of the actual touch. Contrastingly, Paillard (1999) later reported a patient whom after deafferentation, was able to consciously locate the body parts that had been touched when blindfolded, but needed vision to point towards them. Hence, the first case presented with a disrupted body image with preserved body schema, whilst in the second case the reverse pattern was observed. Similarly, hemineglect patients are able to use limbs in motor tasks despite neglecting them, due to a preserved body schema, whereas patients without proprioception show instead a disruption of the body schema, relying on their body image and attention to direct their movements. Thus, these are slow and inefficient (Gallagher, 2005). These dissociations were used as a confirmation of the existence of these two body representations.

Due to the heterogeneity of the components of the body image in dyadic models, others postulated a further subdivision, becoming the *triadic taxonomy* (Schwoebel & Coslett, 2005). The body schema was still considered here, with the same definition, whereas the body image was divided into two: the ‘visuospatial body map’ or ‘body structural description’, which is a topological description of the map of the body (Buxbaum & Coslett, 2001; Sirigu, Grafman, Bressler, & Sunderland, 1991); and the ‘body semantics’, which includes conceptual and linguistic components of the body representation (Di Vita, Boccia, Palermo, & Guariglia, 2016; Schwoebel &

Coslett, 2005). The visuo-spatial body map incorporates knowledge regarding the structure of the body (i.e., where body parts are located, and their boundaries), whilst the semantics of the body is involved with the conceptual and linguistic knowledge of the body.

This taxonomy has also been further supported by dissociations in different disorders of body representation. For example, a patient with apraxia showed a specific deficit in the coding of online positions of the body parts, due to a disorder of the body schema (Buxbaum, Giovannetti, & Libon, 2000). Instead, in autotopagnosia, patients show a specific impairment in the capacity to point to different body parts on one's own body and others' bodies, but this ability is preserved when pointing to animals or objects (i.e., disorder of the visuospatial map). This suggests a particular impairment in the access to the structural component of human body (Buxbaum & Coslett, 2001). Interestingly, the patient reported in this study was still able to point to clothes when asked about the associated body parts, which confirmed preservation of the body semantics. Still, this taxonomy left questions to answer regarding further subdivisions of the body representation.

Sirigu et al. (1991) were supporters of a model that included one more compartmentalization. This was backed by the discovery of a patient with autotopagnosia who showed body-specific aphasia, but was able to provide information about the different function of body parts (Sirigu et al., 1991), and was therefore in contrast to patients in Buxbaum & Coslett (2001). To explain this finding, Sirigu and colleagues (1991) proposed four components of body representation: semantic and lexical (linked to verbal systems), visuospatial (structural body description), dynamic body image (constructed from multisensory online information, which is comparable with the body schema by Head and Holmes), and spatial

representation (constructed from motor programmes). They confirmed that these can interact, and can also be involved in tasks assessing body representation in different degrees, being task-dependent (Sirigu et al., 1991).

As an agreement had not been reached regarding the number of components of body representation, recent models have gone in three different directions. Some continued expanding and increasing the compartmentalization of body representation (independence models); others have proposed a single unified representation (fusion models), whereas new recent proposals focus on the construction of body representation through interactions between the different components (co-construction model) (Pitron, Alsmith, & de Vignemont, 2018; Pitron & de Vignemont, 2017) (see Figure 1.1).

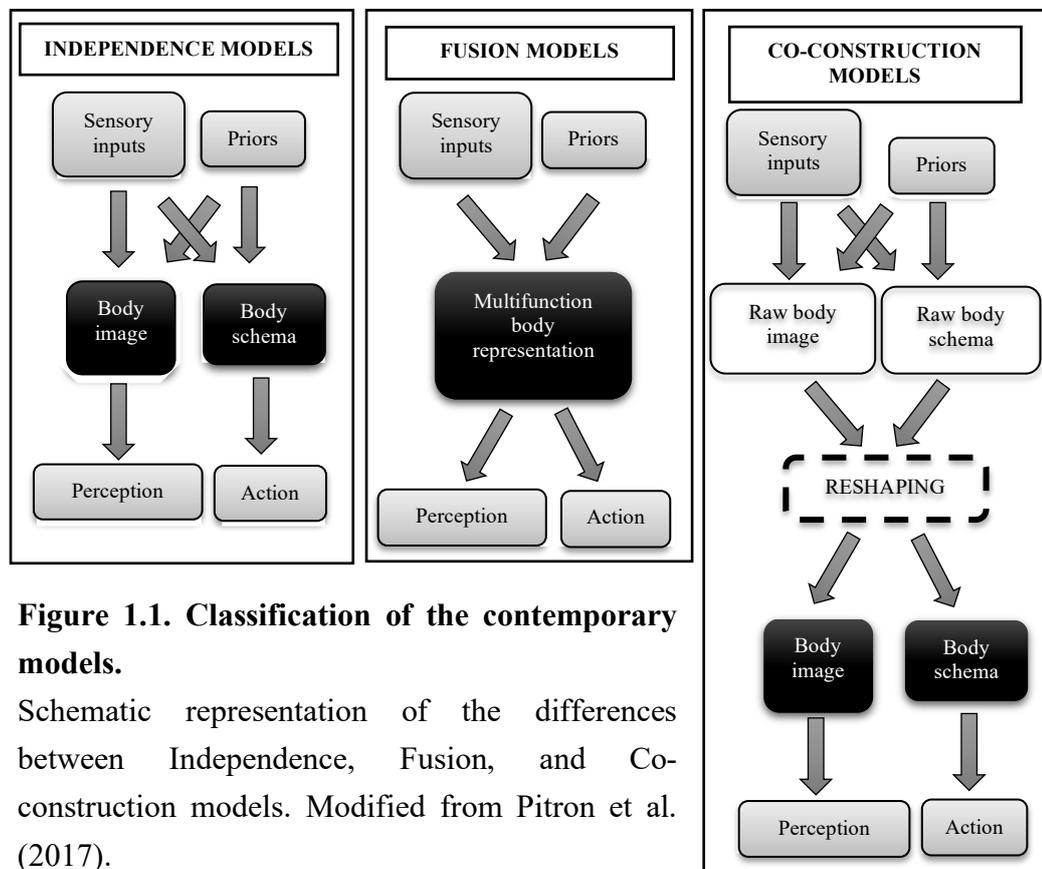


Figure 1.1. Classification of the contemporary models.

Schematic representation of the differences between Independence, Fusion, and Co-construction models. Modified from Pitron et al. (2017).

1.2.2 Contemporary models

1.2.2.1 Independence models

A recent account by Longo, Azañón, & Haggard (2010) has been proposed as an attempt to amalgamate all possible representations within one model. This model supports the idea of mutual interaction between bottom-up sensory signals and stored body representations (top-down percept), with bidirectional interactions between somatosensory and visual systems (Longo, 2015a). Parting from ‘basic’ *somatosensation*, they argue the existence of higher body percepts called *somatoperception*, constructed through the integration of multisensory information; and *somatorepresentation*, which refers to the abstract knowledge of the body, including beliefs and attitudes (Longo, 2016; Longo et al., 2010). This classification reflected the idea of having a body that we perceive and, at the same time, a body that we represent (Di Vita et al., 2019; Longo et al., 2010). According to this model, these two characteristics of body representation are dissociated in different disorders. For example, phantom limb sensations refer to the persistent perception of the missing limb after amputation (Melzack, 1992). In this case, the somatorepresentations have been updated after amputation, whilst somatoperception has not (Longo et al., 2010). Similarly, perceptual experiences can be changed easily, without modifying the higher-order cognitive representation. This can be seen when administering anaesthesia to a body part, which does not feel as if it had ‘disappeared’ or is missing despite the lack of peripheral input (Medina & Coslett, 2016). Within this classification system, they argued the existence of six body representations. *Somatoperception* incorporates the ‘body image’, referred to the conscious experience of body shape, size and physical characteristics; the ‘body schema’, which has the same definition as in previous models (see Head & Holmes, 1911); the ‘superficial schema’, a map of the

skin surface that mediates localisation of touch; and the ‘body model’, a representation of the actual body size and shape (i.e., the metrics of the body). *Somatorepresentation* instead comprises the ‘semantic knowledge’ about the body, that includes the abstract semantic knowledge about shape, location, functions and cultural associations; and the ‘body structural description’, which refers to the topological spatial organisation of body parts relative to each other (Longo, 2016).

Perhaps, from all these representations, the one that has brought more interest and novelty to the field is the *body model* of somatoperception. This is a representation of the metric components of body parts which needs to be integrated to afferent and efferent information to determine the position of body parts in the space (Graziano & Botvinick, 2002; Longo & Haggard, 2010). There is no specific signal that gives information regarding metric components of this representation, so this is presumed stored and pre-existing in the brain. Hence, it includes the relative size proportion of the body segments, such as fingers (Longo et al., 2010; Longo & Haggard, 2010; Serino & Haggard, 2010). This body model is considered a component of the body schema, that supports the position sense, necessary to locate the body in the space (Longo, 2015c).

Lastly, all these representations were conceptualised not only based on perceptual/conceptual dimension, but also on a second dimension which focused on the level of “accessibility to conscious introspection” (Longo, 2016, p. 4), thus having explicit representations (conscious) versus implicit (Longo, 2016; Longo et al., 2010) (see Figure 1.2). This differentiation is supported by the finding that healthy adults may perform more accurately in explicit body size estimation tasks, such as size comparison, whilst a characteristic pattern of distortions is seen in implicit ones (Caggiano & Cocchini, 2020; Longo, 2015a, 2015c).

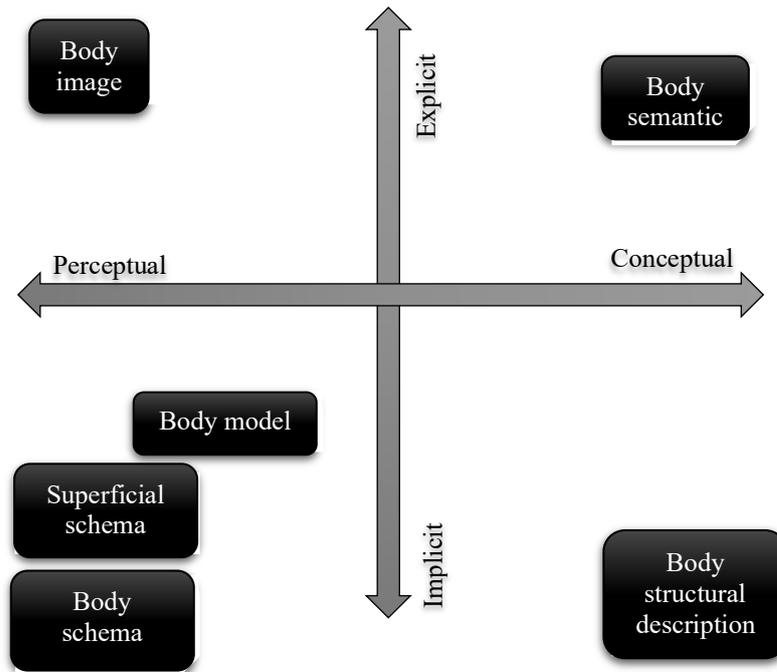


Figure 1.2. Model of body representations by Longo et al. (2010).

Diagram representing the six different representations proposed by Longo et al. (2010) classified in a two-dimensional space according the perceptual/conceptual and explicit/implicit each appears to be. Modified from Longo 2016.

Similarly, alternative classification methods have attempted to provide different labels to arrange the various representations in accordance with their characteristics. For instance, these could be grouped by function, resulting in Action-oriented body representations (encompassing the body schema), and Non-Action oriented body representations (encompassing all the others representations not required for action) (Di Vita et al., 2016). Others, instead, have classified them by the dynamic properties of these representations, and differentiated between short-term and long-term representations (O’shaughnessy, 1980). Following this classification, Gadsby (2017) has recently proposed a model with a long-term body image (LTB) that interacts with more dynamic short-term representations, such as the body schema, tactile form and body percept (mental imagery of the body). This LTB includes spatial

information, which is updated by experience; it is innate, and it develops through life. This stored content acts as a template to adjust other dynamic representations that can be easily modulated. In this proposal, Gadsby further argued that the LTB is the aspect of the body representation that has become distorted in patients with anorexia nervosa, due to affect influences.

Due to this complexity and diverging views in the number of representations, additional recent models have changed the approach in order to avoid increasing the subdivisions, as in Longo et al. (2010), and instead, have looked into an integrated model of multisensory influences.

1.2.2.2 Fusion models

One of these models has introduced the concept of the *body matrix* (Moseley, Gallace, & Spence, 2012). The body matrix is a dynamic online multisensory representation of the body at a given time, which not only includes information about one's own body, but also the body-centred personal space. Moreover, apart from multisensory information from outside the body, it also incorporates homeostatic information from within the body (e.g., temperature). All the different sources of information are then integrated into a network that processes it to construct a body matrix, with the most relevant areas being the posterior parietal cortex (PPC) and insula. This model is supported by findings with bodily illusions. For example, having a body matrix explains the link between the induction of the rubber hand illusion (RHI), in which a fake limb is incorporated in one's own body representation, and reduction of temperature in the 'disowned' hand (Moseley et al., 2012). When ownership of the rubber hand is elicited, the body matrix will include the space around that hand as part of the body, whereas activation of the representation for the 'replaced' hand will be reduced within this matrix, and hence the homeostatic control. Similarly,

this multisensory integrated matrix lends explanation for the fact that stimuli presented near the rubber hand instigate behavioural and neural responses (Ehrsson, Wiech, Weiskopf, Dolan, & Passingham, 2007).

Later, De Vignemont 2014 proposed the *Multimodality Thesis*, in which the focus was given to the interaction between the different sensory modalities to construct a coherent body representation (long-term and short-term body image). De Vignemont (2014) proposed that the underlying process in body representation construction is ‘multisensory binding’, in which characteristics from the same object, in this case the body, are integrated into a unitary representation. De Vignemont then explained that multisensory binding is “constitutive component of the aetiology of bodily experience” (p. 12), in such a way that the most information collected from bodily senses, the better. In this model, vision is primarily responsible of information about the size of the body, which is then bound to proprioceptive and tactile information to localise the body in space (De Vignemont, 2014). This model has again been supported by evidence from bodily illusions, in which contrasting multimodal information compete, resulting in inappropriate binding and causing an altered perception of the body. The key to induce these illusions is cross-modal competition. In the RHI, there is a competition between what the eyes see, and what the hand feels. In these occasions, vision primes over tactile or proprioceptive feedback (De Vignemont, 2014). However, normally the combination of multimodal information helps in the construction of the body representation. For example, viewing one’s own hand improves tactile accuracy (Taylor-Clarke, Kennett, & Haggard, 2002).

1.2.2.3 Co-construction model

An alternative model, that is also based in multisensory integration principles, has recently emerged, in which *co-construction* is proposed between body

representations (Pitron et al., 2018; Pitron & de Vignemont, 2017). The co-construction model entails serial processing of information, in such a way that the body representation becomes more complex after each step (Haggard, Cheng, Beck, & Fardo, 2017; Longo, 2017a). In other words, different body representations “interact and reshape each other” (Pitron & de Vignemont, 2017, p. 116) (see Figure 1.3A). This framework further postulates that the process of co-construction is majorly guided by the body schema, which is a more detailed representation, whereas the body image accommodates a wider margin of error. Specifically, the body schema is built by multisensory signals, combined with prior knowledge that includes motor expertise. This information acts as a prior to then construct one’s own body image, which also needs priors from social expectations, affective factors, etc. In the body image component, greater focus is given to the visual aspect. Overall, the body image becomes a more complex representation throughout this construction process but is also less precise. Lastly, they suggest a feedback loop in which the body image also influences and recalibrates the body schema, but restricted to certain situations in which there is a discrepancy between both (Pitron et al., 2018) (see Figure 1.3). Sometimes, this can be dysfunctional, such as in anorexia nervosa whereby an altered body image will, in turn, disrupt the body schema. This explains why patients act as if they had a larger body than they do (Gadsby, 2017).

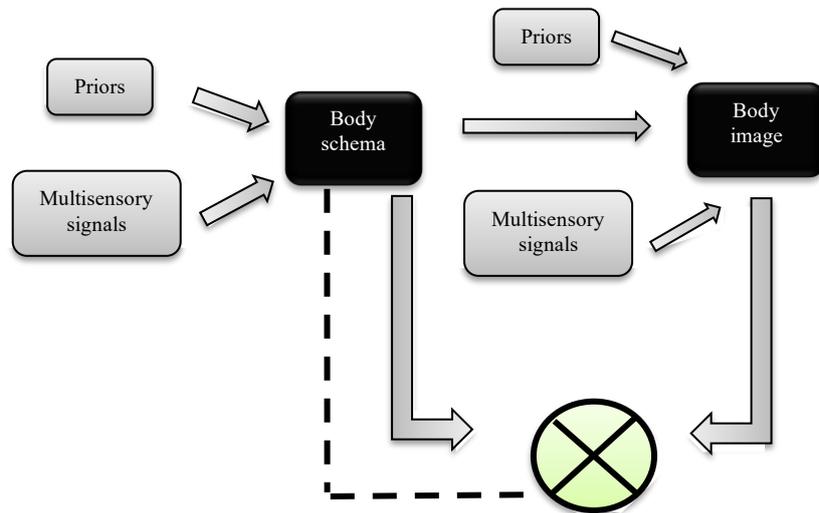


Figure 1.3. Co-construction model.

Schematic representation of serial processing of multisensory signals and priors to construct the body schema and body image. From Pitron et al. (2018).

In summary, no singular model or general theory has emerged, connecting all the different representations (Longo, 2016). Hence, the majority of the research studies tend to focus on one representation at a time rather than multiple, with a predominance to study the body schema and visuospatial body map, in comparison with the semantic components of body representation (Di Vita et al., 2016).

1.3 Neuroanatomical correlates of body representation

Given that multiple body representations have been identified, different brain areas have been also proposed to underlie the different components of body representation. Even though there is no real agreement on the number or characteristics of different body representations, several groups have tried to explore the representation of the body in the brain. Overall, most have accepted the triadic taxonomy agreeing on the existence of three types of representations: the body schema, the body structural description and the body image (Berlucchi & Aglioti, 2010; Schwoebel & Coslett, 2005). However, the localisation of neuroanatomical correlates

has not been an easy task, as most of the studies have only focused on one type of representation at a time. Moreover, the few that have attempted neuroanatomic studies in groups of participants have presented contrasting evidence (Di Vita et al., 2016).

One of the first group studies investigating the underlying neuroanatomic correlates of body representations was carried out by Schwoebel & Coslett (2005). They wanted to provide a study with a large group of subjects, in contrast to previous evidence that had been mostly based on single case studies or small group studies. They considered a large group of stroke patients to shed light into the different neural correlates of body representations within the triadic framework. This study did no more than confirm what had been previously hypothesized in single case studies. Firstly, the subdivision between structural and semantic body image was supported, with representations lateralised to the left temporal regions, whereas impairments in tasks relating to the assessment of the body schema (such as hand laterality and mental rotation tasks) appeared to be due to lesions in the dorsolateral frontal lobe and the PPC. Indeed, posterior parietal areas in particular appear to underlie components of the body schema (Schwoebel & Coslett, 2005).

Following this, the study by Corradi-Dell'Acqua, Hesse, Rumiati, & Fink (2008), focused on the neural substrates of the structural body description. They found activation of the left extrastriate body area (EBA) when viewing body parts, whereas the left superior parietal cortex (SPC) and intraparietal sulcus (IPS) were involved in the processing of spatial relationships between body parts (i.e., body structural description). This same lab investigated the differences in the structures underlying the body schema and the body structural description in a more recent study. In this case, they found activation of the left secondary somatosensory cortex in motor imagery tasks (i.e., body schema), whereas the parietal cortex was active for visual imagery

tasks, which measures the structural body map (Corradi-Dell'Acqua, Tomasino, & Fink, 2009).

Dijkerman & de Haan (2007) instead investigated the neural basis for dyadic models. They found that the right PPC was involved in the body schema, integrating somatosensory inputs, whereas the left was more involved in structural and semantic representations. Hence, they proposed two systems to process somatosensory information: one system starting with the somatosensory cortex, then projecting to the PPC for guided action (body schema); and a second system projecting instead to the insula, involved in conscious perception and memory (body image) (Berlucchi & Aglioti, 2010; Dijkerman & de Haan, 2007). Indeed, the right anterior insula integrates exteroceptive and interoceptive information with a mental image of the body, in order to construct a visuospatial body map (Dijkerman & de Haan, 2007). Further, the temporo-parietal junction (TPJ) and postcentral gyrus are also involved in this process (Di Vita et al., 2019). In detail, the TPJ is involved in generating an internal model of the body against which new stimuli are compared (Tsakiris, Costantini, & Haggard, 2008), whereas the postcentral gyrus links with the insula to construct the visuospatial body map (Di Vita et al., 2019).

A recent review of 'currents affairs' in the neuroanatomic aspect by Di Vita and colleagues (2016), provides an excellent analysis of previous data by considering the differences between action-oriented representations (i.e., body schema), and non-oriented to action representations (i.e., body image) (Di Vita et al., 2016). Firstly, they confirmed the motor nature of the body schema, as activation on the primary motor areas and cerebellum were associated with this type of representation. Secondly, perceptual areas in the occipito-temporal cortex were highly involved in the processing of action-oriented representations. In particular, the EBA and fusiform body area

(FBA) were both activated for body parts or whole bodies, respectively, with a pivotal role of the right EBA, confirming the involvement of vision in the multisensory representation of the body (Corradi-Dell'Acqua et al., 2008). Further, they found bilateral activation in the primary somatosensory areas. Indeed, the somatosensory cortex is organised somatotypically containing the representation of body parts, in such a way that more innervated areas are more extensively represented than the ones with less density of cutaneous receptors (Penfield & Rasmussen, 1950). The information from these somatosensory maps is later integrated for higher order representations (Corradi-Dell'Acqua et al., 2008). These results suggested that the somatosensory cortex stores and/or constructs a spatial body representation from the somatosensory information (Dijkerman & de Haan, 2007). They also highlighted the importance of the right supramarginal gyrus, and right parietal lobe in general, as neural circuits underpinning the visuospatial body map, also supported by previous studies (Corradi-Dell'Acqua et al., 2008; Tsakiris et al., 2008). Lastly, motor circuits on the frontal lobes were involved in the body schema representations, which also engaged the right hemisphere. To sum up, the supramarginal gyrus and the somatosensory areas were mainly involved in the non-oriented to action representations, whilst the right EBA and motor areas were linked to action-oriented representations (body schema). These results confirmed the interaction between somatosensory and visual information to construct the non-oriented to action representations. Further, these results also supported partially distributed networks for the body schema and the non-oriented to action representations.

In the same way that EBA is specialised in body part processing, and FBA in the visual processing of bodies (Downing, 2001; Downing & Peelen, 2016; Taylor, Wiggett, & Downing, 2007), there are two other areas that are analogous and are

involved in face processing. One is the fusiform face area (FFA) and the second is the occipital face area (OFA) (Liu, Harris, & Kanwisher, 2010). Repetitive Transcranial Magnetic Stimulation (rTMS) over EBA disrupts the visual discrimination of bodies, but not faces or objects (Urgesi, Berlucchi, & Aglioti, 2004); whereas targeting the right OFA impairs the processing of faces (Pitcher, Walsh, Yovel, & Duchaine, 2007). However, no specific body representation per se is clearly associated with these areas. More recent studies have shown how EBA may also be involved in the processing of the shape and size of the body (Carey, Knight, & Preston, 2019; Downing & Peelen, 2016; Urgesi, Calvo-Merino, Haggard, & Aglioti, 2007). Indeed, reduced EBA activity (Uher et al., 2005) and structural differences (grey matter reduction) (Suchan et al., 2010) have been found amongst patients with eating disorders (ED), as a core component of body image disturbances (Pazzaglia & Zantedeschi, 2016; Urgesi et al., 2012). Moreover, reduced connectivity between EBA and FBA is associated with the distortion of body image in anorexia nervosa (Suchan et al., 2013).

Subsequent studies confirmed the relevance of parietal areas in the structural map, by testing patients after stroke (Di Vita et al., 2019). Some studies have found that this is lateralised to the right parietal areas (Spitoni et al., 2013), whereas others postulated engagement of the left ones (Corradi-Dell'Acqua et al., 2008, 2009). However, these contrasting results regarding the lateralization of the network processing non-action oriented representations may be due to impairment on semantic components of the representation of the body, and not the visuospatial body map (Di Vita et al., 2019). Indeed, Di Vita and colleagues (2019) have recently confirmed the paramountcy of the right hemisphere for the processing of this map. In particular, they detailed these areas to include the putamen, anterior insula, temporal lobe (middle and superior temporal gyrus extending to TPJ), parietal lobe (postcentral gyrus, angular

gyrus and supramarginal gyrus), frontal lobe (middle and inferior frontal gyri and precentral gyrus), and the surrounding white matter (Di Vita et al., 2019). When these areas are lesioned, patients experience Personal Neglect, a disorder of body representation (Baas et al., 2011; Caggiano & Jehkonen, 2018; Cocchini, Beschin, & Jehkonen, 2001; Committeri, Piervincenzi, & Pizzamiglio, 2018; Coslett, 1998). Moreover, these areas are regions that provide a more “abstract and egocentric representation of the body space, such as the supramarginal gyrus” (Di Vita et al., 2019, p. 504), confirmed also in previous studies in the field (Committeri et al., 2007). To sum up, there is a link between activation on the primary somatosensory cortex and right supramarginal gyrus for non-action oriented representations (Di Vita et al., 2016).

Overall, a wide general network is necessary for the construction of body representations, which mainly include sensorimotor, visual and parietal areas (Di Vita et al., 2016). Indeed, trying to locate specific body representations within specific brain structures will be too simplistic. Firstly, because labels and taxonomies have been used differently depending on the study, and secondly, because the current understanding of brain functioning support the work of distributed systems with areas interconnected in multiple locations (Berlucchi & Aglioti, 2010).

Chapter 2: **Research rationale and overview**



Josephine Cardin Photography

2.1 Body size matters

Knowing the size of our body is essential. For instance, the length of the arms needs to be computed in order to reach for an object (Coelho & Gonzalez, 2018a; Longo & Lourenco, 2007), the length of our legs to walk (K. D. Stone, Keizer, & Dijkerman, 2018), and the height and width of our body to go through a door (Stefanucci & Geuss, 2010). The importance of holding an accurate size representation of our body is perhaps better understood when considering the impact that size distortions can have in daily functioning. For example, increased pain in amputees experiencing phantom limb is linked to an altered perception of limb size (e.g., ‘telescoping’) (Schmalzl & Ehrsson, 2011). Similarly, distorted information about the size of our body is linked to a variety of pathologies such as Anorexia Nervosa (AN), in which patients experience an oversized body (Gadsby, 2017; Riva, 2012; Slade & Russell, 1973). Indeed, information on the size of the body and its segments is required in order to use the body in space (Gandevia & Phegan, 1999).

A large bulk of the recent research on the topic of body metrics has focused on assessing specific body parts. One particular research group, led by Matthew Longo, has predominantly focused on the study of the distortions of the representation of the hands. Following the study of touch anisotropies (i.e., Weber’s illusion), Longo and colleagues (2010) proposed the existence of a *body model*, a stored mental metric representation of the body that includes information about the size of body segments (Longo et al., 2010; Longo & Haggard, 2010; Serino & Haggard, 2010). This body model is an implicit representation, and has been assessed by different variants of the *localisation task* (e.g., Longo & Haggard, 2010). Briefly, participants positioned their hand under an occluded board and had to locate single landmarks on it (i.e., knuckles and fingertips), by pointing with a baton. The goal was to point to the location where

participants *felt* their landmarks to be, relying on their *position sense*. By measuring the distances between pairs of landmarks (e.g., tip of the thumb and the knuckle), these authors were able to compare the real and perceived size judgements, without considering the spatial localisation of these judgements (i.e., distance from real location). Consistent replication of the results showed that fingers were underestimated in length, the hand was overestimated in width, and there was a radial-ulnar gradient in the underestimation of finger lengths (i.e., the thumb was the least distorted, whilst the little finger was the most) (Longo, 2015a).

The finding of a distorted representation of hands in healthy participants was unexpected. Hence, subsequent studies aimed to understand the nature of these distortions. Through this exploration, biases affecting this task were discovered. For instance, Longo (2014) confirmed that, when participants were blindfolded, the implicit hand representation through the localisation task was less distorted (finger lengths were less underestimated) than in full-vision condition. Likewise, perceptual and conceptual distortions were found (Longo, Mattioni, & Ganea, 2015). In detail, Longo et al. (2015) described how healthy participants systematically misallocated their knuckles, locating them as further forward than their real location. The authors proposed that conceptual distortions caused finger underestimation results, due to distal biases when locating the knuckles. In other words, we do not know where our knuckles are. In contrast, perceptual distortions explained hand width overestimation as a true “spatial warping of the representation of bodily tissue itself, [...] reflecting distortions of somatotopic cortical maps” (Longo et al., 2015, p. 1). More recent studies have continued trying to disentangle biases in this task, considering influences due to visual memory (Saulton, Dodds, Bühlhoff, & de la Rosa, 2015; Saulton, Longo, Wong, Bühlhoff, & de la Rosa, 2016), uncertainty (Medina & Duckett, 2017) or motor

control (Peviani, Liotta, & Bottini, 2020). Despite the biases identified, most of the studies that followed have continued implementing the same locational task procedure that was initially introduced 10 years ago. Hence, the main aim of the first experiment in this thesis was to remove the conceptual biases in the task, in order to obtain a more truthful picture of the size distortions for hands. The second aim was to provide a clear account of the localisation judgements that could explain the distorted representation of the hands.

2.2 Size distortions of the hands and face (Chapter 3)

Previous studies have clearly stated that there is a general conceptual misunderstanding in the healthy adult population in locating the knuckles, believing them as being further forward than they really are (Longo et al., 2015). Hence, in the first experiment in Chapter 3, unbiased landmarks were targeted instead (i.e., finger interspaces rather than knuckles) to investigate the distortions of hand representation without conceptual biases. Moreover, a detailed account on the shift of pointing responses was provided to understand the direction of misallocations underlying size distortions.

Although there has been great interest on the implementation of the localisation task for hands, this has not been matched for other body parts. Indeed, only one study by K. D. Stone et al. (2018) has modified this task to measure the metric representation of the legs. Overall, they found a tendency to underestimate the width of the thighs and lower leg length, whereas there was overestimation of upper leg length and ankle width. These results confirmed that, even though there is a characteristic pattern of distortions for the hands, multimodal-based distortions are specific for each body part (K. D. Stone et al., 2018). These findings supported the importance of studying different body parts. Hence, the purpose of the second experiment in this chapter was

to explore the representation of a body part which is extremely crucial for everyday life: the face. Previous attempts to measure self-face representation have been made, but mainly focused on depictive tasks; that is, pointing to different landmarks on a computer screen (Fuentes, Runa, Blanco, Orvalho, & Haggard, 2013) or by using distorted pictures (D'Amour & Harris, 2017). These tasks did not help discern whether they were measuring self-face or a general prototypical representation of faces (Fuentes, Runa, et al., 2013). Also, these tasks lacked the proprioceptive component (pointing towards own body) of the localisation task postulated by Longo and Haggard (2010) and modified by K. D. Stone et al. (2018). With this in mind, a face localisation task was designed for the Experiment 2 in Chapter 3, aimed to measure, for the first time, the body model of the face.

2.3 Effects of long-term expertise on size representation of the hands and face (Chapter 4)

Recent studies have suggested that internal body representations are highly malleable (K. D. Stone et al., 2018; Tsakiris, Tajadura-Jiménez, & Costantini, 2011). Quick modulation can be achieved by simply distorting the viewed size of a limb or by using tools. For example, viewing one's own hand through magnifying lenses affects grasping (Ambron, Schettino, Coyle, Jax, & Coslett, 2017; Ambron, White, et al., 2018), and touch (Haggard, Taylor-Clarke, & Kennett, 2003); whereas arm's length can be modulated through training of specific actions (Cardinali, 2011; Cardinali et al., 2009; Romano, Uberti, Caggiano, Cocchini, & Maravita, 2019). Not surprisingly, long-term training and expertise in the use of a body part also affects the representation of its size. Recently, Coelho, Schacher, Scammel, Doan, & Gonzalez (2019) found that the perceived size of the hands was modulated by extensive practice in baseball due to the use of the mitt to catch the ball.

These studies showed how the metrics of the body can be easily modulated by multisensory information, tool-use and action goals. Despite the interest in the modulation of the size of the body through tools, the effects of long-term practice in the metric representation of hands and face have been rarely investigated. Chapter 4 thus aimed to address this question, considering two groups of adults who have undergone long-term training in complex manual actions: magicians and sign language practitioners. In particular, the effect of expertise in the metric representation of hands and face was explored through the localisation tasks introduced in Chapter 3.

2.4 Effects of brain damage on the size representation of the hands and face (Chapter 5)

Disturbances of the representation of the body are multiple, complex and distinct (Palermo et al., 2018), and insults to its integrity can have devastating effects. These range from brain damaged-related disorders, such as *Personal Neglect* (Benke, Luzzatti, & Vallar, 2004), to psychiatric conditions like *Bulimia Nervosa* (Mölbart et al., 2017), or body injury-derived disorders such as *Spinal Cord Injury* (Magnani & Sedda, 2016; Sedda et al., 2019). Deafferented patients usually present with modulation of their perceived size of the body. After amputation, patients tend to experience a phantom limb that is perceived as getting progressively smaller inside the stump (telescoping phenomena) (Ramachandran, 1993; Ramachandran & Hirstein, 1998). This is due to the maladaptive plasticity of the somatosensory cortex, resulting in incongruent information from afferent and efferent sources (Flor, Nikolajsen, & Staehelin Jensen, 2006; Giummarra, Gibson, Georgiou-Karistianis, & Bradshaw, 2007).

Furthermore, although localisation of the different components of body representation in the brain has been controversial, the study of body disorders has

helped identify a wide network of areas that play a central role (Berlucchi & Aglioti, 2010; Palermo et al., 2018). Hence, Chapter 5 aimed to explore brain insult in areas pertaining to this network and the effects on the representation of hands and face. In particular, Experiment 1 explored the relevance of sensorimotor information on the metric representation of the hands and face in a patient with a left precentral glioblastoma. In Experiment 2, the size representation of the hands and face was instead evaluated for a group of patients experiencing Personal Neglect after brain damage. In this case, the impact of cognitive processes associated to later stages of processing and higher-order body representations were explored.

2.5 Neuroplasticity of hands and face size representation (Chapter 6)

Multiple observations on the modulation of the size of the body in healthy individuals have been reported and have shed light in the underlying mechanisms of size perception. For example, bottom-up modulation of the size of the body is easily achieved by temporary disruption of afferent somatosensory information through anaesthesia, which is associated with a subjective enlargement of the anesthetized body part (Gandevia & Phegan, 1999; Paqueron et al., 2003). Top-down approaches have also been explored, such as repetitive Transcranial Magnetic Stimulation (rTMS), which can modulate size perception by targeting somatosensory areas (Giurgola, Pisoni, Maravita, Vallar, & Bolognini, 2019). This knowledge has supported the development of rehabilitative strategies in disorders characterised by a distorted body representation, such as chronic pain syndrome or AN. In these cases, modulation of the distorted representation has helped rehabilitating functions. For instance, in patients with chronic pain syndrome (who perceive the affected limb as enlarged), watching this limb through minifying lenses successfully instigates a reduction of pain (Moseley, Parsons, & Spence, 2008; Senkowski & Heinz, 2016). Moreover, in the case

of motor impairment after stroke, magnified view of the hand improved motor performance in several tasks, an effect that persisted for almost an hour after the lenses were removed (Ambron, Jax, Schettino, & Coslett, 2019, 2018).

With this in mind, neuroplasticity of the metric representation of the hands and face was explored in Chapter 6. In particular, modulatory top-down mechanisms in the representation of the hands and face were studied through the use of Transcranial Direct Current Stimulation (tDCS) in Experiment 1. In contrast, Experiment 2 explored the bottom-up modulation through the use of passive sensory stimulation delivered by an experimental portable device designed for this research.

2.6 Aims of the thesis

The primary aims of the thesis are detailed in this section.

- I. To review the distortions of the metrics of the hands by removing conceptual biases and to provide a clear account of underlying shifts (Experiment 1, Chapter 3).
- II. To investigate the distortions of the metrics of the face by developing a new task based on locational tasks (Experiment 2, Chapter 3).
- III. To understand the effects of long-term expertise (magic and sign language) in the size representation of hands and face (Chapter 4).
- IV. To investigate the effects of damage to underlying hand cortical area in the representation of hands and face (Experiment 1, Chapter 5).
- V. To study the representation of hands and faces in patients with Personal Neglect after stroke (Experiment 2, Chapter 5).

- VI. To examine the extent to which modulation of the representation of the size of the body (hands and face) can be achieved by tDCS or passive sensory stimulation, as well as consideration of the differential effect of these methods depending in the body part and sensory modality explored (Chapter 6).

Chapter 3: **Size distortions of the hands and face**



Josephine Cardin Photography

3.1 Introduction

We use our hands for a multitude of daily activities, from manipulating objects and tactile perception, to gestural expression and showing affection. No other body part has the ability for movement and interaction with the environment that the hands have, and their relevance has made them the focus of numerous studies (Grob, 2006). Similarly, our face is “us”, the expression of who we are, and centre of our identity. The face area is particularly compelling due to its relevance in constructing our sense of self. Together, the face and hands represent the most social part of our body, as we communicate concepts and express emotions. The interrelationship between hands and face is such that “[s]tates of mind are manifested, almost without exception, in the tensions and relaxations of facial muscles...and in the movements of limbs, and in particular of the hands” (Freud, 1953, p. 286, cited in Grob, 2006). Moreover, hands and face are interlinked not only in the daily functioning, but also due to their proximity in the somatosensory homunculus (Penfield & Rasmussen, 1950). For example, patients that experience phantom limbs after amputations can feel touches on the face also on the phantom limb (Ramachandran & Altschuler, 2009), due to ‘invasion’ of the deafferented hand area by the face area (Ramachandran, 1993). Similarly, others have found topographical invasion of the face area after severing the trigeminal face nerve (Clarke, Ragli, Janzer, Assal, & de Tribolet, 1996). Hence, the close functional and structural relationship between both justifies their concurrent study.

In order to utilize our hands accurately, we need to integrate multisensory information from different sources (i.e., vision, proprioception, motor information, somatosensation) to allow precise location of the limbs in space and to interact with the environment (De Vignemont, 2014). This information allows us to construct

qualitatively different representations, or multiple bodies in the brain, that help build a coherent and entire corporeal representation (Berlucchi & Aglioti, 2010). This representation needs to encompass information about the relative size of body segments (e.g., fingers), which may be stored as an underlying mental metric representation, the so-called *body model* (Longo et al., 2010; Longo & Haggard, 2010; Serino & Haggard, 2010). This model of body shape and size has been thoroughly studied in recent years, and appears to be highly and consistently distorted (e.g., Longo & Haggard, 2012a), even in congenital amputation (Longo, Long, & Haggard, 2012), as discussed in Chapter 2.

The hand's body model has been assessed by different variants of the *localisation task*, which requires participants to locate specific hand landmarks (fingertips and knuckles) whilst the hand is occluded under a board, by pointing on top with a baton (e.g., Longo & Haggard, 2010). The dorsum of the hands is found to be consistently underestimated in length and overestimated in width (e.g., Longo, 2014; Longo & Haggard, 2010; Longo, Mattioni, & Ganea, 2015), a pattern that is mimicked when considering the whole body (Fuentes, Longo, & Haggard, 2013). Interestingly, this is not the case for the palmar surface, which is perceived more accurately (Longo & Haggard, 2012a).

In healthy volunteers, these distortions appear as a result of interactions between somatosensory representation, tactile spatial acuity and other components, such as conceptual factors (Longo, Mattioni, & Ganea, 2015). In particular for somatosensation, body parts required for more precise actions contain a larger number of receptors and are represented more extensively in the cortex, which appears to affect the perceived body size (Linkenauger et al., 2015). The general view is that the distorted pattern of the hand matches the oval-shaped receptive fields on the dorsum,

which are oval-shaped in the proximo-distal axis, explaining the compression of perceived hand length and extension of the width (Longo & Haggard, 2012a; Longo et al., 2015). Tactile spatial acuity studies have also exhibited this effect, where highly sensitive areas perceive objects larger than less sensitive body parts, effect called ‘Weber’s illusion’ (Weber & Ross, 1978).

Other studies have found that a conceptual misunderstanding on the location of the knuckles may explain finger underestimation instead (Ambroziak, Tamè, & Longo, 2018; Longo, 2015b; Longo et al., 2015; Margolis & Longo, 2014). Specifically, location responses to knuckles appear shifted distally, closer to the fingertips than they really are, irrespective of the sensory modality used (e.g. Ambroziak et al., 2018; Margolis & Longo, 2014). Similarly, hip position is also not identified properly due to conceptual misunderstandings (Fuentes, Longo, et al., 2013); that is, healthy adults do not know where exactly they are located. Considering this finding, Longo (2015) proposed that conceptual distortions were underlying finger underestimation results, due to distal biases when locating the knuckles; whereas perceptual distortions (i.e., spatial warping of the hand tissue) were proposed for hand width overestimation (Longo et al., 2015).

Surprisingly, despite the aforementioned difficulties in locating the knuckles, studies still target them as a landmark to measure the metric representation of the hand, which means any results will be subject to this acknowledged bias. In other words, any underlying distortion in the size estimation of the hand will be, in some extent, due to conceptual biases not associated to actual representation. Hence, the first aim of Experiment 1 was to investigate the robustness of these distortions when locating unbiased landmarks. Rather than the knuckles, the hand representation was examined by locating the finger interspaces. These are the areas between the fingers, and

represent clear, salient physical boundaries for their layout. In fact, these are stronger attentional attractors when compared with knuckles (Longo, 2015b). As such, they may well be a clearer boundary to identify for finger length and may be a less ambiguous choice.

As well as spatial warping, another compelling aspect of these body distortions is the shift or displacement of spatial configuration of locational responses. This may account, at least in part, for the distortions. For example, participants may shift their responses towards a specific side of the space, accounting for the overestimation of the hand width. Previous studies have primarily focused on size distortions. The few that have attempted to study the shifts (e.g., Ambroziak et al., 2018; Ingram et al., 2019; Saulton, Bühlhoff, & de la Rosa, 2017) have just considered the shift of knuckles but have failed to provide an account on the shift of all landmarks (i.e., fingertips). As a result, the spatial structure of the location judgements has not been thoroughly explored. With this in mind, the second aim of Experiment 1 was to provide a detailed cartographic representation of the hand, considering proximal-distal and medio-lateral shifts of landmarks, while accounting for possible influences on the spatial shifts and underlying hand representation.

Owing to the predominance of studies focusing on the metric representation of hands, little is known about the metric of other body areas, such as the face. Indeed, face research has been primarily focused on face recognition across sensory modalities (Casey & Newell, 2005), whilst few attempts have been made to study the underlying body model. In general, the representation of the face is distorted, showing a tendency to overestimate width and underestimate length (D'Amour & Harris, 2017; Fuentes, Runa, et al., 2013; Linkenauger et al., 2015). In these studies, there is a predominant use of depictive tasks that rely on visual information, such as pointing to different

locations for size estimation on a computer screen (Fuentes, Runa, et al., 2013), drawing the head's outline (Bianchi, Savardi, & Bertamini, 2008) or using visual estimation tasks (D'Amour & Harris, 2017; Felisberti & Musholt, 2014; Linkenauger et al., 2015). However, it is not clear whether these techniques capture the representation of one's own face specifically, or a prototype face as a category (Fuentes, Runa, et al., 2013). Hence, Experiment 2 aimed to assess the metric representation of one's own face. For this, the size judgements for different face features were considered by developing a novel version of the localisation task, which enables to discern the metric representation of the face within personal space.

To summarise, this chapter sought to examine the following aims: a) to remove potential conceptual biases in hand size perception; b) to study the spatial configuration of locational judgements for the hand, and c) to assess the metric and spatial configuration of the face representation. By studying both hand and face with the same method, qualitative comparisons between both were done.

3.2 Experiment 1: study of the distortions of the metrics of the hands

3.2.1 Introduction

Landmarks on the hands refer to different sections (i.e., fingers or palm), whose functions and degree of movability are profoundly different. For example, the fingers are highly movable, and they are specialised in performing fine movements to interact with objects or reproduce intransitive gestures. On the contrary, the shape of the palm is rather stable, and its movement is much more limited compared to fingers. These aspects may play a crucial role on hand representation and may have a different impact on their localisation (i.e. shift). For these reasons, the first aim of this study was to provide a cartographic analysis of hand metric representation by considering the

underlying proximal-distal and mediolateral shifts of location judgements. To clarify, the shift, which could be understood as error, is the distance from the location of the real landmark (e.g., tip of the thumb) to the location of the pointing judgement performed by the participant.

Further, the second aim of this study was to consider if the previously reported distortion in hand representation will persist after removal of conceptual biases in the localisation task. For this, a modified version of the localisation task was designed, in which the interspaces were targeted rather than knuckles.

3.2.2 Methods and procedure

3.2.2.1 Participants

G* Power 3.1 was used for an a priori power analysis to determine the required sample size (Faul, Erdfelder, Buchner, & Lang, 2009). The effect sizes (Cohen's d) from previous studies were considered for this calculation. Cohen's d were in the area of 0.8 for finger length underestimation, whereas effect sizes for hand width overestimation were in the region of 1.5 (see Ganea & Longo, (2017)). Taking the smaller of these two numbers, a power analysis for one sample t-test (two-tailed) with an effect size of 0.8, alpha of 0.05, and power of 0.8 indicated the adequate sample size would be of 15.

Fifteen participants were recruited (8 females and 7 males) between 19 and 39 years of age ($M = 24.67$; $SD = 5.39$), who had 16.4 years of formal education on average ($SD = 1.76$). There is no clear agreement on gender effect in this task (Longo, 2019); however, previous studies have reported potential differences in hand perception depending on gender, being males more accurate than females (Coelho & Gonzalez, 2018b). Thus, the group had a similar proportion of both genders.

Handedness was assessed with the Oldfield Questionnaire (Oldfield, 1971). Scores range is from -1 to 1; scores below -0.5 indicate left-handedness; scores over +0.5 indicate right-handedness, and scores between -0.5 and +0.5 indicate ambidexterity. All participants but one (score = 0.36) were considered right-handed ($M = 0.86$; $SD = 0.17$). Participants were screened to consider their expertise levels on hand use, as specific exclusion criteria were established (no musicians, magicians, baseball players, etc. were included in this study). All participants gave written consent. This study was approved by Goldsmiths Research Ethics Committee.

3.2.2.2 Hand localisation task

To avoid ambiguity in the hand landmarks considered in the main task, participants were first shown each landmark on a schematic hand picture, and the labelling of landmarks was explained. Participants were then blindfolded and asked to perform a modified version of the localisation task (Longo & Haggard, 2010). In this modified version, the occluded board used in previous studies (e.g. Longo & Haggard, 2010) was replaced with a transparent Perspex sheet. In this way, the examiner was able to monitor the real location of each landmark to account for possible involuntary positional changes that may affect the perceived body structural description (Longo, 2015b; Tamè, Dransfield, Quettier, & Longo, 2017), or that could lead to relatively high rate of data exclusion (Medina & Duckett, 2017).

Blindfolded participants were comfortably seated in front of a table. The horizontal Perspex board (30 x 30 cm) was placed on the edge of the table, resting on four metal posts (each 8 cm high). A remote-controlled camera (Nikon D3200 single-lens reflex digital camera, 24.2 megapixels, 18 – 55 mm VR lens, 1.5x FOV crop, 23.2 x 15.4 mm DX-format CMOS APS sensor) was positioned at 90 centimetres suspended above the Perspex board and aligned with its central point. This was used

to take a picture after each pointing response. The Perspex board had two measuring tapes attached on the top and on the left sides to facilitate conversion of pixel units into centimetres for further analyses (see Figure 3.1A).

The experimenter positioned the participant's left hand underneath the Perspex board, whilst he/she was blindfolded. Hence, participants did not have any vision of the hand under the board. The middle finger was positioned in line with the participants' body midline. Fingers were spread out to a comfortable degree and participants were asked to keep their hand still for the entire duration of the task. This position of fingers has been consistently used in previous studies, as it increases the distinctiveness of fingers in somatosensory processing, in comparison with close posture (see Longo, 2015c). A small black dot (approx. 1-2mm diameter) was drawn on the tip of the right index fingernail to be used as reference for later analyses.

Nine landmarks were read aloud, one at a time (e.g., 'point to the interspace between middle and ring fingers'), corresponding to the 5 fingertips and the 4 finger interspaces (see Figure 3.1B). To avoid influences from added distortion to consecutive judgments (Medina & Duckett, 2017), landmarks were given in a randomised order, which was counterbalanced across participants. The method adopted to implicitly calculate the length and width of the hand may be biased by the misallocation of a single landmark. Therefore, each landmark was requested 6 times to minimize possible bias due to occasional misallocation of a single landmark, resulting in a total of 54 trials for each participant.

Participants were required to use their right index finger to point to the different landmarks requested (as in Blangero, Rossetti, Honoré, & Pisella, 2009; Ingram et al., 2019) rather than a baton. They were also allowed to clarify the landmark requested if investigator suspected there was a misunderstanding. As in previous studies, pointing

adjustments were allowed to prevent the variability of ballistic responses (Kammers, de Vignemont, Verhagen, & Dijkerman, 2009; Króliczak, Heard, Goodale, & Gregory, 2006; Longo & Haggard, 2012a). A picture of each response was taken for later coding. Following this, the participant was asked to place their right index finger back on the right side of the table and wait for the next command. Feedback was not given at any time.

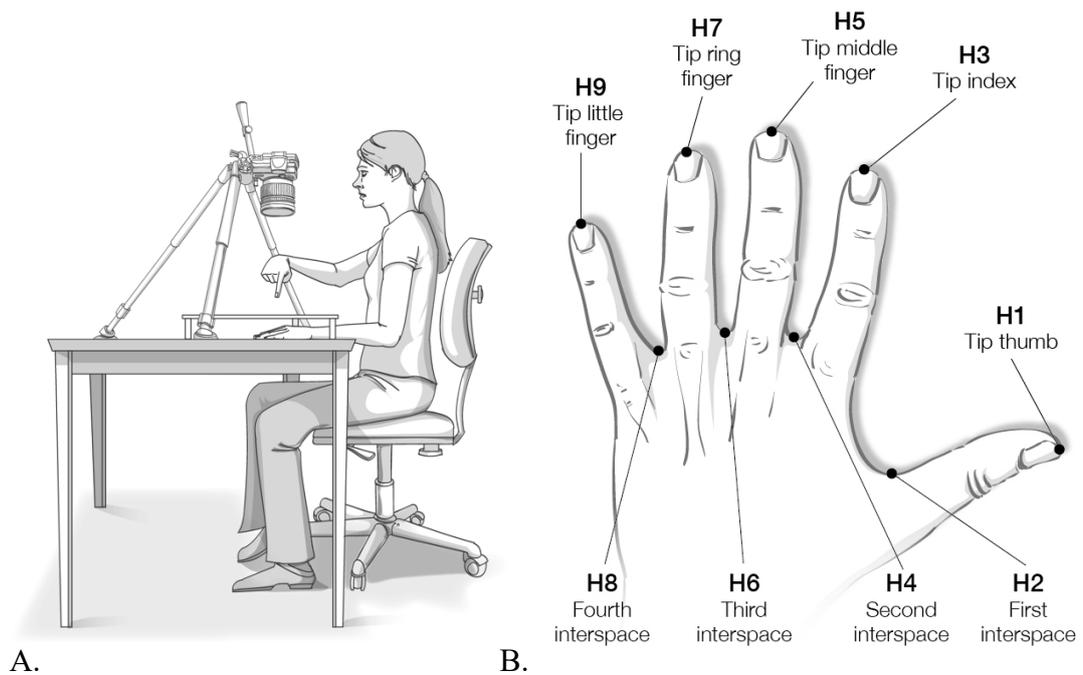


Figure 3.1. Hand localisation task.

Illustration of hand apparatus (A) and hand landmarks (B).

3.2.2.3 General analyses

Individual data was averaged across the 6 attempts at each finger landmark. An image analysis program developed using Borland C++ Builder (2007), converted pixel units into centimetres, with the origin at the bottom right corner of each picture. Responses were expressed as x and y coordinates and represented in a graph (see Figure 3.2A). The location of each pointing response was directly compared with the real location of the landmark, in order to calculate the shift in each axis.

The coordinate data was also used to calculate the inferred hand size (lengths and widths) and underlying shift of landmarks. Previous studies have used the information on the coordinates for single pointing responses to calculate distance between landmarks, and decode the so-called body model (e.g., Longo & Haggard, 2012). These distances are chosen between meaningful pairs of landmarks in order to calculate the length of fingers and the width of the hand (e.g., between H2 and H3 for the length of the thumb; see Figure 3.1B). Thus, the finger lengths, the hand's dorsum length, the hand's width and the width of the wrist were calculated for each hand.

These data were then used to: a) analyse the proximal-distal shift of perceived landmarks compared to real positions; b) to analyse the mediolateral shift of perceived landmarks, and c) to calculate the size perception (percentage of distortion). Proximal-distal shift was the y-axis difference between perceived and real coordinates; a positive value indicated a shift away from the body (distal bias). The mediolateral shift was the x-axis difference between perceived and real coordinates (in cm); a positive value indicated a rightward shift.

3.2.2.4 Statistical analyses

One sample t-tests were used to test the averaged shifts and size distortions against zero (no distortion). Paired samples t-tests were run to compare differences in shift or distortion between landmarks. Bonferroni correction was applied for multiple comparisons.

3.2.3 Results

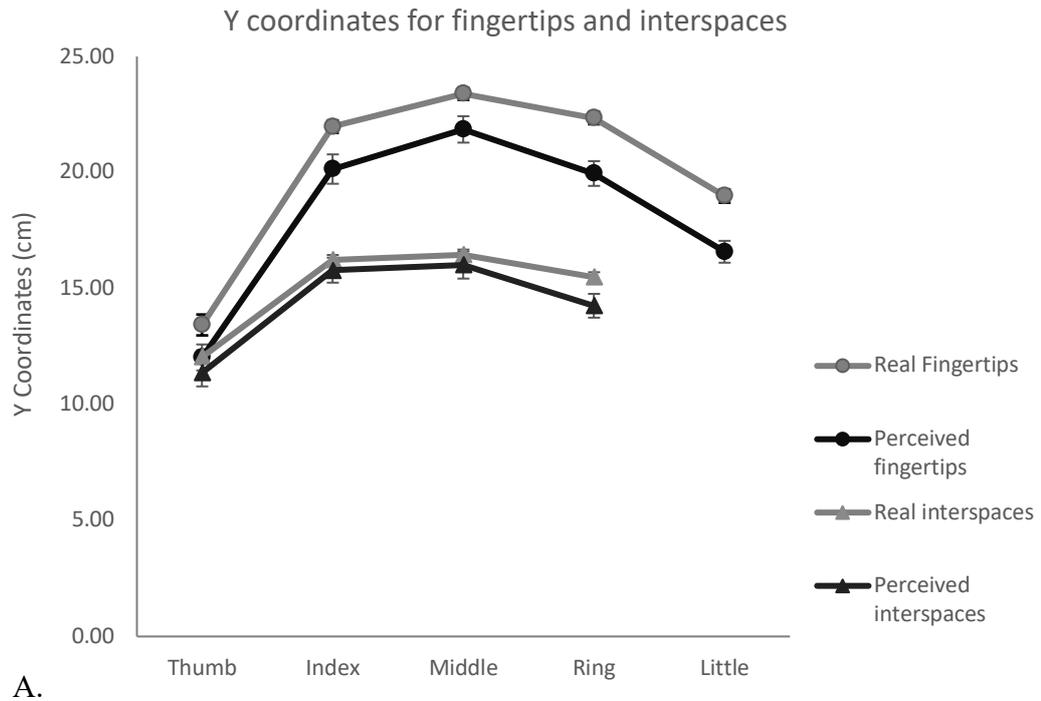
3.2.3.1 Proximal-distal shift of landmarks

The y coordinates (cm) of real location and location judgements are presented in a graph in Figure 3.2A. Visual inspection showed a proximal shift of fingertips,

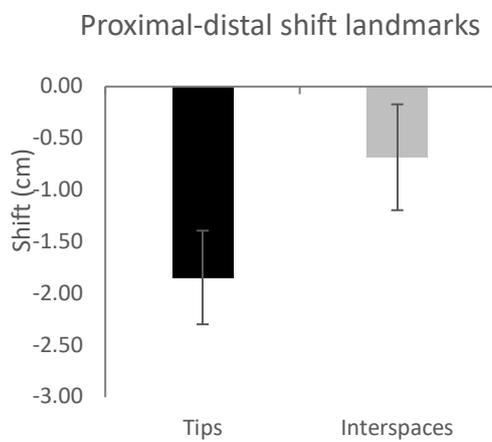
whilst the interspaces showed minimal shift in the y-axis. To explore the displacements of landmarks, the mean perceived shift per landmark was calculated (see Figure 3.2B).

Fingertips were perceived as shifted significantly closer to the body ($M = -1.84$ cm, $SD = 1.75$) than they really were [$t(14) = -4.08$, $p = .001$; $d = 1.05$]. Interspaces also showed proximal shift ($M = -.68$ cm, $SD = 1.98$); however, the overall difference between real and perceived positions was not significant [$t(14) = -1.34$, $p = .23$; $d = 0.34$]. A paired-sample t-test revealed significant differences in the perceived shift of landmarks [$t(14) = -4.35$, $p = .001$, $d = -1.12$], confirming fingertips were shifted significantly more than interspaces in the proximo-distal axis. As fingertips were the landmarks that were misallocated, further Bonferroni-corrected one sample t-test analyses (corrected p value of .01) were run to consider the proximal shift for each of them. With the exception of the thumb ($p = .025$), all the non-thumb fingertips were significantly shifted: index fingertip [$t(14) = -3.31$, $p = .005$, $d = -0.85$]; middle fingertip [$t(14) = -3.15$, $p = .007$, $d = -0.81$]; ring fingertip [$t(14) = -4.82$, $p = .001$, $d = -1.24$]; and little fingertip [$t(14) = -4.26$, $p = .001$, $d = -1.1$] (see Figure 3.2C for graphic representation).

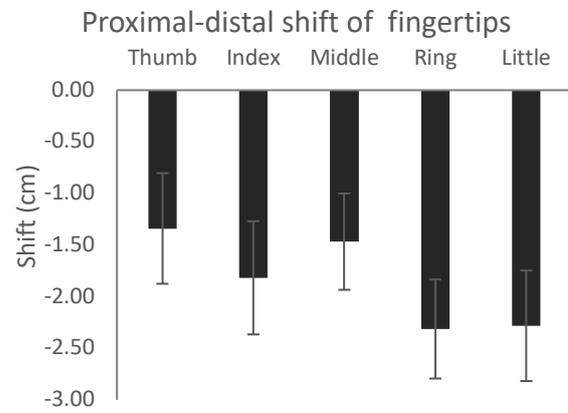
In summary, these results showed that participants shifted the location of their fingertips more than interspaces, which was in particular evident for the non-thumb fingers.



A.



B.



C.

Figure 3.2. Proximal-distal shift.

Representation of the real and perceived y coordinates (in cm) for fingertips and interspaces (A); proximal-distal shift of landmarks (cm) averaged across fingertips and interspaces for all participants (B), and averaged proximal-distal shift of fingertips per finger (C). Error bars represent the Standard Error of the Mean.

3.2.3.2 Mediolateral shift of landmarks

Interspaces were, on average, shifted towards the left hemisphere ($M = -.59$ cm, $SD = 1.88$); however, this shift was not significant [$t(14) = -1.21$, $p = .25$, $d = -0.31$].

Similarly, the fingertips were also shifted towards the left ($M = -.22$ cm, $SD = 1.79$), but not significantly so [$t(14) = -.47$, $p = .65$, $d = -.12$] (see Figure 3.3A).

As with proximal shift, Bonferroni-corrected one sample t-tests were run to compare the shifts of single fingers against zero (corrected p value of .01). There was a significant difference for the ring finger [$t(14) = -3.17$, $p = .007$; $d = -0.82$] and a trend for the little finger [$t(14) = -2.46$, $p = .027$; $d = -0.64$]. No other comparisons provided significant results for the other fingers (for the thumb [$t(14) = .41$, $p = .69$, $d = .1$]; for the index finger [$t(14) = .89$, $p = .39$, $d = .23$]; and for the middle finger [$t(14) = -1.32$, $p = .21$, $d = .34$]) (see Figure 3.3B).

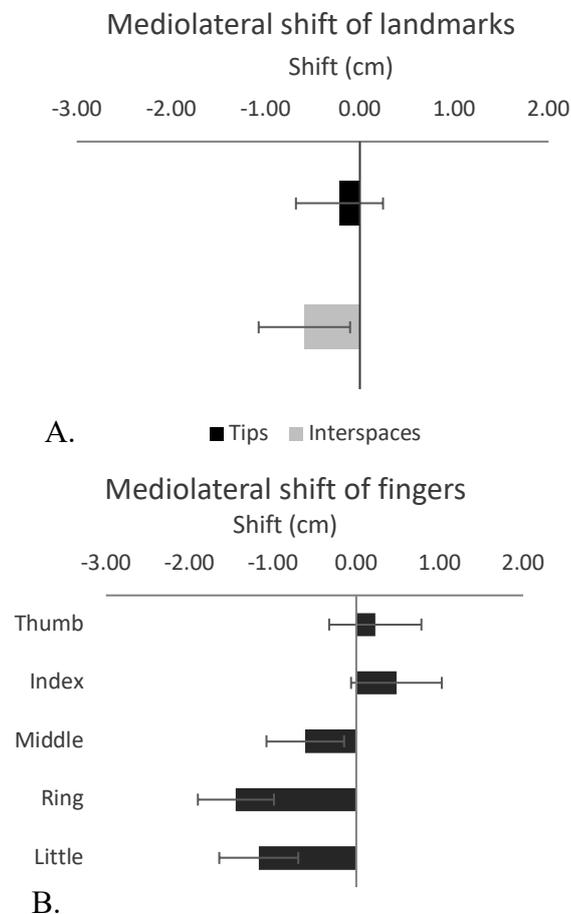


Figure 3.3. Mediolateral shift of landmarks.

Mediolateral shift averaged for fingertips and interspaces (A), and mediolateral shift per finger (B). Error bars represent the Standard Error of the Mean.

3.2.3.3 Inferred hand size

The real and perceived size of fingers and width of hand was calculated to then obtain the percentage of over/underestimation of their real size. On average, participants perceived the length of their fingers underestimated ($M = -9.53\%$, $SD = 15.99$) and the distortion was significant [$t(14) = -2.31$, $p = .04$, $d = .6$].

Since the underestimation of fingers was not equally distributed (e.g., Longo, 2015a), the distortion of each finger was tested against zero (no distortion) via one-sample t-tests (Bonferroni corrected critical p value of .01). The distortion was not significant for the thumb ($M = 3.22\%$, $SD = 19.16$), index ($M = -9.49\%$, $SD = 15.94$) or middle finger ($M = -8.36\%$, $SD = 21.3$) (all $ps. > .01$). Instead, the ring ($M = -13.83\%$, $SD = 19.95$) and little fingers ($M = -19.18\%$, $SD = 27.25$) were, overall, the most underestimated in size. The distortion was close to significance for both (ring: [$t(14) = -2.68$, $p = .018$, $d = -.69$]; little: [$t(14) = -2.73$, $p = .016$, $d = -.7$]) (see Figure 3.4A).

The width of the hand was calculated from the distance between the second interspace (between index and middle fingers) and the fourth interspace (between the ring and little fingers, see Figure 3.1B). The width of the hand was overestimated ($M = 44.54\%$, $SD = 23.45$), distortion that was significant [$t(14) = 6.11$, $p < .001$, $d = 1.58$] (see Figure 3.4B).

To explore these results further, the spacing between interspaces was calculated, as in Longo & Haggard (2010). The distance between the first and second interspaces (between thumb and index, see Figure 3.1B) was overestimated by a 6.32% ($SD = 17.25$), distortion that did not reach significance [$t(14) = 1.42$, $p = .18$, $d = .37$]. In contrast, the distance between the second and third interspaces (between index and middle fingers) was overestimated by a 57.69% ($SD = 40.45$), which was significant

[$t(14) = 5.52, p < .001, d = 1.43$]. Similarly, the distance between the third and fourth interspaces (between middle and little fingers) was also overestimated by a 43.38% (SD = 49.94), and significantly so [$t(14) = 3.3.6, p = .005, d = .87$] (see Figure 3.4B).

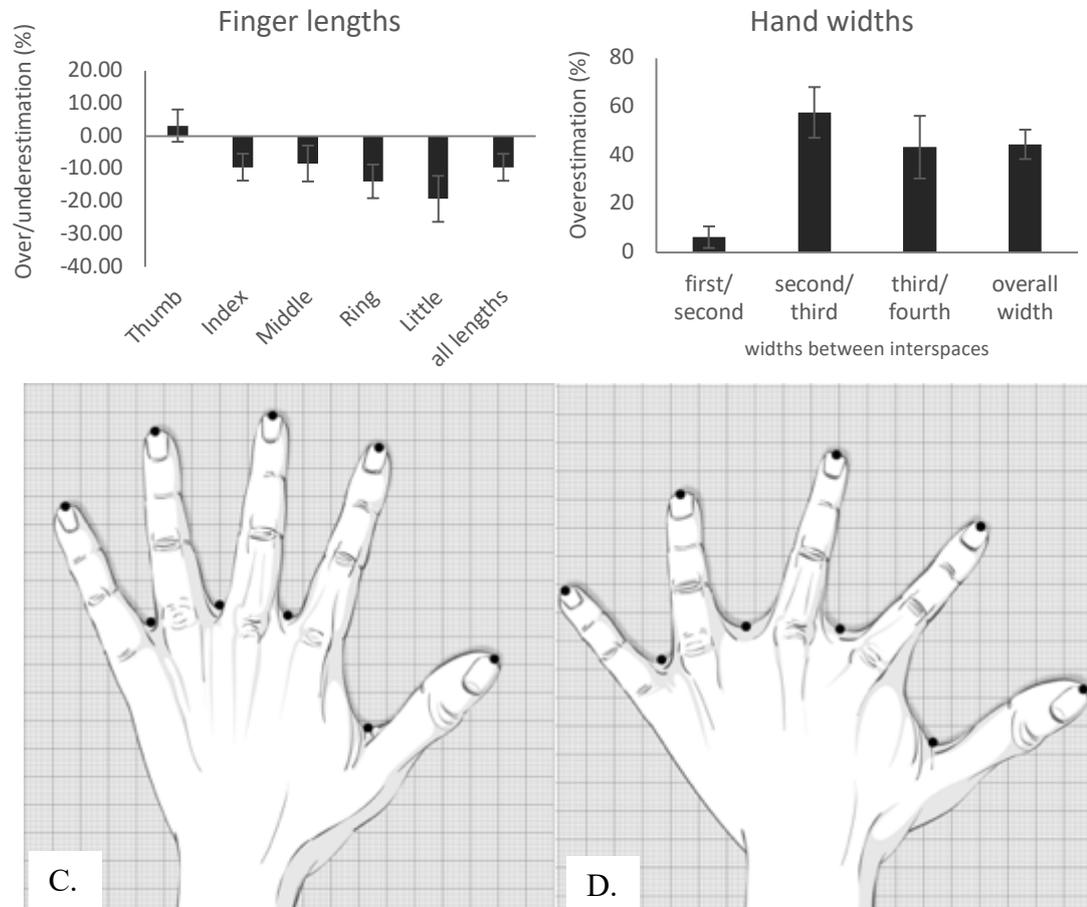


Figure 3.4. Inferred hand size.

Graph representing finger length underestimation for all fingers and averaged across them (A); graph representing the widths between adjacent interspaces, and the overall width of the hand (B), and pictorial representation of the real sized hand (C) and the perceived hand size (D).

These results confirmed that the reported shifts of location judgements were translated into distorted representation of the hand, which mimics the pattern previously reported in numerous studies (see Longo (2019) for a recent summary) (see Figure 3.4C and D for pictorial representation of real and perceived hand size).

3.2.4 Preliminary discussion

This study has explored the different influences in the location task used to assess the representation of the size of hands. Previous studies had reported conceptual biases in the understanding of the location of knuckles which ought to be removed to obtain a more truthful depiction of the metrics of the hands. Hence, in this study, instead than the knuckles, participants were required to locate the finger interspaces. Further changes to the task to remove other biases saw participants pointing with their index finger, rather than a baton. Lastly, no previous studies had fully explored the spatial distribution of the location judgements in this task. Thus, a full account of the shifts of location responses was provided.

The findings in this study confirmed the typical distortion of hand representation, consisting of shorter fingers and wider hand dorsum. Interestingly, the misallocation of pointing responses in the localisation task was not uniform across landmarks and fingers. Specifically, the study of the fingertips' localisation provided a characteristic pattern of shifts, with a tendency to displace their location closer to the interspaces than they really were, leading to underestimation of finger length. A possible reason for this type of bias is that fingers are involved in precision movements where fingers close around an object, normally seen contracted. Therefore, we construct a mental image from this experience, storing information about typical position of hand segments (Bremner, Holmes, & Spence, 2008). In order to judge the representation of a body part, we then use this stored mental image (Smeets, Klugkist, Rooden, Anema, & Postma, 2009). Thus, it is possible that this mental image of typical posture may influence location of landmarks (Fraser & Harris, 2017) and explain the proximal shifts found for the fingertips. Interestingly, a recent study has shown how location error for fingertips reduced when the fingers were all flexed under the palm

(Dandu, Kuling, & Visell, 2018), supporting this hypothesis. In line with this interpretation, other studies have also reported how the functional workspace and manual experience influence the localisation judgements of the hands (Fraser & Harris, 2016). That is, the typical position of the hand will influence location judgements by shifting them towards the direction of usual movement or standard positions. This is supported by studies using manual training in which the proprioceptive shifts changed direction towards the new task space (Ghilardi, Gordon, & Ghez, 1995). Similarly, size distortions in upper and lower limbs have been found to be guided by the functional use of these limbs (Caggiano & Cocchini, 2020; K. D. Stone et al., 2018).

Moreover, it is plausible that misallocation judgements of the fingertips are also influenced by uncertainty. It cannot be forgotten that this task involves the use of afferent proprioceptive information to locate different landmarks on the hand. Fingertips are very movable and can assume many different locations, therefore their position is more variable and uncertain as the hand is kept still (De Vignemont, 2014; Gritsenko, Krouchev, & Kalaska, 2007; Medina & Duckett, 2017). In fact, distal body parts, such as fingertips, are considered harder to locate due to required computations from receptors, joints, and muscles (De Vignemont, 2014). Owing to the uncertainty of their location, localisation is biased towards frequently held positions, based on experience, towards central positions (Gritsenko et al., 2007). Hence, there is a bias to locate these landmarks towards the centre of the ‘prototype’ or target area: the dorsum of the hand. This effect has been also found when estimating the remembered location of dots within given boundaries (Huttenlocher, Hedges, & Duncan, 1991), which is associated with other perceptual processes related to somatosensation (Medina & Coslett, 2016).

To support this, the accuracy improved for landmarks that do not show this range of movement or uncertainty; that is, interspaces. Indeed, contrary to previous studies (Medina & Duckett, 2017), the proximal-distal shift of interspaces was not significant. Similarly, in Longo & Haggard (2012), the perception of the palm was explored by targeting the crease at the base of the fingers, rather than the knuckles. They found less distortion (both in width and length) in the perception of the palm, and postulated differences in size due to different perception of hand regions (i.e., palm versus dorsum). However, it may have actually been due to removal of the confounding effect of conceptual biases for the knuckles (Saulton et al., 2017). Thus, interspaces may represent clearer boundary for the fingers, a potentially more robust landmark to consider in future studies.

Further, the less-functional fingers (ring and little fingers) were the ones 'harder to locate', with larger shifts both in the proximal-distal and mediolateral axes. This difference across fingers cannot be entirely explained by a finger difference on predictability of position, as there is not a higher degree of movability for ring and little fingers compared to the other fingers. This misallocation seems to reflect a different use and role on finger movement. Fingers involved in fine motor actions (thumb and index) are represented more accurately in the body model (Coelho, Zaninelli, & Gonzalez, 2017; Longo & Haggard, 2012a), and more extensively in primary somatosensory cortex (Duncan & Boynton, 2007), especially for the thumb (Martuzzi, van der Zwaag, Farthouat, Gruetter, & Blanke, 2014; Penfield & Boldrey, 1937). These fingers are used for more dexterous tasks, such as grasping, and their localisation has developed to be more accurate (Dandu et al., 2018). On the contrary, ring and little fingers are less crucial for fine movements and it follows that their representation may be less accurate, making location judgements less precise. The

impact of body part function during actions has been considered in recent studies (e.g., Caggiano & Cocchini, 2019; Ferretti, 2016), underlying the functional relationship between everyday actions and the role of different body parts.

In summary, these results have shown a specific pattern of shifted location judgements that underlies the distorted representation of the metrics of the hand, which was not uniform across different sections (i.e., fingertips and interspaces). Hence, the hand size is closely related to misallocation judgements, which may be affected by different degrees of movability, functionality, and typical posture. Thus, a combination of factors modulates the final metric representation of our hand. However, it is unclear how this would generalise to other body parts. This has been rarely attempted, with only a recent study adapting the location task to measure the metric representation of lower limbs (K. D. Stone et al., 2018). Surprisingly, no previous studies have attempted to investigate the implicit body model of the face. Thus, there remains an important gap in understanding how one's own face is represented. Experiment 2 was designed with this purpose in mind.

3.3 Experiment 2: study on the distortions of the metrics of the face¹

3.3.1 Introduction

The face represents one of the most social parts of our body, it is our presentation to the world and how others remember us. The face defines us more than any other body part, and is involved in important and complex functions, such as eye-hand coordination, eating and speaking. The face is instrumental to create a sense of self, and to construct our identity (Tsakiris, 2008). Threats to the integrity of the face

¹ The information from this experiment is also included in a publication by Mora, Cowie, Banissy & Cochini (2018). I had a major role in the design, data collection, analysis and writing up of the article.

cause severe loss of the sense of identity, such as after face disfigurement (Callahan, 2005). The face is a singular element of the body, which is considered distinct and separate to others, as it is processed by a highly specialised network (Webster & MacLin, 1999). In order to recognise one's own face, a mental representation of the self-face needs to exist (Tajadura-Jiménez, Longo, Coleman, & Tsakiris, 2012). This knowledge is not a priori, as the infant would have never seen oneself on the mirror, and it must develop overtime, to accommodate changes due to aging. This requires also a matching between sensorimotor experience and behaviour seen in the mirror, which will allow successful self-identification (Tajadura-Jiménez et al., 2012). Self-face is better discriminated and perceived than other familiar and non-familiar faces (Keenan et al., 1999; Sui & Han, 2007). Hence, a robust representation needs to be stored (Keyes & Brady, 2010), and the more robust it is, the better. Furthermore, face features are processed in a configural manner, and spacing between them is required for discriminating between one's own face and other individual faces (Tsao & Livingstone, 2008). This ability, interestingly, appears to rely on two sources of information: first-order configuration (e.g., mouth below the nose), and second-order configurations, which refer to the spacing between features (Diamond & Carey, 1986). The second-order configurations are of interest when discriminating faces and are more complex than the first-order (Piepers & Robbins, 2012). Beyond the question of whether faces are discriminated or perceived in a holistic or configural manner, there is interest to further understand the structure of the self-face representation, which should be affected by all these factors.

In this second experiment, the self-face representation was explored, with a number of predictions. Previous studies on structural representation have suggested an influence of somatosensory representation on size perception (e.g. Longo, Azañón, &

Haggard, 2010), and it has been proposed that the somatosensory homunculus may provide the base system from which an implicit body model is based. Facial features occupy differently sized areas in the somatosensory homunculus, with overrepresented mouth and tongue (McCormack, 2014). If homuncular size representation influences perceived size of the body part, highly represented features will be perceived as bigger. Thus, a distorted representation of face features was hypothesized, with an overestimation of areas such as the mouth, compared to the nose. Additionally, different face portions have different mobility, which may affect body size perception, as seen for the hands. Previous studies have shown overestimation of highly movable body parts, such as the ankle (K. D. Stone et al., 2018) and wrists (Longo, 2017c), and a compartmentalised representation of upper and lower face regions (Fuentes, Runa, et al., 2013). Thus, this study sought to explore the size differences between the representation of top (eyes) and bottom (mouth) face areas anticipating overestimation for areas whose movement tends to change shape and size to a much greater extent (bottom). Lastly, the spatial shift that underlies the aforementioned distortions of face representation was analysed, as in the previous experiment. In detail, the horizontal and vertical shifts in pointing judgements were calculated, to consider the symmetry of these judgements.

3.3.2 Methods and procedure

3.3.2.1 Participants

Following the hand study, an a priori power analysis for one sample t-test (two-tailed) with an effect size of 0.8, alpha of 0.05, and power of 0.8 was carried out to set the sample size in G* Power 3.1 (Faul et al., 2009). The power analysis indicated the adequate sample size would be of 15.

Seventeen participants (10 females and 7 males) between 19 and 39 years of age ($M = 24.67$; $SD = 5.39$) were recruited. On average, participants had 16.5 years of formal education ($SD = 1.2$).

Handedness was assessed with the Oldfield Questionnaire (Oldfield, 1971), on which scores range from -1 to 1. Scores below -0.5 indicate left-handedness, scores over +0.5 indicate right-handedness and scores between -0.5 and +0.5 indicate ambidexterity. All participants but one (score = 0.36) were considered right-handed ($M = 0.90$; $SD = 0.11$; range -1 to +1).

The study was approved by the Goldsmiths Research Committee and it was carried out in accordance with the Declaration of Helsinki. All participants gave written informed consent.

3.3.2.2 Face location task

Participants were comfortably sat in front of a table. A vertical acrylic sheet (30 x 30 cm) resting on two metal posts (20 cm of height) was placed in front of them. A chin rest was positioned on the edge of the table, between the participant and the acrylic sheet. To take into consideration the curved shape of the face introducing some lateral distortion, the face was positioned very close to the acrylic setting (1 cm from the tip of the nose).

A Nikon D3200 camera (single-lens reflex digital camera, 24.2 megapixels, 18 – 55 mm VR lens, 1.5x FOV crop, 23.2 x 15.4 mm DX-format CMOS APS sensor) was positioned on a tripod in front of the sheet at 90 cm from it. The camera focus was exactly on the centre of it, and camera lens was set at 18mm. Attached to the sheet there were two measuring tapes, one along the left edge and another along the top edge, to facilitate conversion of pixels into centimetres for later analyses (see Figure 3.5A).

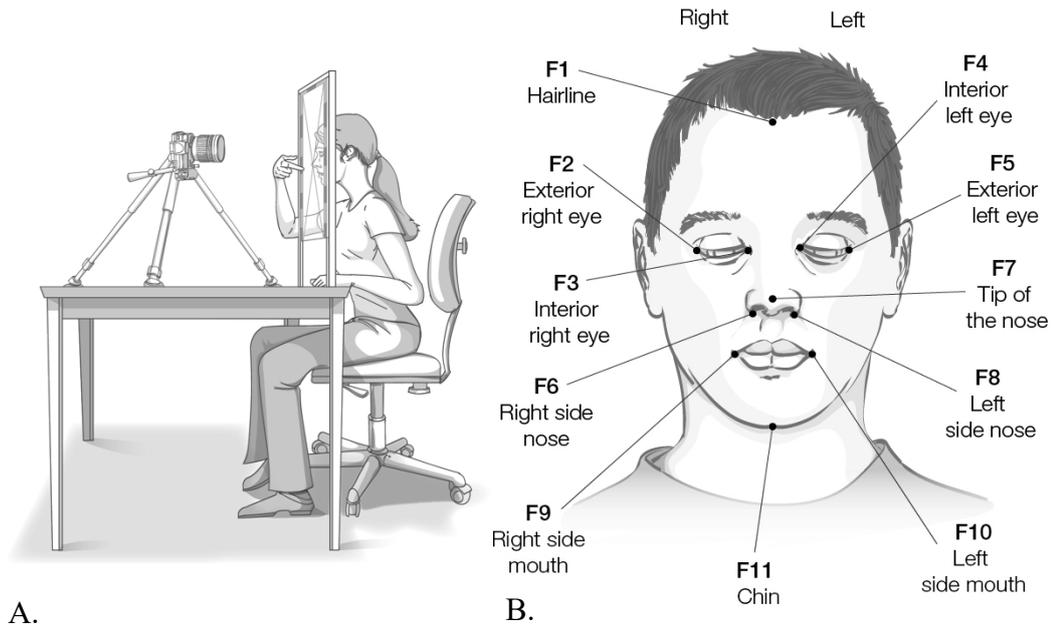


Figure 3.5. Face localisation task.

Depiction of the face setting (A) and drawing with face landmarks and labels considered in the localisation task (B). From Mora et al. (2018).

A small black dot (1-2 mm of diameter) was drawn on participants' right index fingernail as reference for later analysis of pointing responses. Participants were asked to position their head on the chin rest so that the tip of the nose was aligned with the camera focus. They had to remain silent and avoid any movement of the face for the entire experiment. Following a pilot study and previous literature (Fuentes, Runa, et al., 2013; Linkenauger et al., 2015), 11 unambiguous face landmarks were identified (i.e., hairline, corners of each eye, tip of nose, lateral side of both nostrils, corners of the mouth and chin) to be located (see Figure 3.5B). To ensure participants understood the labels given to the different landmarks of the face, they were asked to identify these landmarks on a schematic picture placed in front of them. Then, they were asked to close their eyes and imagine the landmarks on the acrylic sheet as if they were projected in a straight line. They were asked to point on the acrylic sheet with their right index finger to the different landmarks, which were read aloud, one at a time, in

random order and counterbalanced across participants. The task was repeated six times for a total of 66 trials per participant. The method adopted to implicitly calculate the length and width of face structures may be biased by the misallocation of a single landmark. Therefore, each landmark was requested 6 times to minimize possible bias due to occasional misallocation of a single landmark.

Pointing corrections were allowed to adjust the position of the right index finger, as ballistic pointing tends to be highly variable (Kammers, de Vignemont, et al., 2009; Króliczak et al., 2006). A picture was taken (6016×4000 pixels) of each response for later coding. Following this, the participant was asked to place the right index finger back on the right side of the table and wait for the next command. Feedback was not given at any time.

3.3.2.3 General analyses

A total of 66 pictures (6 for each of the 11 landmarks) were collected for each participant. An image analysis program was developed *ad-hoc* for this study using Borland C++ Builder (2007), as in the previous experiment. This program converted pixel units into centimetres. Responses were expressed as x and y coordinates, with the origin at the left top corner of each picture. For each pointing response, the x and y coordinates of the real and the perceived location were collected. Data was averaged across the 6 attempts at each landmark. Following this, shifts were calculated. The vertical shift was the y-axis difference between perceived and real y-coordinates; a positive value indicated the landmark was perceived higher than real location, whilst a negative value indicated the landmark was perceived lower than real location, towards the body. Horizontal shift was the x-axis difference between perceived and real coordinates; a positive value indicated a rightwards shift. Further, the distance between two landmarks (e.g., F2 and F3, see Figure 3.5B) was considered to calculate

length and width (in cm) of the different face features (i.e., nose, eyes, mouth); which were then averaged across the recruited participants. Comparison of the real and the perceived distances provided information about the percentage of over and underestimation. To sum up, this data was then used to: a) create schematic map of real and perceived faces; b) to analyse the shift of perceived landmarks compared to real position; and finally, c) to analyse face length and width of its features.

3.3.2.4 Statistical analyses

One sample t-tests were used to test the averaged shifts and size distortions against zero (no distortion). Paired samples t-tests were run to compare differences in shift or distortion between facial features. A repeated-measures ANOVA was run to investigate the differences in the distortion of facial features. Bonferroni correction was applied for multiple comparisons.

3.3.3 Results

3.3.3.1 Perceived shift of landmarks

Averaged coordinates for x and y axes between the 17 participants were used for analyses and to produce pictorial representations of real and perceived face sizes (see Figure 3.6A). Perceived and real conditions were compared for each feature by means of a one sample t-test (Bonferroni corrected $p < .01$). When considering vertical shift, all areas were perceived to be significantly lower (closer to the trunk) than their real location (right eye [$t(16) = -6.34, p = .001, d = 1.53$]; left eye [$t(16) = -4.7, p = .001, d = 1.14$]; nose [$t(16) = -3.36, p = .004, d = 0.82$]; mouth [$t(16) = -6.44, p = .001, d = 1.56$], and other areas (hairline and chin) [$t(16) = -3.93, p = .001, d = 0.95$] (see Figure 3.6B).

For the horizontal shift, all face areas were perceived shifted further to the right than the real position, except for the left eye (see Figure 3.6C). However, only the right eye showed a significant rightward shift [$t(16) = 5.38, p = .001, d = 1.3$].

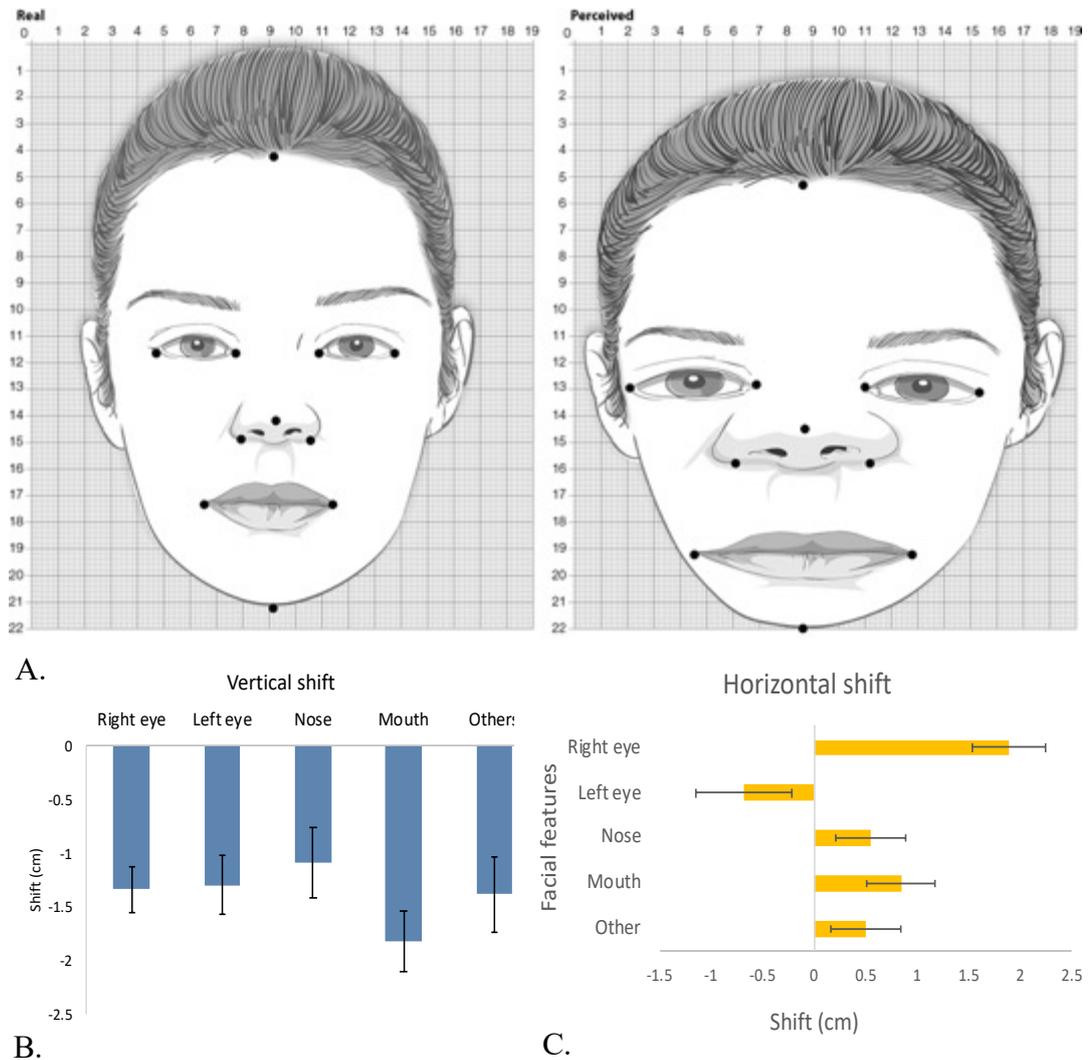


Figure 3.6 Face results.

Pictorial representation of the real and perceived face representations (A); bar graph representing the vertical shift of landmarks (B), and bar graph representing the horizontal shift of landmarks (C). Error bars represent the Standard Error of the Mean.

3.3.3.2 Face length

The real and perceived length of three distances were considered: i) overall face length (i.e., from hairline F1 to chin F11; see Figure 3.5); ii) top-half length (i.e., from hairline F1 to tip of the nose F7), and iii) bottom-half length (i.e., from tip of the nose F7 to chin F11). These distances were averaged across all participants.

The overall face length was slightly underestimated ($M = -1.62\%$; $SD = 9.55$), but not significantly so [$t(16) = 0.759$, $p = .46$; $d = 0.18$]. When considering different halves of the face, the top half of the face was significantly underestimated ($M = -6.81\%$, $SD = 12.47$), [$t(16) = 2.37$; $p = .03$; $d = 0.58$], whereas the bottom half showed overestimation ($M = 6.60\%$, $SD = 17.74$) but not significantly so [$t(16) = -1.45$; $p = .16$; $d = 0.35$] (see Figure 3.7). When correction for the two comparisons is applied (p value of .25), the difference in top face areas becomes a trend. Nevertheless, the percentage of over/underestimation between face halves was significant, [$t(16) = -2.42$, $p = .03$, $d = 0.59$], indicating that the top half of the face is perceived to be significantly shorter than the bottom half.

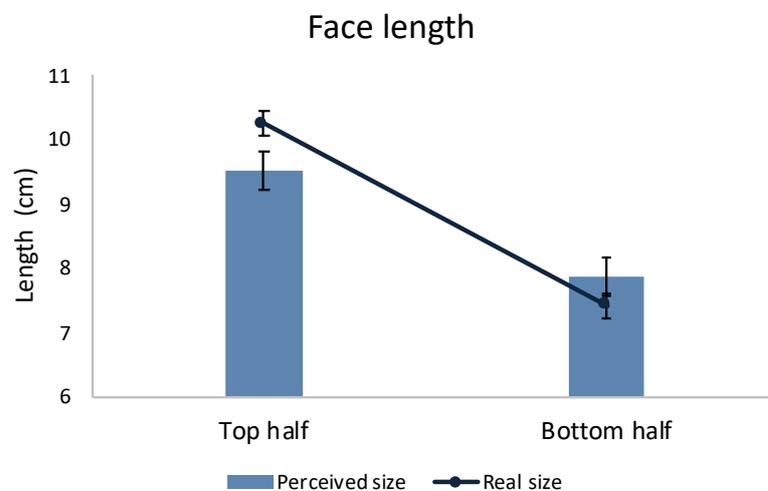


Figure 3.7. Face length.

Graph representing the real (line) and perceived (bars) length of the top and bottom halves of the face in centimetres. The error bars represent the Standard Error of the Mean.

3.3.3.3 Face widths

Five different widths were considered: right eye (i.e. F2 to F3; see Figure 3.5B), left eye (i.e., F4 to F5), distance between eyes (i.e., F3 to F4), nose (i.e., F6 to F8), and mouth (F9 to F10). Distances were calculated in centimetres and results were averaged across all participants (see Figure 3.8).

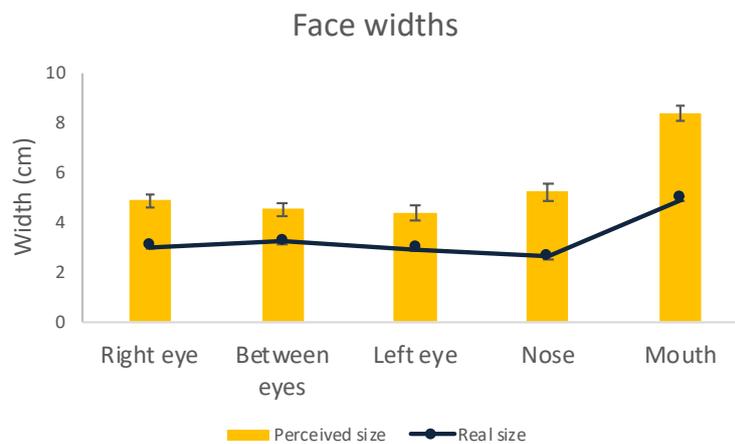


Figure 3.8. Face widths.

Graph representing the real (line) and perceived (bars) widths of the face features in centimetres. The error bars represent the Standard Error of the Mean.

A repeated-measures ANOVA was run with two factors: Condition (real versus perceived width in centimetres) and Area (the five facial features detailed above). There was a significant effect of Condition [$F(1,16) = 91.79, p = .001; \eta^2 = 0.85$], suggesting that participants showed an overall distortion of perceived face width. There was also a significant effect of Area [$F(4,64) = 111.79, p = .001, \eta^2 = 0.88$] and a significant interaction between Condition and Area [$F(2.66, 42.51) = 12.68, p = .001; \eta^2 = 0.44$] (Greenhouse – Geisser correction), indicating variability in the magnitude of width perception depending on the facial area considered. Bonferroni corrected post-hoc analyses (critical p value $< .01$) showed that all areas were

perceived significantly larger than their real size: right eye [$t(16) = -6.58, p = .001; d = 1.6$]; between eyes [$t(16) = -5.91, p = .001; d = 1.43$]; left eye [$t(16) = -4.29, p = .001; d = 1.04$]; nose [$t(16) = -7.04, p = .001; d = 1.71$]; and mouth [$t(16) = -10.44, p = .001; d = 2.53$]. However, there were differences in the degree of distortion depending on the facial feature considered. This was most apparent for the nose (103.03%), followed by the mouth (70.38%), right eye (64.30%), left eye (52.81%), and between eyes (40.4%). Bonferroni corrected t-tests (critical p value $< .008$) were run to check if the differences in the degree of distortion were significant between facial features. Significant differences were found between the distortion for the nose and all the other facial features, indicating that the nose is perceived significantly more distorted than the right eye [$t(16) = -3.46, p = .003, d = -0.84$]; the left eye [$t(16) = -3.51, p = .003, d = -0.85$] and the mouth [$t(16) = 3.37, p = .004, d = 0.82$]. No significant differences were found in the distortions between the other facial features (all $ps. > .008$).

3.3.4 Preliminary discussion

For the first time the metric and locational representation of facial features have been assessed with a proprioceptive localisation task. For this, a new location task was developed, in which participants were required to point to specific landmarks on the face to then discern the metric representation of the face and its features. Results showed a significant shift of landmarks, both in the proximo-distal and mediolateral axes. These shifts in location judgements meant that there were distortions in the representation of the size of the face. Specifically, there was overall overestimation of the width of facial features, with minimal underestimation of face length, which was compartmentalised into upper and lower regions.

This shift could be explained due to the stored mental image of the face, which includes the possibility of movements, shifting responses towards most typical position of the body part. It has been found that the visual experience with a body part will, in turn, affect the size this body part is perceived. For instance, this happens with the width of thighs, which are overestimated, as we normally see them wider when seating (K. D. Stone et al., 2018). A mental image of a body part is needed in order to judge its metric representation (Smeets et al., 2009) and to compare to others too (Walton & Hills, 2012). A particular quality of the mental image of the face in comparison to the hands or other body parts is that is constructed secondarily; that is, we only see our face reflected on a mirror, captured in a picture or recorded in a video. Furthermore, the face is normally seen in movement (Piepers & Robbins, 2012; Tsakiris, 2008), and the stored image of the face may include details of motor capabilities and its layout, as it occurs for other body parts, such as the hands (Bremner et al., 2008) or wrists (Longo, 2017c). To explore this, the shift of locational responses was analysed. All face areas were perceived shifted down, closer to the body than they really were, confirming this hypothesis.

Further, the horizontal shifts of locational responses were also explored to consider any differences in the perception of the body in the personal space. Rather than showing a symmetrical representation of the face, there was a predominance to shift responses to right landmarks towards the right hemispace. The rightward shift might be due to the fact that the participants were asked to use the right hand to point. However, if this was the case, the leftwards shift for the left eye should not have been found. This finding seems more in line with previous studies on body space representation, which showed that right-handers tend to overestimate the size of the right portion of the body (Hach & Schütz-Bosbach, 2014). In particular, pointing

responses to rightwards areas of the hip and waist were located further from midsagittal plane than left areas, even when pointing was performed with the contralateral hand (Hach & Schütz-Bosbach, 2010). Furthermore, right-handers perceive their right hand and arm to be longer than the left one (Linkenauger et al., 2009). This asymmetry is usually reported in more implicit tasks of body representation, such as the pointing task, but not with more explicit tasks, such as body image (Hach & Schütz-Bosbach, 2014). However, this is a debatable issue and a recent meta-analysis study suggests that facial self-processing may be more related to activity of the right hemisphere (Hu et al., 2016), rather than handedness.

As initially hypothesized, length perception was not unitary and appeared to be compartmentalised into two separate sections: the upper (underestimated) and bottom (overestimated) regions. The compartmentalised representation of face length may be associated with the different functionality and relevance of each face portion, but also with the capacity of facial areas to change size and shape. Apart from the eyebrows, the upper face areas are relatively stable in size and shape, whilst the bottom areas are subject to more positional changes. During a wide array of daily functions, such as speech or feeding (Cavina-Pratesi, Kuhn, Ietswaart, & da Milner, 2011; Fuentes, Runa, et al., 2013), movement of the lower jaw means that the effective size and shape of the lower face is subject to changes. This may lead to a perceived overestimation of its length. Similar to observations of size overestimation for ankles and wrists (Longo, 2017; Stone et al., 2018), the direction of distortion for the lower face follows the direction of movement. That is, the mouth and chin are perceived lower, shifted towards the body, increasing the perceived length of this region. Indeed, functionality of a body part also affects its size perception (Linkenauger et al., 2009).

Further, the neural representation of these two face portions is distinct (Jain, Qi, Catania, & Kaas, 2001; Ullrich & Woolsey, 1954; Woolsey, Marshall, & Bard, 1942), supported by different innervation of upper and lower areas by the trigeminal nerve (Dreyer, Loe, Metz, & Whitsel, 1975). These findings are consistent with face image studies where this compartmentalisation has also been reported (Fuentes et al., 2013). However, in this study, the overall perceived length is more accurate than previously reported, probably due to the pointing task used here. In fact, increased accuracy in the representation of the body model is also shown for the hands, when vision is removed, and participants rely in proprioceptive/mental imagery information instead (Coelho & Gonzalez, 2018a; Longo, 2014). These results support the idea that pointing tasks show the more implicit representation of the body model, underlying the position sense and allowing us to know the online location of the body (Longo, 2015a).

All facial features were perceived to be much wider than their true size, confirming the tendency to perceive the face as wider (D'Amour & Harris, 2017; Fuentes, Runa, et al., 2013). Width overestimation may be also associated with representation in the somatosensory cortex. In fact, Longo & Haggard (2011) postulated a shared implicit representation of the body size and shape, discerned both by touch and position sense, which preserves characteristics of somatosensory homunculus. The cortical representation of face features is also not uniform: for example, the lips occupy a larger region than cheeks (Nguyen, Inui, Hoshiyama, Nakata, & Kakigi, 2005). Data here follows this pattern, finding different magnitude of distortions for different features. The nose was the most overestimated area (103.84%), whilst the left eye was the least (54.29%). Similarly, a recent study in self-face perception (using two-alternative forced choice task with distorted images) has

shown how the accuracy to recognise the real size of face features is worse for the nose, followed by the mouth, and lastly by the eyes (Felisberti & Musholt, 2014). Yet, if somatosensory representation was causing these distortions, there would have been larger overestimation of the lips in comparison with the nose or eyes; however, this was not found. A potential explanation for this finding is the *reversed distortion* hypothesis, which proposes that bodily areas with lower number of tactile receptive fields are overrepresented in the cortical body map in order to compensate for this lack of resolution (Linkenauger et al., 2015). This could explain why, in the present data, the nose is largely overestimated, as this area is less well represented in the somatosensory and motor homunculi, but it does not explain why the mouth is also perceived larger than its real size. Perhaps it is due to a combination of both influences explained above. Lastly, another possibility is that there is more uncertainty when locating nose landmarks, due to its particular shape. Hence, responses are less accurate.

Other studies in self-perception and size have found biases to identify the self with larger size stimuli (Sui & Humphreys, 2015), which may explain, in part, the tendency to perceive the face much larger than its real size. This self-bias effect has been associated with the emotional and power significance of larger stimuli (Sui & Humphreys, 2015), with strong influences in size perception. Previous studies have shown how width distortion of facial features is also associated with self-esteem, and there is a preference for larger sized features for the eyes and mouth, and smaller for the nose. Overall, it appears that there is an intrinsic believe that noses are too large (Felisberti & Musholt, 2014). Others, by employing the collision judgement method, found that healthy adults overestimate the width of their face, owing to a ‘safety margin’ that participants may have applied around the head (Nico et al., 2010) as seen in monkeys (Graziano & Cooke, 2006). Width distortions after finger anesthesia have

been also associated to this safety margin to protect the deafferent segment from harm (Walsh, Hoad, Rothwell, Gandevia, & Haggard, 2015).

In summary, this study allows a better understanding on previous self-face perception research, providing a structural metric map of single facial features. This is the first study to investigate self-face representation through first-person perspective pointing, showing implicit characteristics of body representation. Interestingly, the distortions of self-face representation are qualitatively similar to those observed for other body parts when similar tasks are used, suggesting a related underlying mechanism. Further, the proximal shift implies a general shift of perceived body location towards the centre of the self, whereas there is an overall tendency to overrepresent the right side of the face. The explanations considered to account for these distortions emphasise the reliance on a mental image of one's own face based on the combination and mental reconstruction of sensory information and experience.

3.4 General discussion

The present research aimed to investigate further the metric representation of two of the most relevant body areas: the hands and the face. In Experiment 1, important influences in hand representation have been presented. Specifically, it has shown how the finger underestimation consistently found in previous studies, appear to be due to misallocation of fingertips, when conceptual biases for the knuckles are removed. Similarly, the overestimation of width is associated with misallocation of less-functional fingers. Experiment 2 has presented the first study reporting the body model of the face, with a thorough analysis of the shifts of locational responses and perceived size.

In both cases, the underlying shifts of pointing responses have helped understanding the distortions of size perception. When looking at the proximo-distal shifts for the hand, and the vertical shifts for the face, similar results are found. That is, areas appeared shifted towards the body, in such a way that it acts as a frame of reference (Gritsenko et al., 2007). This effect has been also explained due to usual movement and stored mental image of the body, which depends on the experience with the body part.

Instead, there are some differences in the mediolateral shift of landmarks between these two body parts. In particular, the overestimation of hand width is due to a leftwards shift of the less-functional fingers; whereas the overestimation of face width is guided by an overall tendency to shift responses towards the right hemispace. These results pinpoint the idea that the functional use of body parts will affect their representation. As seen in previous studies, others have found elongated arms and legs associated with their functionality (Caggiano & Cocchini, 2020), whereas ankles are overestimated as they have larger range of movement than the knees (K. D. Stone et al., 2018). Moreover, these results support the need to investigate the metric representation of different body parts with the same methods, as each has their own intrinsic distortions due to their use and visual experience (K. D. Stone et al., 2018). In detail, the leftwards shift in the left hand was due to finger functionality, whereas the overrepresentation of the right side of the face was due to representational components.

As with hands, the dimension where more distortion is found is the width. The size distortions found in the face support previous studies that reported overestimation of width perception for the face, consistently found with a variety of methods (D'Amour & Harris, 2017; Fuentes, Runa, et al., 2013). Indeed, the perception of the

body seems to be overestimated in width consistently across body parts and groups (see Longo, 2017).

These results confirm the idea that distortions are intrinsic to healthy representation (Longo, 2017b). However, little is known about the modulatory potential of these representations. Indeed, if functionality is affecting them, long-term use of a body part should, in turn, modify this representation. Hence, in the next chapter two studies will be presented in which hands and face representation is explored in two groups of experts: magicians and sign language interpreters.

Chapter 4: **Effects of long-term expertise on the size representation of the hands and face**



Josephine Cardin Photography

4.1 Introduction

As seen in Chapter 3, distortions in body representation are part of healthy experience. By using the well-known localisation task, researchers have been able to collect information on the body model of the hands (e.g., Longo & Haggard, 2012 and Chapter 3) and the face (as seen in previous Chapter 3), which are intrinsically distorted. Hand distortions are assumed to be quite robust and resistant to changes depending on the type of instructions (Longo, 2018), task modality (Ambroziak et al., 2018; Peviani & Bottini, 2018), or hand orientation (e.g., Longo & Haggard, 2010; Saulton, Longo, Wong, Bühlhoff, & de la Rosa, 2016). Distorted representation has even been observed in a case of congenital absence of the left hand (Longo et al., 2012). However, other studies have shown how the extent of the distortion can be modulated by multisensory information, such as positional changes (Longo, 2015c); vision (Longo, 2014); tool use and type of action (Romano et al., 2019) or even sound (Tajadura-Jiménez et al., 2017), confirming that the representation of the body is highly malleable (Ambron, White, et al., 2018; Medina & Coslett, 2016; Medina, Jax, Brown, & Coslett, 2010).

A growing body of evidence demonstrates that long-term training can modulate our body representation. For example, professional dancers show better capacity for proprioceptive localisation of their hand (Jola, Davis, & Haggard, 2011) and single joints (Kuni & Schmitt, 2004; Ramsay & Riddoch, 2001). Interestingly, the effect of practice not only translates into behavioural differences in perceptual performance, but also in cortical excitability (Hallett, 2001). That is, structural (Meier, Topka, & Hänggi, 2016) and connectivity brain changes are found in expert dancers (Burzynska, Finc, Taylor, Kramer, & Knecht, 2017), whereas improved dexterity of fingers through training brings cortical long-term activation adjustments in motor cortex (Kami et al.,

1995). On the contrary, reduced use is associated with a shrinkage of representation due to decreased cortical excitability, such as in the case of cast use (Liepert, Tegenthoff, & Malin, 1995; Lissek et al., 2009), or short-term immobilization (Opie, Evans, Ridding, & Semmler, 2016). These structural and functional changes are seen even after short-lasting tactile training for Braille reading in healthy volunteers (Debowska et al., 2016).

Similarly, illusions can also lead to body representation changes (Cavina-Pratesi et al., 2011; D'Angelo, di Pellegrino, Seriani, Gallina, & Frassinetti, 2018; Ekroll, Sayim, Van Der Hallen, & Wagemans, 2016; Pitron & de Vignemont, 2017; Tajadura-Jiménez et al., 2017). For example, Ekroll and colleagues (2016) described the 'shrunk finger illusion', which occurs when a hollow ball cut in half is placed on a finger. If this is looked at from above, it creates the illusion that the finger has shrunk as the ball is perceived as a complete sphere. Lastly, modulation of the size of the body also occurs due to actions and repetitive use of tools (Cardinali, 2011; Cardinali et al., 2009; Farnè, Serino, & Làdavas, 2007; Garbarini et al., 2014, 2015; Maravita & Iriki, 2004; Romano et al., 2019; Sposito et al., 2012). For example, this has been observed after extensive cane use by blind people (Serino, Bassolino, Farnè, & Làdavas, 2007), robotic hands (Marini et al., 2014), or sport equipment (Fourkas, Bonavolonta, Avenanti, & Aglioti, 2008). These studies demonstrated the multidimensional plasticity of our body representations. Undoubtedly, implementation of visuo-spatial, proprioceptive, somatosensory and motor information leads to the formation of internal body representations (De Vignemont, Majid, Jola, & Haggard, 2009; Longo et al., 2010).

Most of the studies looking into the body model of hands have looked into healthy performance. However, the modulatory effects of long-term training on the

metric representation of hands and face are still unclear. To this aim magicians and Sign Language (SL) professionals may offer a unique opportunity to investigate modulation of the size of the body through long-term expertise. For instance, magicians rely on their highly developed manual dexterity (i.e., sleight of hand) to trick or deceive their audiences (Rensink & Kuhn, 2015). In a traditional magic trick, called ‘the French Drop’, the spectator believes a coin has vanished when this coin has been concealed in one hand by the magician (Phillips, Natter, & Egan, 2015). Likewise, SL professionals expertly use the hands and face as mean of communication, having to move their hands rapidly and precisely and use their face simultaneously to convey meaning (Bettger, Emmorey, McCullough, & Bellugi, 1997; Muir & Richardson, 2005). Signers rely on somatosensory processing for signing processes (Emmorey, Bosworth, & Kraljic, 2009), associated with better overall kinesthetics and visuo-motor skills, as in the case with magicians (Cavina-Pratesi et al., 2011). Hence, these two groups of experts help to explore whether influences of improved somatosensory processing will help construct a more precise mental representation of the body.

The long-term effect of practice in the metric representation of the body is still unclear (specifically for the body model). This chapter aims to address this question, considering a population of adults who have undergone a prolonged training in complex manual actions, and disentangling proprioceptive information from mental representation of own hands. Two experiments were designed to investigate this. Experiment 1 explored the metric representation of hands in a group of expert magicians who used sleight of hand as the main aspect of deception; whereas Experiment 2 investigated the representation of the face and hands in a group of

experienced British SL professionals. The performance from both expert's groups was compared with matched control groups.

4.2 Experiment 1: the magic hand²

4.2.1 Introduction

Magicians are experts in prestidigitation (or 'sleight of hand'), with extremely developed fine motor skills for their tricks. In these sleights, they normally pretend to do one thing, whilst actually doing something else. In order to achieve this, an accurate representation of the size of the hands needs to be stored (i.e. real position and shape of hand and fingers) (Cavina-Pratesi et al., 2011). It is also crucial to retain the 'illusory' or 'pretended' representation and position of the hand. Indeed, sleight of hand demands a precise mental representation of one's own hands and fingers, as these need to be expertly moved in different positions at the right speed, and often with little visual input. This requires magicians to train and rehearse these movements for a long time (Rissanen, Pitkänen, Juvonen, Kuhn, & Hakkarainen, 2014), and it is likely that this extensive experience modulates their visuomotor processing, resulting in long-term changes in mental hand representations (Cavina-Pratesi et al., 2011).

This unique type of expertise is an excellent opportunity to also explore a separate aspect, highlighted in recent studies. Specifically, proprioception had been given greater relevance in previous studies, whereby the metrics of the hands were explored (e.g., Longo & Haggard, 2012). In contrast, most recent accounts had postulated that imagery, instead, may be more instrumental (Ganea & Longo, 2017). This point can be further explored here. If proprioception was predominant in the

² The information from this experiment is also included in a publication by Cocchini, Galligan, Mora, & Kuhn (2018). I had a major contribution in the design, data collection and writing up of the final article. All authors have given their authorisation to use this information in this thesis.

localisation task, magicians would show an advantage when the hand is held in a ‘congruent’ position (i.e., holding hand open) for pointing responses. In such a case, this advantage would be lost when presented with an ‘incongruent’ position, in which the hand is held in a different position to the actual image required (i.e., holding hand in a fist).

In this study, participants were asked to localise landmarks of their fingers in two different conditions, in order to investigate mental representation of participants’ own hands when proprioceptive information was congruent (Experiment 1A) or incongruent (Experiment 1B). It was hypothesized that long-term training in sleight of hand would result in better performance for magicians in the first experiment, when compared with a control group. The outcome of the second experiment would depend on the type of information that primes for this task and the effect of long-term training. If the task relies on proprioception and training improves the processing of afferent information, magicians should show improved performance in the first experiment, but not the second. Alternatively, if sleight of hand training refines, overall, the long-term hand representation, then magicians should maintain the same advantage over controls in the second experiment.

4.2.2 Experiment 1A: congruent condition (holding hand open)

4.2.2.1 Methods and procedures

4.2.2.1.1 Participants

An a priori power analysis was run to determine the required sample size by using G* Power 3.1 (Faul et al., 2009). The effect sizes (Cohen’s *d*) from previous studies were considered for this calculation (see Ganea & Longo, (2017) and Experiment 1 in the previous chapter). Effect sizes for finger underestimation were in the area of 0.7, whereas the effect size for hand overestimation was in the area of 1.6.

Taking the average between these two numbers, a power analysis for the difference between two independent means (two groups) with an effect size of 1.15, alpha of 0.05, and power of 0.8 indicated the adequate sample size would be of 13.

Twenty male adults aged between 18 and 58 years of age ($M = 31.78$ years; $SD = 11.16$) were recruited. Eleven participants were expert magicians, all members of the Magic Circle in London. All passed the Magic Circle entry exam, demonstrating high proficiency in practical conjuring (i.e., sleight of hand) and in theoretical knowledge. They all had at least 5 years of training and performed at least one show each month (two participants were excluded as they did not fulfil the latter criteria).

Demographic details, handedness scores and degree of expertise of the 9 magicians who finally entered the study are reported in Table 4.1. Handedness was assessed through the Edinburgh Handedness Inventory (Oldfield, 1971). Scores range from -100 to 100, where scores below -50 indicate left-handedness; scores over +50 indicate right handedness and scores within -50/+50 indicate ambidexterity. According to this scoring system, 2 participants were ambidextrous with right hand preference (+40 and +45, respectively) and 7 participants were right-handed.

Table 4.1. Demographic details.

Participants' demographic and handedness characteristics with magicians' degree of expertise.

		Magicians	Controls
		N = 9	N = 9
Age	mean	42.44	31.78
	sd	13.76	11.16
	range	26-67	23-58
Formal education (years)	mean	17.33	18.56
	sd	2.53	1.13
	range	12.21	16-20
Edinburgh Handedness Inventory	mean	79.89	87.13
	sd	26.22	21.39
	range	40-100	40-77
<i>Degree of expertise as magician</i>			
Years of practice	mean	23.89	==
	sd	14.26	
	range	6-50	
Practice per week (hours)	mean	6.67	==
	sd	9.17	
	range	1-30	
Shows per month	mean	4	==
	sd	2.7	
	range	1-10	

A group of 9 naïve control participants were recruited. The groups were matched by gender (all males), age, formal education, and handedness (see Table 4.1). One participant was ambidextrous (Handedness score = +40) and 8 were right-handed. T-test analyses did not show significant differences between the two groups on age, level of education, or handedness scores (all $ps. > .05$). None of the control participants played musical instruments or use their hands for other artistic or professional activities requiring fine movements of hands and related training.

The study was approved by the Goldsmiths Ethics Committee, and participants provided written consent to take part in the study.

4.2.2.1.2 Preliminary tests

To ensure that participants showed no general difficulty in pointing to specific locations, nor relevant differences between hands, they were asked to point as quickly and accurately as possible to 10 targets (small numbered dots of 0.5 cm of diameter), printed on an A1 sheet displayed in front of them. The examiner read the numbers aloud in a random order and participants had to point with their right or left hand to the corresponding stimulus. With the exception of three errors (<1%) across both groups and both hands, all participants performed flawlessly.

4.2.2.1.3 Experimental task

The experimental task was very similar to previous studies on the locational task, making use of the occluded board and pointing stick whilst participants had their eyes opened. This contrasts with the method in Chapter 3. Like previous research on mental hand representations (e.g., Longo & Haggard, 2012), participants were required to indicate the location of specific landmarks on a blank piece of paper whilst their hand was occluded from view. Participants were asked to close their eyes and place their hand wide open, with all fingers straight and spread apart on an A1 sheet located on a table in front of them. The middle finger was in line with the midline of their body. The distance from the hand to the body was adjusted to avoid uncomfortable positions. Participants were then instructed to relax and not move their hand for the entire test.

A picture of the hand was taken for later analyses from a fixed position camera (Canon EOS 700D), suspended directly overhead at about 50 cm above the hand (see Figure 4.1A). Four marks were placed on each of the four A1 sheet corners for later reference, when images of hand and participant responses were superimposed for measurements. An occluding box (39 cm x 29 cm x 7 cm) was placed over the hand.

Participants were then instructed to open their eyes and to point with a short stick held on the other hand (14 cm), to nine landmarks of the occluded hand.

As seen in previous Chapter, finger interspaces are not subject to conceptual biases, as knuckles are (Longo, 2015b). Therefore, the locations of the five fingertips and the four interspaces of the fingers were considered as landmarks for this experiment (see Figure 4.1B). Participants were asked to indicate the tip of each finger and their interspace. The landmarks were asked in a set order (e.g. tip of little finger; interspace between little and annular fingers; tip of annular finger; etc...), starting from the little finger (for half of the participants) or from the thumb (for the other half of participants). Before reading each landmark aloud, the participant was asked to point with the short stick to a starting point located in the lowest part of the sheet and align with the midline of their body. After each pointing, participants held the stick in place for a few seconds so that a picture could be taken for later analyses, they were then asked to point to the starting position before hearing the next landmark. After the last trial, the cardboard was removed, and a final picture of the hand was taken to control for possible minor movements. In case of movement, the initial and final pictures of the participant's hand were combined, and the averaged position was considered.

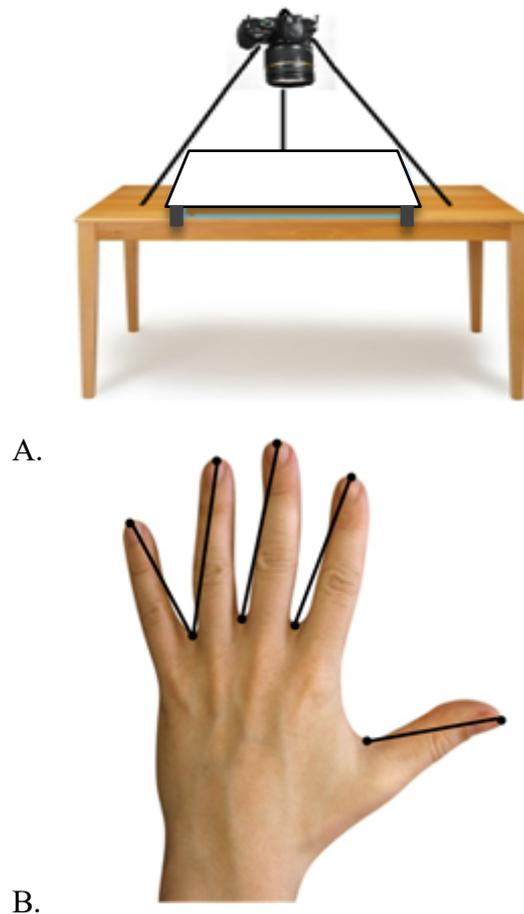


Figure 4.1. Hand localisation task.

Experimental setting (A) and finger lengths considered of the right-hand view (B). From Cocchini et al. (2018).

The task was repeated for each hand (Side condition), and for dorsal and palmar positions (i.e. palm of hand facing down or facing up, respectively) of the hands (View condition). View condition was counterbalanced with participants following ABBA order, and Side condition was counterbalanced across participants. Therefore, each participant performed the pointing task four times, for a total of 36 trials.

4.2.2.1.4 General analyses

For each condition, every photograph indicating the participant's response (i.e., the position indicated with the stick) was digitally placed over the initial photograph, using Photoshop software CS6. An IBM Lenovo T60 computer with screen resolution

1600 x 1200 pixels was used to carry out the measurements. Measurements were recorded in centimetres. Each finger length was calculated by measuring the distance between the tip of the finger and the closest interspace toward the little finger. For the little finger the interspace shared with the annular finger was considered (see Figure 4.1B).

The percentage of error was calculated as follows:

$$\frac{SubjectiveLength - ObjectiveLength}{ObjectiveLength} \times 100$$

A negative value indicated underestimation of the finger length; a positive value indicated overestimation; and a value equal to zero represented a perfect estimation. The same measurements were considered for both hands and both views.

4.2.2.1.5 Statistical analyses

T-tests for independent samples were used for group comparisons of real hand sizes. T-tests for repeated samples were used to compare distortion (real versus perceived sizes) for each group. A Group x Hand x View x Fingers ANOVA was conducted. Appropriate post-hoc analyses were run on main effects only.

4.2.2.2 Results

Overall magicians' real finger length (M = 6.96cm; SD = 1.16) was very similar to controls' real size (M = 6.83cm; SD = .42), and the difference was not significant [t(16) = .332; p = .74, d = .15]. Both groups showed an overall distortion of their own finger lengths with magicians perceiving their fingers underestimated by a -20.4% (i.e., M = 5.54 cm; SD = 2.17), and controls perceiving their fingers -39.4% shorter than actual size (i.e., M = 4.14cm; SD = .79). The distortion was significant for

magicians [$t(8) = 3.31$; $p < .01$, $d = 1.1$] and controls [$t(8) = 12.13$; $p = .001$, $d = 4.04$], but significantly smaller for the magicians [$t(16) = 2.59$; $p = .02$, $d = 1.22$].

More detailed analyses were run to consider distorted representation of each hand, view, and fingers between groups. Figure 4.2 shows the mean percentage of distortion for groups, hands, fingers, and views. Inspection of Figure 4.2 suggests that both groups showed a persistent underestimation for both hands, all fingers, and under both views. A 2 (Group) x 2 (Hand) x 2 (View) x 5 (Fingers) ANOVA on percentages of error estimations confirmed a significant effect of Group [$F(1,16) = 4.58$; $p = .048$; $\eta^2 = .22$], demonstrating that the magicians were significantly better at estimating their finger position than the control participants. There was also a significant effect of Fingers [$F(4,64) = 7.61$; $p = .001$; $\eta^2 = .32$]. Pairwise comparisons (Bonferroni correction for 10 comparison; $p < .005$) amongst fingers revealed significantly smaller errors in the thumb than the middle ($p < .001$, $d = 1.08$) and annular fingers ($p < .001$, $d = .97$), and significantly smaller errors in the little finger compared to the annular finger ($p < .001$, $d = .91$). There were no significant main effects of View ($p = .17$) or Hand ($p = .803$), but there was a significant View by Finger interaction [$F(4,64) = 3.52$, $p = .01$, $\eta^2 = .18$], and an interaction between Groups*View*Hand*Finger [$F(4,64) = 3.33$, $p = .01$, $\eta^2 = .17$].

Clearly there were many ways to interpret such an interaction. Firstly, results for magicians and controls were compared in each combination of view, hand, and finger, with the highest differences between groups reported here. The thumb and the index fingers of the left hand in palmar view showed the highest group differences (i.e. 40.3% and 27.5%, respectively) and a significant group effect ([$t(16) = 2.94$, $p = .01$, $d = 1.39$]; [$t(16) = 2.98$, $p = .009$, $d = 1.4$] respectively; Bonferroni correction not applied). Secondly, as performance for thumb and index fingers did not differ

significantly (see above post-hoc analyses), groups were compared for the combined performance of these two fingers (thumb-index) for both Hands and Views. Considering Bonferroni corrections for 4 comparisons (i.e. $p < .0125$), a significant group effect was found for the combined fingers of the left palmar hand condition [$t(16) = 3.23, p = .005, d = 1.61$], whereas other Hand by View combinations for these fingers fell far from significance (lowest $p = .12$).

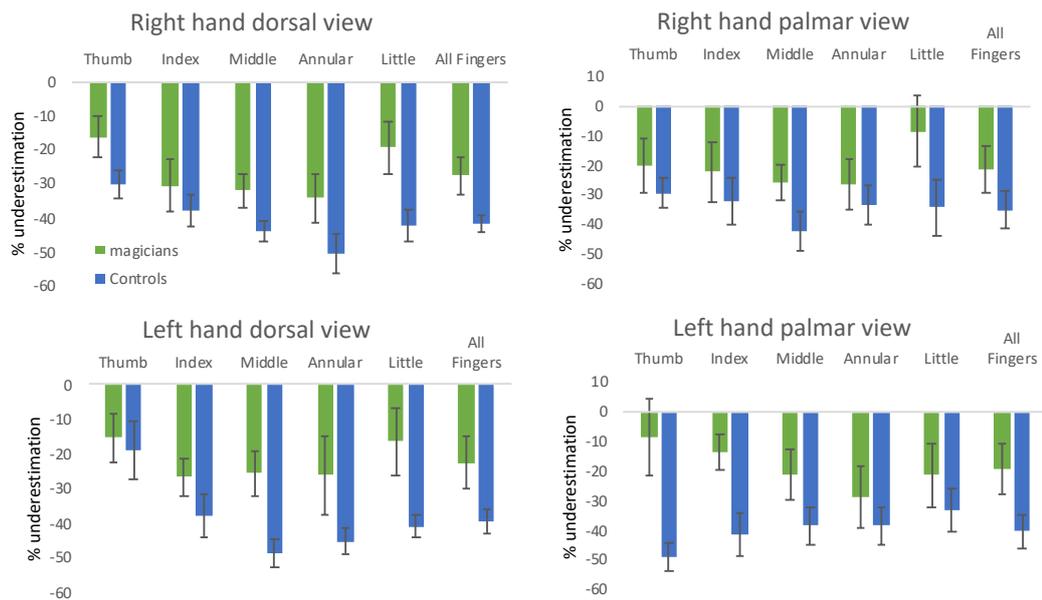


Figure 4.2. Perceived length of fingers in Experiment 1A.

Percentage and standard error of participants' underestimation of their right and left hands under both views.

4.2.2.3 Preliminary discussion

In line with previous studies (e.g., Longo & Haggard, 2012), control participants showed a significant distortion of hand representation as they consistently underestimated their finger lengths for both hands and under both dorsal and palmar views. Overall, magicians performed significantly better than controls; however, they also showed a tendency to underestimate their finger length.

This data further supports the improvement on accuracy of finger underestimation due to the removal of conceptual biases when considering the knuckles, as seen in Chapter 3. Therefore, the underestimation cannot be explained by a conceptual distortion. Instead, and as discussed in Chapter 3, the findings in this study support the idea that the specific direction of distortion relies on the fact that fingers are highly movable parts of the upper limbs and that fingers are moving towards the body which cannot prolong beyond their actual length (Caggiano & Cocchini, 2020; Ferretti, 2016) unless using tools (Pitron et al., 2018). Moreover, distal parts are harder to locate, as more computations need to be carried out compared to proximal parts (De Vignemont, 2014). This aspect becomes particularly important during sleight of hand, where finger movements are a crucial aspect of the tricks. Therefore, it is not surprising that magicians performed significantly better than controls, though their performance was far from perfect.

The pattern of finger distortion was like that reported in the literature (e.g. Longo & Haggard, 2012), whereby fingers were not equally distorted in both groups. The thumb was generally less underestimated than the middle and the annular fingers, and the little finger was less underestimated than the annular finger. Notably, most participants were right-handed, and the highest group difference was found when estimating the size of the left thumb and index fingers under palmar view, for the non-dominant hand. A possible interpretation of these findings may be linked to the fact that only magicians used both hands extensively to practice and perform their tricks. Moreover, palmar view of hands seems to represent a less common representation, demonstrated by slower processing and less accurate responses in mental rotation tasks (Ionta & Blanke, 2009). Also, studies investigating visual awareness during perceptual suppression found that dorsal view pictures of the hands reach consciousness faster

than palm view (Salomon, Lim, Herbelin, Hesselmann, & Blanke, 2013). When control participants were asked to localise landmarks of the less used hand (i.e. left hand) and to represent it in the less usual way (i.e., the palmar view). These combined detrimental conditions may have maximised the group differences. Interestingly, the two fingers showing the highest group difference are those more heavily used for fine motor actions (Coelho et al., 2017; Longo & Haggard, 2012a) and magic tricks (Cavina-Pratesi et al., 2011). This result supports previous findings by Cavina-Pratesi and colleagues (2011), who found that extensive practice in sleight of hand improved performance of pantomime reaching action, specifically for the ‘grip component’ (i.e., using two fingers) of the reach-to-grasp task. The authors suggested that magicians’ ability lies in their capacity to “calibrate the grasping action” (p. 4). In view of these findings, the successful ‘calibration’ could be interpreted to result, at least in part, from a better finger representation.

These outcomes advocate for a generally better performance in representing own finger length in magicians. It follows that magicians may implement proprioceptive and somatosensory information more successfully than controls. It therefore remains unclear as to whether the magicians’ advantage reported in the first study, was mainly due to a better implementation of afferent proprioceptive and somatosensory information of the hand lying flat on the table, or whether the substantial gain reflects a more accurate internal mental representation (Ganea & Longo, 2017; Longo & Haggard, 2012a). To address this question, the proprioceptive and somatosensory information contrasted with the internal mental representation requested to perform the task in Experiment 1B.

4.2.3 Experiment 1B: incongruent condition (holding hand in a fist)

According to Longo and Haggard (2012; Longo et al., 2015) and findings in Chapter 3 (Experiment 2), localising external body landmarks requires us to successfully implement somatosensory information with our long-term internal spatial representation. Experiment 1A suggests that extensive motor training can significantly improve body-part localisation. However, there is a need to clarify if this extensive training improves the processing of online sensory information during the task (i.e., proprioceptive), or if, instead, it modulates the long-term size representation of the hands. In order to address this question, Experiment 1B was designed.

In Experiment 1B, participants were asked to locate landmarks on their imagined open hand, as in Experiment 1A, whilst holding their hand in a fist shape under the cardboard. Similar paradigm has been used in a recent study (Ganea & Longo, 2017) where authors concluded that “proprioception and proprioceptive imagery rely on a common stored model of the body’s metric properties” (p. 41). The mismatch between imagined representation and online sensory information from the hand can help discern in which way extensive training in sleight of hand influences its representation. If the magicians’ advantage observed in the previous experiment was guided by a better implementation of afferent information, overall worse performance of magicians should be found in Experiment 1B compared with Experiment 1A. In Experiment 1B, afferent inputs would not provide useful information about the finger locations and both groups would show an equivalent degree of distortion. As a result, the group difference would be negligible or considerably reduced. Alternatively, if extensive practice in sleight of hand leads to qualitative more refined mental representations of this specific part of the body, a relatively unchanged group effect

should be found as magicians would still be able to capitalise on their better mental representations of hands.

4.2.3.1 Methods and procedures

4.2.3.1.1 Participants

A subgroup of 15 participants (7 magicians and 8 controls) who took part in Experiment 1A, were also recruited for the Experiment 1B, which was performed later the same day. No feedback was provided after Experiment 1A, and participants were engaged in general conversation before carrying out Experiment 1B.

4.2.3.1.2 Experimental task

The main task, the method and the procedure were identical to Experiment 1A; however, now participants had their hand in a fist shape (with the thumb on the top) rather than spread out under the box. They were then instructed to imagine their hand wide open with the middle finger aligned to the mid-line of their body, and to point to the different nine landmarks that were read aloud as in Experiment 1A. Both hands and views were tested, and the order of presentation was counterbalanced as in Experiment 1A. Also, the order of landmarks (i.e., starting with the tip of thumb or the tip of little finger) was counterbalanced across participants as in the previous experiment.

4.2.3.1.3 General and inferential analyses

The pointing data were compared with actual finger lengths as measured in Experiment 1A. All other analysis methods were the same as for Experiment 1A. In addition, an ANOVA and a Pearson correlation were conducted to compare group performance across the two Experiments.

4.2.3.2 Results

The magicians' overall real finger length ($M = 7.47$ cm; $SD = .65$) was similar to those of the control subgroup ($M = 6.90$ cm; $SD = .38$), and the difference did not reach significance [$t(13) = 2.11$, $p = .054$, $d = 1.07$]. Both groups showed an overall underestimation of own finger lengths, with magicians perceiving their fingers -7.82% shorter on average (i.e., $M = 6.89$ cm; $SD = 1.95$), and controls -31.87% shorter (i.e., $M = 4.70$ cm; $SD = .98$) than their actual size. The control group significantly underestimated their finger length [$t(7) = 6.68$, $p < .001$, $d = 2.36$], whilst for the magicians there was no significant difference between the real and the estimated finger length [$t(6) = 1.06$, $p = .33$, $d = .4$]. A group effect was found between real and perceived lengths [$t(13) = -2.60$, $p = .02$, $d = 1.32$], suggesting that controls underestimated their finger size significantly more than magicians, who estimate their finger lengths very close to actual size.

More detailed analyses were run to consider performance for each condition during Experiment 1B. Figure 4.3 shows the mean percentage of estimation errors for both Groups, Hands, Fingers and Views. Both groups underestimated finger lengths for both hands and under both views. A 2 (Group) x 2 (Hand) x 2 (View) x 5 (Fingers) ANOVA on estimation errors confirmed a significant main effect of Group [$F(1,13) = 7.02$, $p = .02$, $\eta^2 = .35$], again illustrating that the magicians were more accurate in estimating their finger length than the control participants. There was also a main effect of Fingers [$F(4,13) = 7.25$, $p < .001$, $\eta^2 = .36$], and a series of post-hoc paired t-tests (Bonferroni corrections for 10 comparisons; $p < .005$) revealed a significantly larger difference between the annular and all the other fingers ($p < .001$ with thumb; $d = 1.03$, index; $d = 1.35$ and little; $d = 1.35$; $p < .005$ with middle; $d = 0.93$). No significant

main effect of View ($p = .48$) or Hand ($p = .13$) were observed nor interactions between factors (Groups*Hand* View*Finger interaction, $p = .16$).

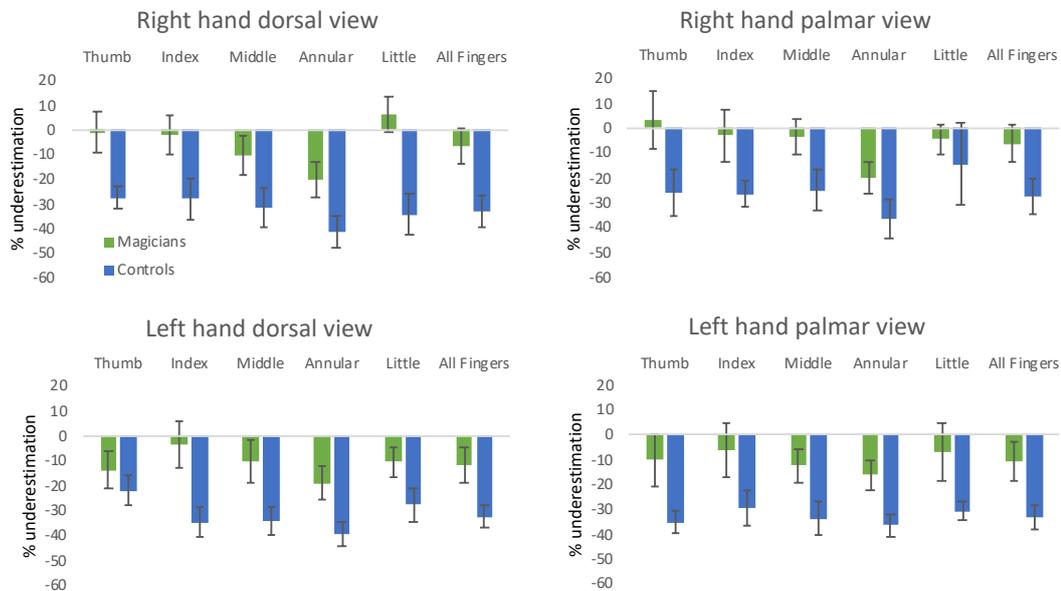


Figure 4.3. Perceived length of fingers in Experiment 1B.

Percentage and standard error of participants' underestimation of their right and left hands under both views.

4.2.3.2.1 Comparisons between experiments

Figure 4.4 shows the overall underestimation for each finger of both subgroups (i.e. 7 magicians and 8 controls) who took part in both Experiments. A 2 (Groups) x 2 (Experiment) ANOVA showed a significant effect of Experiment [$F(1,13) = 11.39, p = .005, \eta^2 = .47$], and a significant effect of Group [$F(1,13) = 8.06, p < .01, \eta^2 = .38$], but no interaction ($p > .05$). Pearson's correlations of finger estimations between Experiments 1 and 2 were significant for both magicians ($r = .89; p < .01$) and controls ($r = .80; p < .05$). Pictorial representations of the distortions are presented in Figure 4.5.

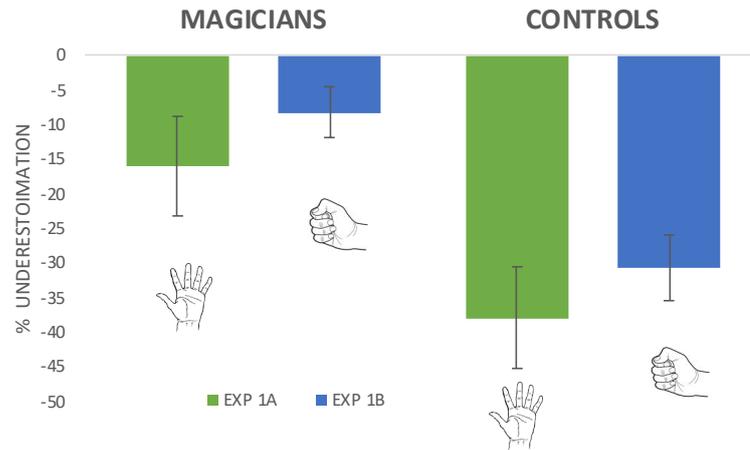


Figure 4.4. Comparisons between studies.

Percentage and standard error of participants' performance during Experiment 1A (holding hand open) and Experiment 1B (holding hand in a fist).

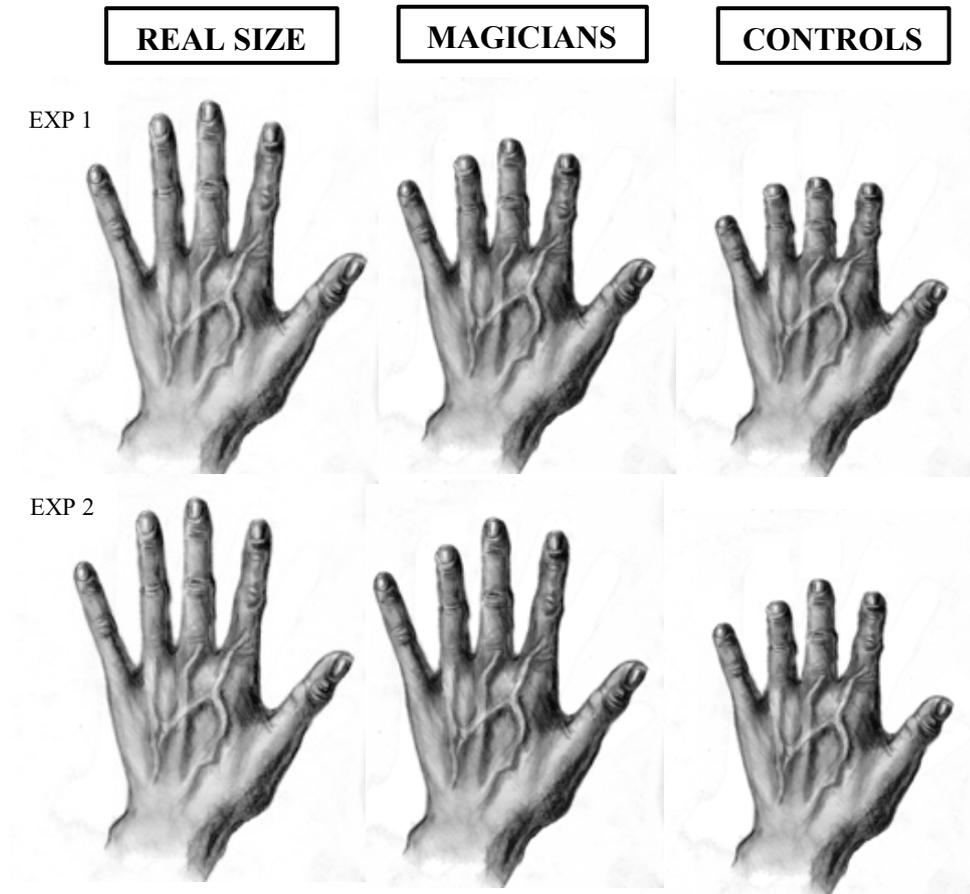


Figure 4.5. Pictorial depiction of finger length distortion.

Hands depicting the overall length distortion per finger for each group and each experiment, averaged across participants and views. The first column represents undistorted picture of the hands, to help comparisons.

4.2.4 Discussion

Several previous studies have shown that participants hold a distorted metric representation of their own hands, consistently finding underestimation of finger lengths (see Longo, 2019 for a review). This was replicated in both experiments, for both hands, and under dorsal and palmar views. Further, magicians using sleight of hand considerably outperformed controls in estimating their own finger lengths. These results therefore demonstrate that intensive and long-lasting training can modulate our metric body representation.

Similarly, a recent study suggested that proprioceptive imagery and proprioception hinge on the same stored body model (Ganea & Longo, 2017). In Experiment 1A, representation and actual locations of landmarks were congruent, and it was therefore not possible to discern whether the sleight of hand expertise influenced the processing of afferent information or whether it changed internal representation. For this reason, these two types of information were in contrast in the second study (i.e., imagine own hand wide open while holding it in a fist). The purpose was to explore the reason for improved size perception in Experiment 1A. If this gain was due to better integration of online proprioceptive information, differences between groups would be reduced in Experiment 1B, in which the proprioceptive information would, instead, disrupt performance. On the contrary, in the second study magicians showed an almost identical advantage over controls (i.e. 21.97% in the first study and 22.49% in the second study). Interestingly, both groups were significantly better in Experiment 1B. Even though there is a likely order effect of experiments, these results better suggest the interference of proprioception in the task. In other words, whilst proprioceptive information is fundamental for action (De Vignemont, 2014), it plays a marginal role on the representation of own hand when measured by the location task.

This has also been seen with lower legs (K. D. Stone et al., 2018) and in a case with congenital hand loss (Longo et al., 2012), whereby the representation was equivalent in imagined conditions. These findings support the existence of a stored body model that relies on mental imagery, and not only on somatosensory representation (Ganea & Longo, 2017; Longo et al., 2012; K. D. Stone et al., 2018). Owing to these findings, sleight of hand may contribute in the formation of more accurate internal metric hand representation than controls. Indeed, long-term manual practice translates into long-term activation adjustments, as seen after finger dexterity training (Kami et al., 1995).

However, it remains unclear as to why congruent proprioceptive information resulted in worse rather than better performances. Although some degree of familiarization or practice may be playing a role in the second study, a third possibility ought to be considered. Somatosensory information is crucial for the formation of body representation (Canzoneri, Ferrè, & Haggard, 2014; De Vignemont et al., 2009); however, under some circumstances (e.g., when contrasting) this information can be detrimental, and it can interfere with our internal representations. For example, in situations in which proprioception contrasts with visual information, such as in mirror drawing, deafferented patients have an advantage as proprioception becomes an obstacle to accurate performance (Balslev et al., 2004). Moreover, in recent studies using the localisation task, participants showed less distortions to localise landmarks on a rubber hand than on their own hand (Longo et al., 2015; Saulton et al., 2016). It therefore seems likely that under specific circumstances, knowing that proprioceptive information is clearly irrelevant (as in Experiment 1B) may have facilitated performance on a task, as this information will not interfere with the mental representation of this body part. In these instances, participants will fully rely on their mental imagery to complete the task (Ganea & Longo, 2017; Longo et al., 2012). The

stored mental representation will be more accurate for magicians, due to practice, as it relies on a more developed occipito-parietal cortex to utilise visual information (Cavina-Pratesi et al., 2011). This, together with the likely order effect of experiments, may explain why both groups performed better when they were asked to imagine their hand wide open while keeping it as a fist. Further studies would be needed to disentangle the role of these two variables.

A further possible limitation of this study is the sample size. There was highly stringent inclusion criterion in selecting only highly experienced magicians who use sleight of hand magic. Inevitably, this resulted in a relatively small sample size for this group. This did not have an effect in the main findings of the studies. Yet, a larger sample of participants may allow to reach more influential conclusions on correlation analyses and interactions amongst factors.

To sum up, findings in these two experiments suggest that long-term expert manual use of hands can modulate the representation of their size. Moreover, this modulation is not due to just better processing of proprioceptive information, but due to a more refined mental representation. Moreover, the impact of training seems to have a high body-part specificity, with a maximum impact for those body sections used more often during training. However, possible generalisation of the ‘benefit’ in the metric representation of the body width has not been explored in this experiment and should be investigated in further studies.

In the next experiment, this aspect will be explored in more detail. In Chapter 3 and the magicians’ study, evidence has been provided to support the idea that functional differences in the use of a body part could bring changes to its representation. In keeping with this, not only is the function that is important, but also the space where action is performed (Fraser & Harris, 2016). Hence, it is possible that

the representational gain seen in magicians could just be found within the manual space of action, but not in a less frequent space, such as far-reaching space or behind one's own back. In order to explore this aspect of body representation, SL professionals were considered in the next study. Due to their particular expertise, the representation of hands and face can be explored simultaneously, to further understand the overall modulatory effects in the body representation. Moreover, SL is a visuo-spatial language which is performed within a confined space around the body, considered part of the near-space (Emmorey, 2001). This particular space-dependent expertise is an advantage in exploring whether the metric representation of hands is linked to the manual workspace (as hypothesized in previous studies), or whether it relies on a stored model not related to space. With these aims in mind, the next experiment is presented.

4.3 Experiment 2: the signing body

4.3.1 Introduction

Proficient SL users need to be able to move their hands rapidly and precisely and use their face simultaneously to convey meaning (Bettger et al., 1997; Muir & Richardson, 2005). Moreover, SL users have to coordinate between a range of positions, movements, and locations altogether. Particularly, handshapes (configurations of fingers and palm) have to be combined with changes in location (position of the hand relative to the other hand, face, trunk, or in signing space), movement (action performed) and orientation (direction of the palm) to provide meaning (Sehyr & Cormier, 2016). For example, in British SL (BSL), vowels are spelled by pointing to the fingertips of the non-dominant hand (Sutton-Spence, Woll, & Allsop, 1990). The words 'pig' and 'witch' are both signed at the nose but with different handshapes, whilst the words 'name' and 'afternoon' have a shared

handshape, only varying on their location (head and chin, respectively) (MacSweeney, Capek, Campbell, & Woll, 2008). Further, the face is not only used as location for manual gestures; SL users need to identify and distinguish quick facial expressions that have linguistic or emotional connotations for the perception of meaning (Bettger et al., 1997; Emmorey & McCullough, 2009). For example, negation in BSL is indicated with non-manual gestures (headshake, furrowed brow or frowning) (Campbell, MacSweeney, & Waters, 2007), whilst mouth configurations indicate adverbial meaning when accompanied by American SL (ASL) verbs (Emmorey & McCullough, 2009) (see Figure 4.6A for schematic representation of how hands, face and body are used).

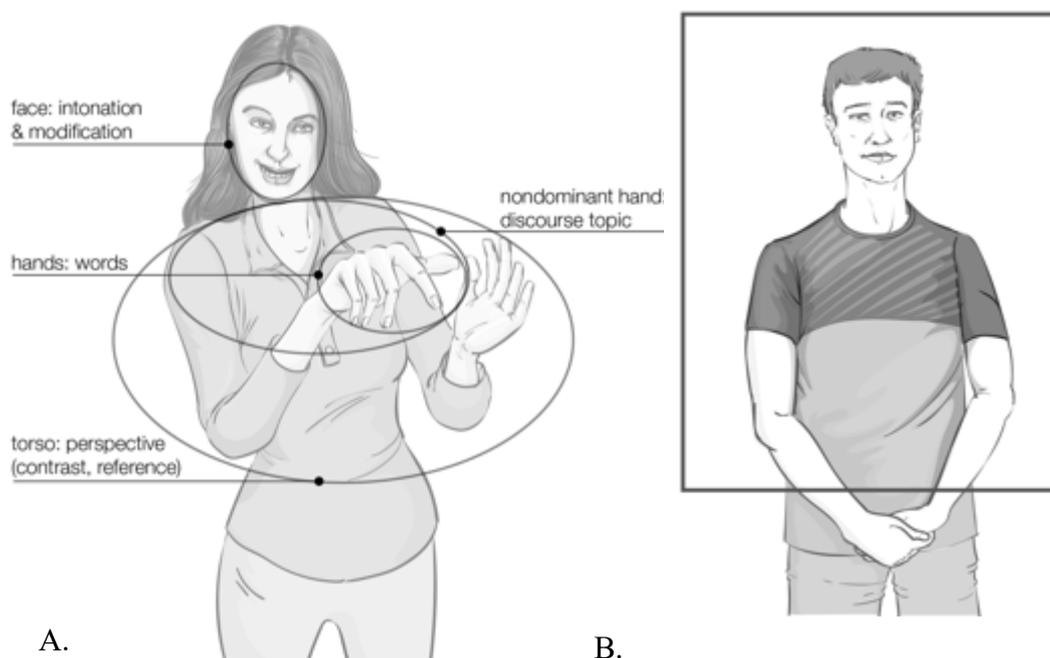


Figure 4.6. Space and SL.

Organization of body and discourse components (A) based on Sandler (2018); and representation of signing space surrounding the body (B).

When interpreting, SL practitioners need to simultaneously process heard language, maintaining the message in short term memory at the same time as signing the message coherently with the language format used (Klein, Metz, Elmer, & Jäncke,

2018). This linguistic experience of manual and non-manual gestures and complex cognitive skills translates into better perceptual abilities. In particular, functional gains in visuo-spatial abilities have been reported for mental rotation (Emmorey, Kosslyn, & Bellugi, 1993; Keehner & Gathercole, 2007), and in generating mental images (Emmorey et al., 1993). Moreover, SL use improves working memory, as addressees need to retain visual sequences of hand shapes, and face and body movements in order to convey meaning (Arnold & Mills, 2001). Further, signers rely on somatosensory processing for signing processes (Emmorey, Bosworth, et al., 2009), associated with better overall kinesthetics and visuo-motor skills, as seen in magicians (Cavina-Pratesi et al., 2011). Similarly, long use of SL results in “enhanced processing of hands” in the left hemisphere (dominant for language), even when not signing (Mitchell, 2017, p. 159). These gains also result in long-term brain changes. Expert SL users show differences in cortical thickness (Hervais-Adelman, Moser-Mercer, Murray, & Golestani, 2017), hyperconnectivity in prefrontal regions during resting state (Klein et al., 2018), and more bilateral activation when processing emotional facial expressions (Emmorey & McCullough, 2009). Further, SL practice is associated with left hemisphere superior and inferior parietal lobe activation (MacSweeney et al., 2002), whilst other studies have found bilateral recruitment of parietal cortices (Emmorey, 2006), areas presumed to store the structural representation of the body (Corradi-Dell’Acqua et al., 2009; Tamè et al., 2017).

Moreover, all these manual and facial actions are space-dependent, as these are performed within a circumscribed area around the body in near-reaching space (Arnold & Mills, 2001; Emmorey, 2001) (see Figure 4.6B). Indeed, there is a close link between space and body representation. For example, studies have shown how the perceived length of the arms or their affordances, can extend the size of peripersonal

space (Longo & Lourenco, 2007) or reduce it (Lourenco & Longo, 2009). Hence, size perception appears to be linked to space and to the possibilities of action (Bassolino, Finisguerra, Canzoneri, Serino, & Pozzo, 2015; D'Angelo et al., 2018). As seen before, spatial organisation is characteristic of visual-gestural languages (Bellugi & Klima, 2015), and this may have an effect on the metric representation of their body. Moreover, visuo-motor-proprioceptive cross-modal interactions are intrinsic to hand use (Korb, Osimo, Suran, Goldstein, & Rumiati, 2017). The evidence above makes a strong case to study the representation of hands in different portions of space (i.e. near- or far-reaching space). If the metric representation of hands is associated with the manual workspace and type of expertise, the SL practitioner's advantage in the metric representation of hands should be found only in near-reaching space, whereas no differences should be found in far-reaching. Indeed, previous studies have linked the representation of the body with the actions, functionality, and space where these occur (Caggiano & Cocchini, 2020; D'Angelo et al., 2018). Hence, in Experiment 2A the representation of the hands in 'near' and 'far' reaching space was explored, to elucidate any differences on representation due to expertise and space localisation.

Additionally, SL uses the face for non-manual gestures and expressions, and this use may also influence face representation. Hence, a second aspect of this study is to further understand if signing has a relevant impact on the metric representation not only of the hands, but also of the face (Experiment 2B).

4.3.2 Experiment 2A: effects of expertise and space of manual action on the size representation of the hands

4.3.2.1 Methods and procedures

4.3.2.1.1 Participants

An a priori power analysis was run to determine the required sample size by using G* Power 3.1 (Faul et al., 2009). The effect sizes (Cohen's d) from the magicians' study (Experiment 1) were considered for this calculation. In this case, the effect size for the independent t-tests for finger lengths was 1.32. A power analysis for the difference between two independent means (two groups) with an effect size of 1.32, alpha of 0.05, and power of 0.8 indicated the adequate sample size would be of 11.

Twenty participants (16 females and 4 males) between 24 and 63 years of age (mean age = 40.85 years, SD = 10.8) took part in this study. Ten of them (8 females and 2 males) were recruited as expert SL professionals (mean age = 45.4, SD = 8.69) from SL associations and educational settings, such as Heriot-Watt University, and through snowball sampling. SL use is associated with different activation patterns in the brain; however, plasticity of these networks varies depending on the hearing status of the user, when language acquisition occurs and the levels of exposure to the SL (Campbell et al., 2007). For example, studies have shown thicker white matter connections between auditory regions in hearing users, when compared with deaf users (Emmorey, Allen, Bruss, Schenker, & Damasio, 2003). In order to control for variability, only bimodal signers were recruited (i.e., hearing bilingual signers with both oral and signed languages). These participants were required to have at least 3 years of professional practice, with over 10 hours of use per week, and at least 3 years of previous formal training.

Table 4.2. Participants' demographics.

Demographic and handedness characteristics with the SL practitioners' degree of expertise (SD = standard deviation).

		<u>SL group</u>	<u>Control group</u>
		(N = 10)	(N = 10)
Age (years)	Mean	45.4	36.3
	SD	8.69	11.16
	Range	35 - 60	24 - 63
Post-secondary school education (years)	Mean	5.6	5.2
	SD	2.32	2.15
	Range	2-9	2-8
Edinburgh Handedness Inventory	Mean	.67	.68
	SD	.48	.6
	Range	-.09 - 1	-1 - 1
<i>Degree of expertise as sign language practitioner</i>			
Years of practice	Mean	20.34	-
	SD	9.89	
	Range	3.5 - 39	
Practice per week (hr)	Mean	38.4	-
	SD	25.69	
	Range	15 - 84	

Handedness was assessed with the Edinburgh Handedness Inventory (Oldfield, 1971). Values range from -1 to 1, with scores below -0.5 indicating left-handedness; scores between -0.5 to +0.5 indicating ambidexterity; and scores over +0.5 indicating right-handedness. From the ten participants, two were ambidextrous (scores = -.32 and -.09, respectively), whilst eight were right-handed. All SL professionals used the right hand as the dominant hand for signing. Demographic details, handedness and expertise details are reported in Table 4.2.

The other ten participants acted as control group, and they were matched by Age (M = 36.3, SD = 11.16), Gender (8 females) and Handedness (one left handed participant; score = -1) (see Table 4.2). Analyses did not show any differences by Age

[$t(18) = -2.04, p = .06, d = .91$], Handedness [$t(18) = .06, p = .96, d = .03$] or Education [$t(18) = -.4, p = .69, d = .18$] between groups. Frequency of females in each group was identical (see Table 4.2). None of the control participants had practiced or learned SL or used their hands or faces for any other professional or artistic purposes requiring specific training and ability. Goldsmiths Research Committee approved this study. All participants provided written informed consent.

4.3.2.1.2 Hand localisation task and procedure

A modified version of the hand localisation task (Longo & Haggard, 2012) was used in this study, a replica of the procedure presented in Chapter 3, Experiment 1, with some modifications for the ‘far space’ condition. A horizontal transparent Perspex board (50 x 55 cm) resting on four wooden posts (each 10 cm high) was positioned on a table in front of the participant. A remote-controlled camera (Nikon D3200) was used to record participants’ responses, positioned over the board (90 centimetres high) with a tripod, with its focus aligned to the centre of the board. A small 20 x 20 cm white canvas was positioned underneath, onto which the participants rested their hands (one at a time). This canvas was positioned at two different distances from the body for two different conditions: ‘near’ and ‘far’ distances. In the ‘near’ condition, the canvas was placed at a distance of around 15 cm to the body, in such a way that the canvas was just at the edge of the table, allowing participants to only position the hand and wrist under the Perspex board. In contrast, in the ‘far’ condition, the canvas was moved further forward, at the edge of the individual’s reaching space (at about 45 cm from the body). Participants rested their elbow on the table, whilst extending their arm as far as it was comfortable underneath the board (see Figure 4.7A). Both conditions were counterbalanced. A measuring tape was attached to the top and right edges of the

Perspex board, to allow later conversion of pixels into centimetres for each pointing response.

Participants were sat in front of a table whilst keeping their eyes closed. One hand (either the right or left, counterbalanced) was positioned underneath the Perspex board, and on top of the white canvas frame (see Figure 4.7A). The middle finger was aligned with the participant's body midline, whilst the other fingers were spread out comfortably. Participants were asked to keep the hand under the board completely still, whilst using the other hand's index finger to point to the required locations. A small dot (around 1mm diameter) was drawn on the tip of the index's fingernails as reference for later analyses.

A total of eleven hand landmarks were read aloud (see Figure 4.7B), one at a time (5 fingertips, 4 interspaces and the two sides of the wrist's bones, ulna and radius). Participants were previously trained to understand the different labels for each landmark by identifying these on a schematic drawing. Landmarks were given in order, starting either from the interior bone of the wrist, the radius (H1 landmark, see Figure 4.7B); or from the exterior bone, the ulna (landmark H11). The starting landmark was randomized across participants. Each landmark was requested twice, with a total of 22 trials per hand (final total of 88 pictures considering two hands and two conditions). Participants were required to point to each landmark on top of the board by using their index fingers. They were allowed to make pointing adjustments to avoid ballistic responses' variability (Kammers, de Vignemont, et al., 2009; Króliczak et al., 2006). Once the landmark was located, a picture of the response was taken for later analyses. Participants were then required to remove their index finger (right or left) and place it back on the table, before the next landmark was read. Participants did not receive any feedback during the experiment.

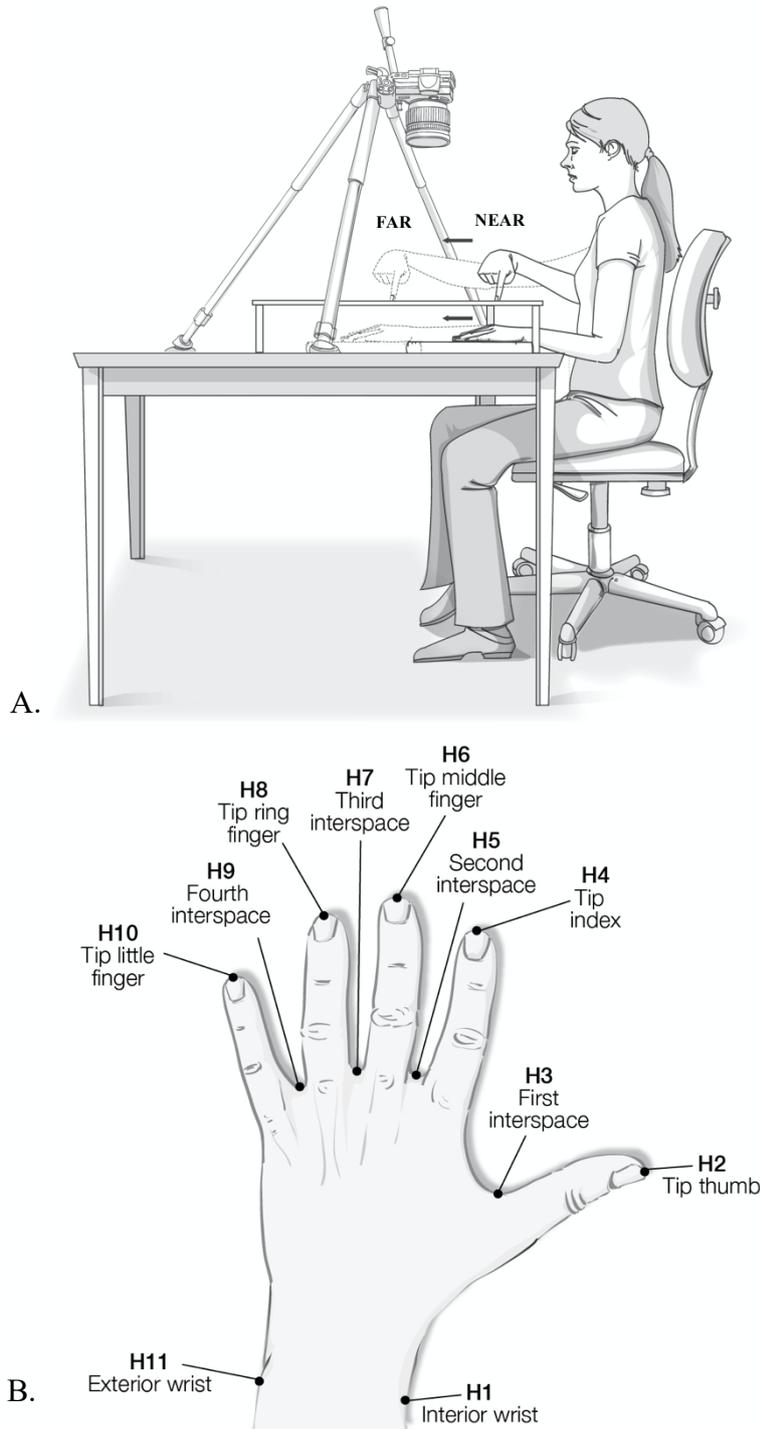


Figure 4.7. Hand setting and landmarks.

Picture of hand setting showing hand position in near and in far conditions (A); and illustration of hand's and wrist's landmarks (B).

4.3.2.1.3 General analyses

Information on the coordinates for single pointing responses was used to calculate the misallocation judgements of each landmark. Thus, from each individual picture taken, the x and y coordinates were calculated for the real and perceived location per landmark (origin was located at the bottom right corner of each picture). For this, a programme developed with Borland C++ Builder (2007) was used, allowing conversion of pixel units into centimetres.

The coordinate data was further used to calculate the inferred hand size (lengths and widths), and underlying shift of landmarks. Previous studies have used the information on the coordinates for single pointing responses to calculate distance between landmarks, and decode the so-called body model (e.g., Longo & Haggard, 2012). These distances are chosen between meaningful pairs of landmarks in order to calculate the length of fingers and the width of the hand (e.g., between H2 and H3 for the length of the thumb; see Figure 4.7B). Thus, the finger lengths, the hand's dorsum length, the hand's width and the width of the wrist, were calculated for each hand in near and far conditions.

4.3.2.1.4 Statistical analyses

The results on the representation of the hands are considered in Condition A (near-reaching space), and again in Condition B (far-reaching space). Firstly, the overall distortion for each condition was calculated and tested against zero (no distortion) for each group. Differences between groups were tested by means of independent two-tailed t-tests. Pairwise t-tests were used to test differences in the representation of different dimensions within participant groups (e.g., difference in hand width versus wrist width).

4.3.2.2 Results

Cartographic maps of the real and perceived hands for both groups were produced by using the x and y coordinates, showing the differences between the real and perceived hand sizes between conditions and groups (see Figure 4.8).

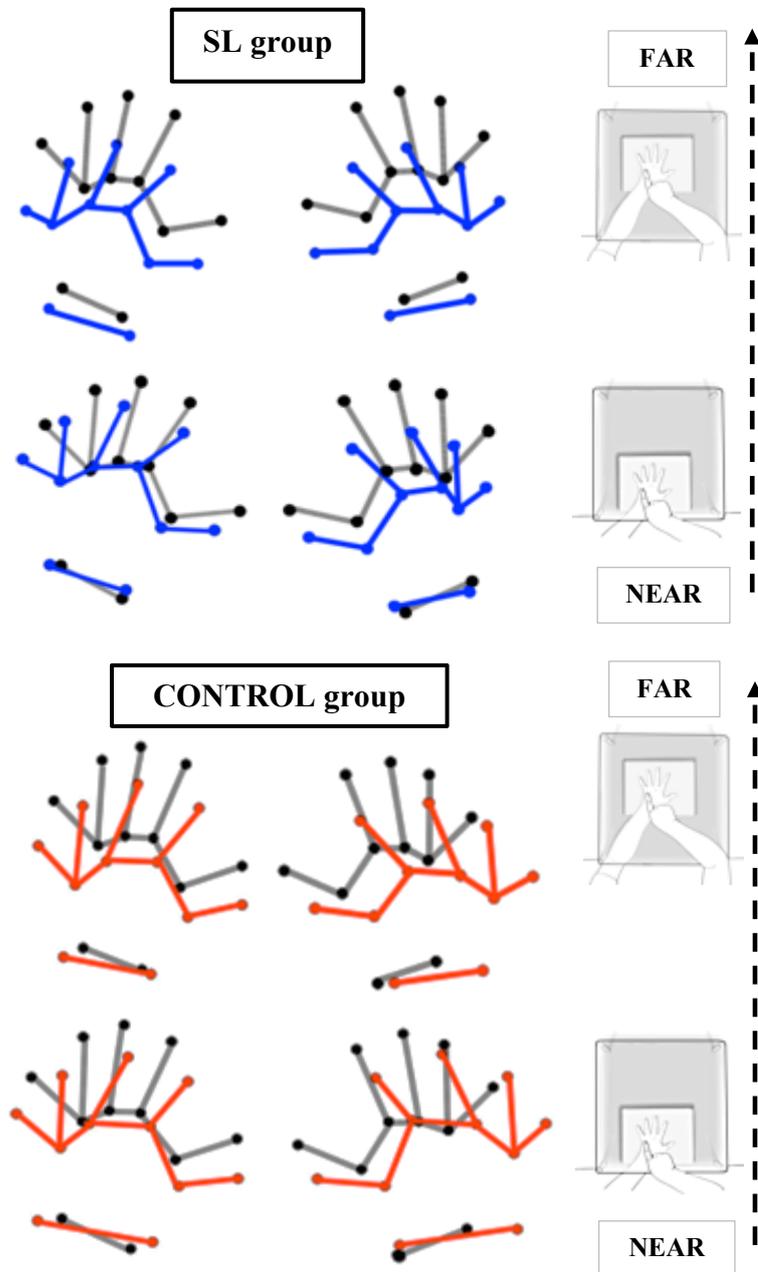


Figure 4.8. Cartographic hand maps.

Maps for real (grey lines) and perceived hands' representation in SL (blue lines) and Control (red lines) groups, in near and far conditions.

4.3.2.2.1 Condition A: near-reaching space

Length of fingers and dorsum

Differences between left- and right-hand size estimations were not significant (all p s. $> .05$ for both groups and lengths); hence, size (percentage of over/underestimation) was averaged across hands for further analyses. There was overall underestimation of finger lengths, with SL participants underestimating their length by a -21.23% (SD = 11.24) and controls by a -12.53% (SD = 14.11). The distortion of length was significant for both SL [$t(9) = -5.97, p < .001, d = -1.88$] and controls [$t(9) = -2.82, p = .02, d = -.88$]. Differences between groups did not reach significance [$t(18) = 1.53, p = .15, d = .68$].

The length of the hand's dorsum was calculated as the distance between the second interspace (H5) and the interior part of the wrist (H1) (see Figure 4.7B). Overall, the perceived length of the dorsum was underestimated in both groups. SL group underestimated the size of the dorsum by -9.96% (SD = 13.1) and the distortion was significant [$t(9) = -2.4, p = .04, d = .76$]. Controls underestimated in similar magnitude (M = -9.56%, SD = 21.49) but in this case not significantly so [$t(9) = -1.41, p = .19, d = .44$]. Differences between groups did not reach significance [$t(18) = .05, p = .96, d = .02$]. These results confirmed there were no significant differences in length perception between groups in the near condition.

In order to compare if the length distortion was different between fingers and the dorsum, two pairwise t-tests were run within each group (Bonferroni corrected p value of $p = .025$). Interestingly, there were significant differences in the SL group [$t(9) = -3.75, p = .005, d = 1.19$], whereas no differences were found for controls [$t(9) = -.46, p = .66, d = .14$]. These results indicated that length of fingers in SL group was more underestimated than the dorsum (see Figure 4.9).

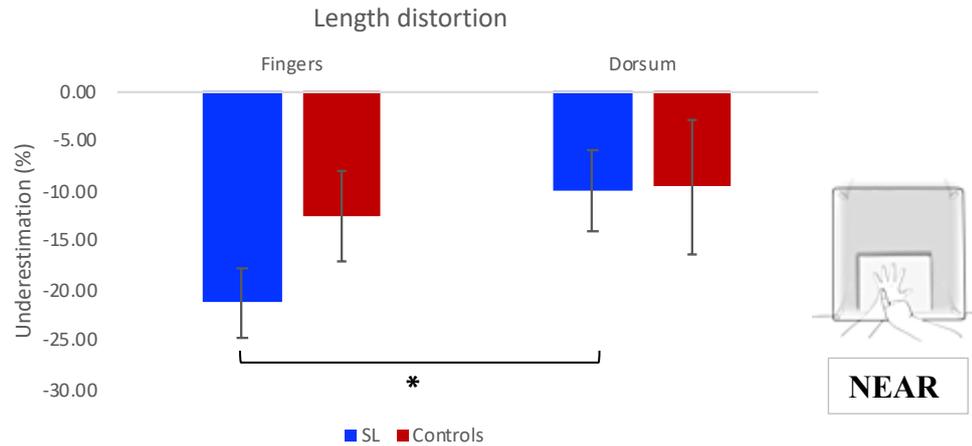


Figure 4.9. Length distortion near-reaching space.

Averaged underestimation for finger lengths and length of hand's dorsum across hands for controls and SL participants. Error bars represent Standard Error of the Mean. * denotes significant differences.

Width of the hand and wrist

The real and inferred perceived distance between second (H5) and fourth interspace (H9) was calculated as a measure of overall width of the hands (see Figure 4.7B). Equal to length findings, differences between the widths of the left and right hands (dorsum and wrists) were not significant (all p s. > .05); hence, these were averaged across both for analyses. Both groups overestimated the width of their hands, with SL users ($M = 35.09\%$, $SD = 14.56$; $t(9) = 7.62$, $p < .001$, $d = 2.41$) and controls ($M = 73.55\%$, $SD = 26.16$; $t(9) = 8.89$, $p < .001$, $d = 2.81$) showing a significant distortion. The difference between groups was significant [$t(18) = 4.06$, $p = .001$, $d = 1.82$], confirming that the SL group was more accurate than controls in the representation of the width of their hands (see Figure 4.10).

In order to explore the effect on width representation further, the width of the wrists was considered (see Figure 4.10). SL participants did not show a significant overestimation of their width ($M = 15.65\%$, $SD = 24.65$; $t(9) = 2.01$, $p = .08$, $d = .63$). In contrast, controls perceived their wrists to be wider than their real size ($M = 54\%$,

SD = 39.27; $t(9) = 4.35$, $p = .002$, $d = 1.37$). Group differences were significant [$t(18) = 2.62$, $p = .018$, $d = 1.17$], confirming that the SL participants were more accurate when estimating the size of their wrists

As with lengths, the perceived width distortion was compared between hands and wrists (Bonferroni corrected p value of .025). There was a trend in SL group [$t(9) = 2.36$, $p = .04$, $d = .75$], indicating a more distorted representation of the hand in comparison with the wrist. This was also the case for controls, who also perceived the hand significantly more distorted than the wrist [$t(9) = 2.74$, $p = .02$, $d = .86$]. Hence, it appears that the hand width overestimation is more accentuated in the hand than the wrist.

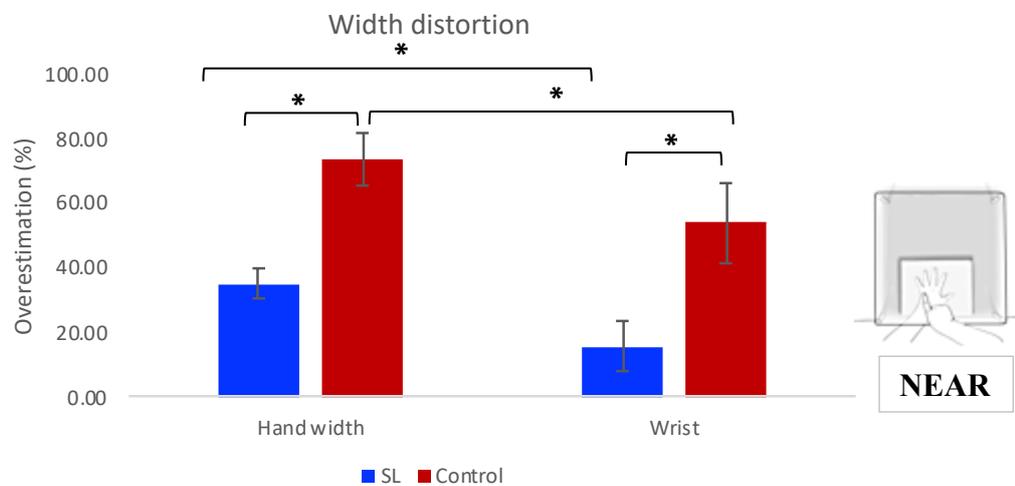


Figure 4.10. Width distortion in near-reaching space.

Representation of the distortion of hands' and wrists' widths averaged across hands for both groups. Error bars represent the Standard Error of the Mean. * denote significant differences.

4.3.2.2.2 Condition B: far-reaching space

Length of fingers and dorsum

In the far distance, SL participants significantly underestimated the length of fingers ($M = -17.99\%$, $SD = 15.74$; $t(9) = -3.62$, $p = .006$, $d = -1.14$), whilst controls did not show a significant distortion of their finger length ($M = -4.64\%$, $SD = 21.09$; $t(9) = -.696$, $p = .5$, $d = -.22$) (see Figure 4.11). However, differences between groups were not significant [$t(18) = 1.61$, $p = .13$, $d = .72$].

When considering hands dorsum's lengths, SL participants underestimated by -10.91% ($SD = 22.09$), but the distortion was not significant [$t(9) = -1.56$, $p = .15$, $d = .49$]. Similarly, controls showed underestimation of the size of the dorsum ($M = -9.91\%$, $SD = 26.5$) but not significantly so [$t(9) = -1.18$, $p = .27$, $d = .37$]. Differences between groups did not reach significance [$t(18) = .09$, $p = .93$, $d = .04$].

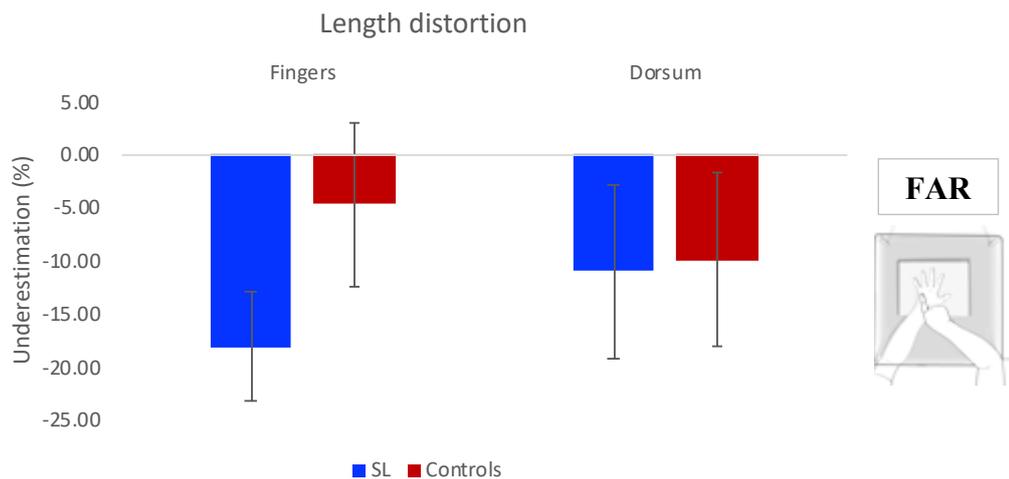


Figure 4.11. Length distortion far-reaching condition.

Representation of the averaged distortion for the length of fingers and the length of the hand's dorsum averaged across hands for both groups. Error bars represent the Standard Error of the Mean.

Differences between the underestimation of finger lengths and dorsum were not significant for either the SL group [$t(9) = -.98, p = .35, d = .31$] or for control group [$t(9) = .52, p = .61, d = .17$].

Width of the hand and wrist

In the far distance, SL participants significantly overestimated the width of their hands ($M = 41.93\%$, $SD = 16.55$; $t(9) = 8.01, p < .001, d = 2.53$). Similarly, controls also showed a distortion for the width of their hands, and was found to be significant ($M = 59.81\%$, $SD = 27.13$; $t(9) = 6.97, p < .001, d = 2.21$) (see Figure 4.12). Differences between groups were not significant in this case [$t(18) = 1.78, p = .09, d = .8$].

Similarly, overestimation of width was present for the wrists in both the SL group ($M = 38.56\%$, $SD = 42.2$; $t(9) = 2.89, p = .02, d = .91$) and the control group ($M = 49.68\%$, $SD = 39.66$; $t(9) = 3.96, p = .003, d = 1.25$). As with the hands, differences between groups did not reach significance [$t(18) = .61, p = .55, d = .27$], and is in contrast with the near space condition.

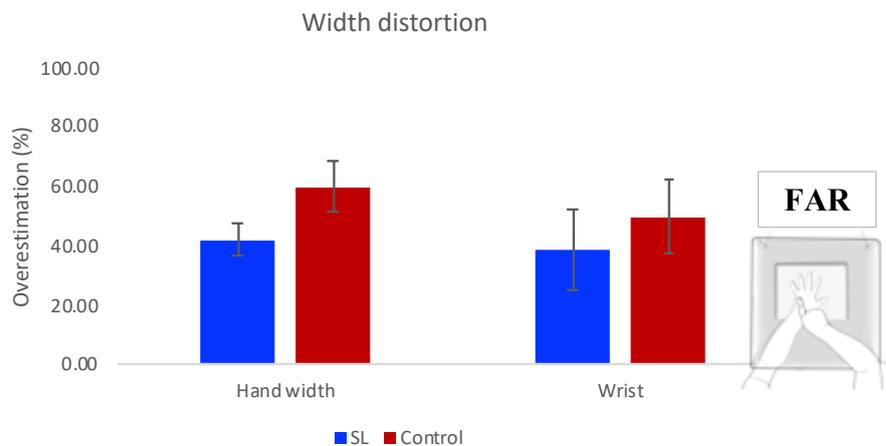


Figure 4.12. Width distortion far-reaching space condition.

Representation of the averaged width of hands and wrists for both groups. Error bars represent the Standard Error of the Mean.

Lastly, differences between the perceived width of the hands and wrists were not significant in either the SL [$t(9) = .26, p = .8, d = .08$] or control groups [$t(9) = .86, p = .41, d = .27$], confirming that hands and wrists were equally distorted in far reaching space condition.

4.3.2.2.3 Comparisons between conditions

In this case, the differences found in the perception of the size of the hand and wrist across distance conditions were directly compared. Mixed model ANOVAs were run with two factors: Distance (near and far) and Group (control and SL groups), for each dependent variable (finger lengths, dorsum length, hand width and width of wrists). Averaged results are presented in Figure 4.13.

The ANOVA for the length of fingers showed a trend for the Distance factor [$F(1,18) = 4.01, p = .06, \eta^2 = .18$], as there was an overall reduction of the underestimation in the far-reaching space condition. Results did not reach significance for the Group factor [$F(1,18) = 2.82, p = .11, \eta^2 = .14$], or for the Distance by Group interaction [$F(1,18) = .7, p = .41, \eta^2 = .04$].

For the dorsum's length, neither Distance [$F(1,18) = .02, p = .89, \eta^2 = .001$], Group [$F(1,18) = .01, p = .93, \eta^2 < .001$] nor Distance by Group interaction [$F(1,18) = .004, p = .95, \eta^2 < .001$] were significant.

When considering the hand width, the ANOVA did not reveal significant results for the main factor of Distance [$F(1,18) = .39, p = .54, \eta^2 = .02$]. However, there were significant results for the main effect of Group [$F(1,18) = 12.27, p = .003, \eta^2 = .41$], confirming a better overall estimation of hand width in the SL group. Lastly, there was a trend for the Distance by Group interaction [$F(1,18) = 3.46, p = .08, \eta^2$

= .16], as the SL group perceived the width of their hand more accurately in the near space condition.

Lastly, the ANOVA for the wrist did not reveal significant results for Distance [F (1,18) = 1.33, p = .26, $\eta p^2 = .07$], Group [F (1,18) = 2.91, p = .11, $\eta p^2 = .14$], or for the Distance by Group interaction [F (1,18) = 2.85, p = .11, $\eta p^2 = .14$].

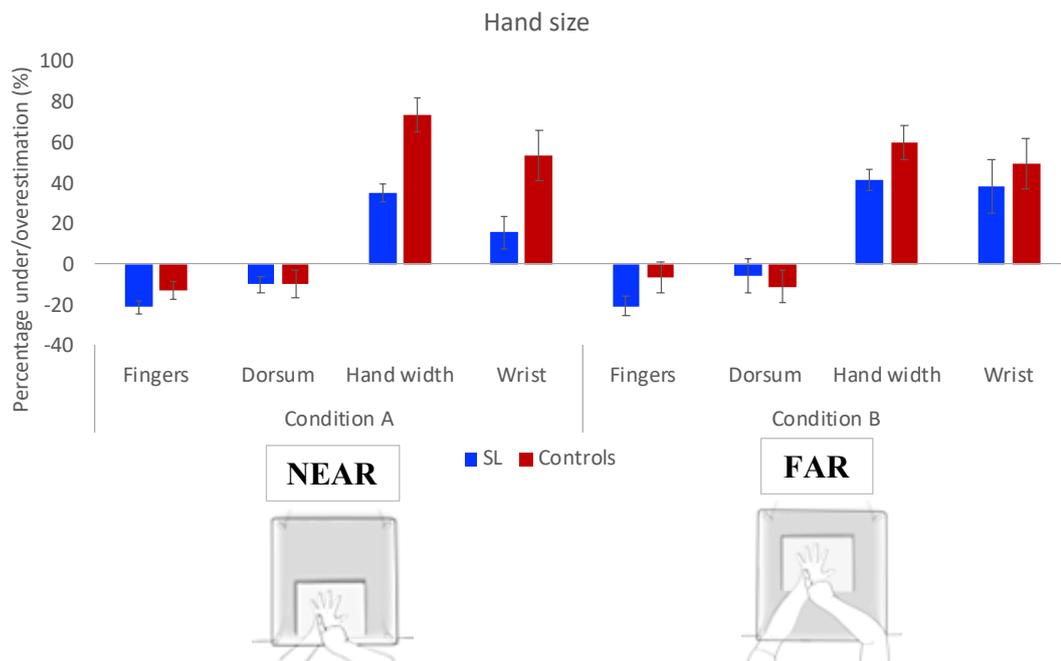


Figure 4.13. Comparisons between conditions.

Averaged size distortion for finger lengths, hands' dorsum, hands' width and wrists for all participants across conditions. Error bars indicate the Standard Error of the Mean.

4.3.2.3 Preliminary discussion

Results in this study have shown how expert signing modulates the representation of hands. Specifically, although distortions in near reaching space follow the characteristic pattern for both groups (i.e., underestimation of length and overestimation of width), the SL group showed more distortion of length of fingers (but not significant), and a significant reduction of distortion for width. Hence, the SL

group was not better than the control group when estimating their finger lengths. Moreover, this increased distortion was specific to fingers and was not seen in the dorsum of the hands. These results are in line with Coelho et al. (2019) study, in which a smaller hand was seen as advantageous to catching the ball in baseball, reducing the margin of error. Extrapolating to SL users, it is possible that the way the hands are used also affects how these are represented. In order to sign, hands need to be moved accurately, and in a quick and timely fashion, coordinating complex movements. Therefore, it could be argued that a smaller hand may be of more benefit, in the same way that certainty reduces the size of hand aperture for grasping (Jakobson & Goodale, 1991).

Regarding the specific direction of the distortions, SL and control groups did not significantly differ in the perception of finger lengths and did not reflect any clear effects of expertise. However, within the SL group, worse performance was demonstrated at the estimation of finger length compared to that of the dorsum. This confirmed the association of body size representation with specific use and functional experience (Caggiano & Cocchini, 2020; Ferretti, 2016; Fraser & Harris, 2016, 2017; Romano et al., 2019), and not with an overall bias to underestimating lengths. In other words, the larger underestimation of length was specific for fingers, and not an overall bias affecting the whole hand. As seen in Chapter 3, repeated skill work in a given manual workspace will prime the perception of hand position towards usual locations, biasing localisation towards them (Fraser & Harris, 2016). In this case, SL practitioners vary the position of their fingers frequently, perhaps increasing the uncertainty of their localisation. Hence, functionality becomes a main factor that guides proprioceptive localisation of fingers (Dandu et al., 2018). Further, the specific distortions directly depend on the perceptual experience with the body part (Bettger et

al., 1997). Supporting this, other studies have postulated that dancers are only better in the localisation of highly trained postures, which does not necessarily transfer to non-trained postures (Jola et al., 2011; Schmitt, Kuni, & Sabo, 2005).

On the contrary, SL participants showed a clear advantage in the representation of the width of hands and wrists. Width is believed to be the dimension with more variability, as it is intrinsically related to more representational flexibility to accommodate growth (De Vignemont, Ehrsson, & Haggard, 2005; Hashimoto & Iriki, 2013). Moreover, width is the dimension that appears more linked to own body representation (Ganea & Longo, 2017), as length underestimation is also found when judging the size of a rubber hand (Longo et al., 2015; Saulton et al., 2016). Hence, and as hypothesized in Chapter 3, width appears more susceptible to modulation than length. In any case, it follows that expert use of the hands modulates influences in width perception (e.g., homuncular characteristics (Nguyen et al., 2005); reversed distortion (Linkenauger et al., 2015); self-perception biases (Felisberti & Musholt, 2014; Sui & Humphreys, 2015), and safety margin (Nico et al., 2010)) (see Chapter 3 for discussion), in such a way that it becomes more accurate.

Owing to the idea of manual practice and functional workspace (Fraser & Harris, 2016, 2017), differences in the representation of the hands were only seen in the near-reaching space, and not in the far-reaching space, whereby performance between groups was not significantly different. This was due to a reduction of the gain by the SL group in near reaching space from 38.46% to 17.88% in far-reaching space. As signers produce all their communication within a confined three-dimensional signing space that extends from the forehead to the waist, to the front of the face and chest, and laterally beyond the elbows (Arnold & Mills, 2001; Emmorey, 2001), differences in experience may only be found within this confined space. In particular,

BSL signs occur near the other hand, face or trunk (Woodward, 1982) and the categorisation of handshapes in space is important to provide meaning (Cormier, Fenlon, & Schembri, 2015; Sandler, 2018) (see Figure 4.6).

Not only do SL practitioners use the hands to a greater extent than the typical population, they also sign around the face, as well as using facial expressions to communicate (Emmorey & McCullough, 2009). Thus, the next experiment looked into the effect of expertise for the metric representation of the face.

4.3.3 Experiment 2B: face representation in SL

Head tilts, movements of the brows, squinting of eyes and mouth movements are used independent of the hands in SL, and each component provides meaning in different ways. That is, upper face areas, such as brows or eyes, when combined with hand gestures provide intonation to the expressions (Sandler, 2018). In contrast, the lower face areas are involved in different functions. *Mouthings* are speech-like mouth movements, and have phonological function; whilst *mouth gestures* are non-speech like movements that are inseparable, and guided by the manual action not deriving from words (Capek et al., 2008).

SL proficient users focus on the addressee's face, and seldom look to their hands (Capek et al., 2008; Siple, 1978). Similarly, the addressee focuses on the signer's face, where gestures are seen in high acuity (foveal vision), which becomes the centre of attention (Muir & Richardson, 2005). In contrast, eye fixations to manual gestures are minimal and only present when gestures occur near the face, otherwise being processed by peripheral vision (Muir & Richardson, 2005; Siple, 1978). The specialised use of the face in SL not only translates in attentional differences, but also on improved perceptual abilities. For example, SL proficiency is associated with enhanced lip-reading skills, in particular for deaf people (MacSweeney et al., 2008),

and improved local facial feature recognition (Emmorey & McCullough, 2009). In fact, better discrimination of self-face is linked to a more robust stored representation (Keyes & Brady, 2010). These findings support the importance of the face in SL, and the relevance of studying the effects of expertise on its representation. In this second study, improved ability of SL practitioners to localise face landmarks is predicted in comparison with controls.

4.3.3.1 Methods and procedures

4.3.3.1.1 Participants

The same group of participants took part in this second study. See demographic information in Table 4.2. Experiment 2B took place on the same day as the previous one, and the order was counterbalanced across participants to control from order or practice effects. No feedback was provided after Experiment 2A, and participants were engaged in general conversation before carrying out Experiment 2B (or vice versa).

4.3.3.1.2 Face localisation task and procedure

Participants were required to locate different face landmarks on command whilst keeping their eyes closed. The overall method was like those adopted for Chapter 3, with slight variations. A vertical transparent Perspex board (50 x 55 cm) resting on two wooden legs (20 cm height) was positioned on a table, in front of the participant. A chin rest was on the edge of the table, between the Perspex board and the participant. The Nikon 3200D camera was positioned on a tripod at 120cm. The centre focus of the camera was aligned with the centre of the board and the tape measures were attached to the top and right side of the board for later analyses.

Participants were required to rest their head on the chin rest, aligning the tip of the nose with the camera focus. They were asked to avoid movements of the face for

the whole duration of the experiment, to maintain a relaxed facial expression (not smiling), and to keep their eyes closed (see Figure 4.14). As in Chapter 3, 11 landmarks were read aloud in random order (see Figure 4.15). The landmarks had to be located by pointing towards the face, on top of the Perspex board, with their right index finger. A picture (6016 x 4000 pixels) was taken for each pointing response. Following this, the hand had to return to the initial position on the table, before the next landmark was requested. Each landmark was repeated twice, with a total of 22 trials per participant. Participants did not receive any feedback for the whole duration of the experiment. As in Experiment 2A, participants practiced identifying the landmarks on a schematic drawing prior the experiment.



Figure 4.14. Face localisation task.

Face apparatus and participant positioning during the face localisation task.

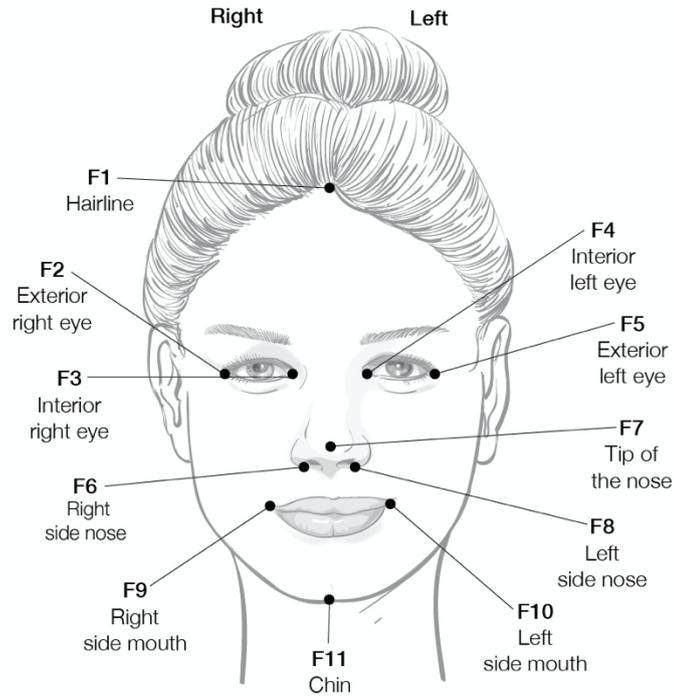


Figure 4.15. Illustration of face landmarks.

11 facial landmarks requested during the face locasiation task.

4.3.3.1.3 General analyses

Pictures were analysed by using Borland C⁺⁺ Builder (2007). A total of 22 pictures (2 for each of the 11 landmarks) were collected. Pixel units were converted into centimetres, to obtain the x and y coordinates for each real and perceived landmark location. The origin in this case was at the left top corner of each picture. The real and perceived distances between landmarks was then calculated for specific areas. The length of the face was calculated by obtaining the real and perceived distances between the F1 and F11 landmarks. Further to this, the distance between different facial features were calculated: right eye (distance from F2 to F3); between eyes (distance between F3 and F4); left eye (distance from F4 to F5); nose (F6 to F8); and mouth (F9 to F10) (see Figure 4.14B). Percentage of over/underestimation was calculated from this data.

One participant (SL003) had a missing data point for the right eye. The missing data was replaced with the series mean for analyses.

4.3.3.1.4 Statistical analyses

As in the previous experiment, initial one-sample t-tests were run to investigate if the distortions of size were significantly different from zero (no distortion). Group differences were then investigated by means of mixed-model ANOVAs or independent t-tests.

4.3.3.2 Results

As in previous experiments, the coordinates were used to produce schematic maps of the real and perceived face for both groups (see Figure 4.16).

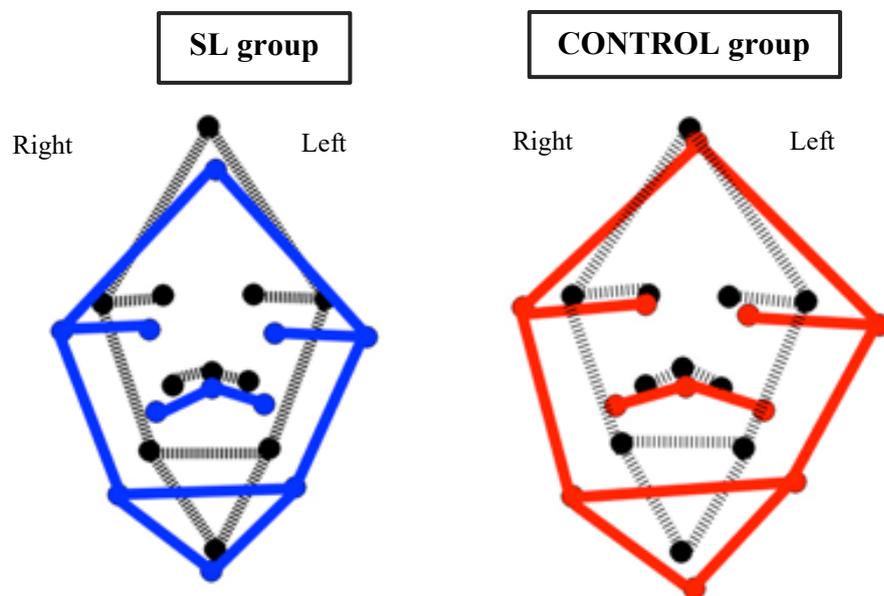


Figure 4.16. Face maps.

Representation of real (continuous lines) and perceived face size (black dotted lines) in SL (blue) and Control (red) groups.

4.3.3.2.1 Face length

SL and control participants showed opposite trends in length perception, but the distortion was not significant (i.e. different from zero) for either the SL ($M = -4.5\%$, $SD = 19.87$; $t(9) = -.72$, $p = .49$, $d = -.23$) or control groups ($M = 5.39\%$, $SD =$

16.51; $t(9) = 1.03$, $p = .33$, $d = .33$). An independent samples t-test confirmed these differences were not significant between groups [$t(18) = 1.21$, $p = .24$, $d = .54$] (see Figure 4.17).

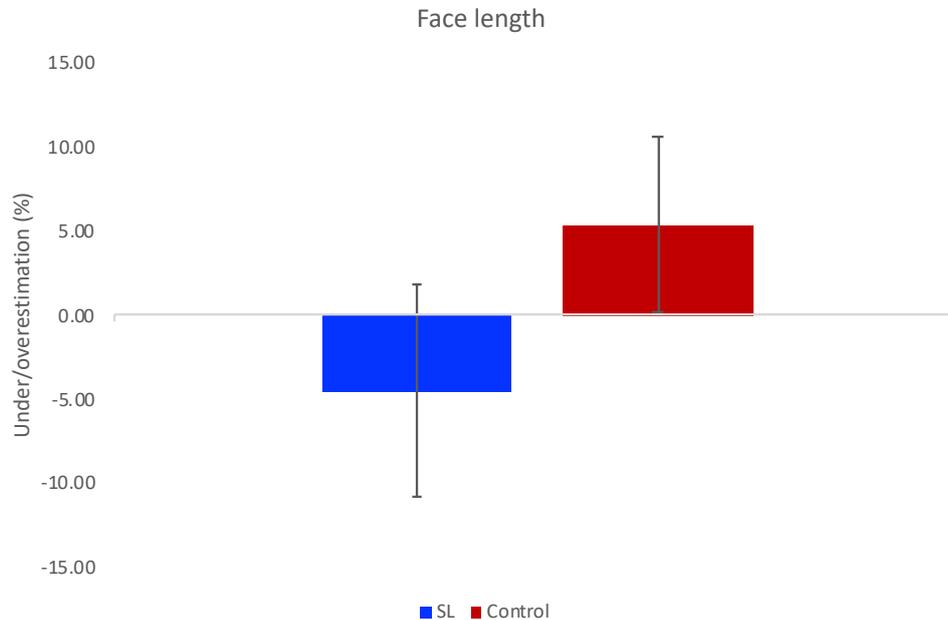


Figure 4.17. Face length.

Representation of the length of the face for both SL and controls. Error bars represent the Standard Error of the Mean.

4.3.3.2.2 Face widths

On average, the SL group showed more accuracy in the perception of the width of the face. The control group overestimated the width of face landmarks by 73.76% (SD = 19.64) a distortion that was significant [$t(9) = 11.87$, $p < .001$, $d = 3.75$]; whereas the SL group overestimated by 36.55% (SD = 19.92), again, significantly so [$t(9) = 6.78$, $p < .001$, $d = 2.14$].

Figure 4.18 illustrates the width sizes for each face Landmark. A mixed model ANOVA (Landmarks (5) x Group (2)) revealed a significant main effect of Landmarks [$F(4, 72) = 4.74$, $p = .002$, $\eta^2 = .21$], indicating different width size representation

depending on the landmark considered. Bonferroni corrected pairwise comparisons (cut off p value of .005), showed that the mouth was more overestimated than the right eye ($p = .003$; mean difference = 31.81) and the between eyes area ($p = .003$; mean difference 34.46). It also showed that the nose width was more overestimated than the between eyes area ($p = .003$; mean difference = 34.36). No other comparisons reached significance (all p s. $> .005$). Furthermore, there was a main effect of Group [$F(1,18) = 19.02, p < .001, \eta^2 = .51$], confirming that SL participants represented the width of the face more accurately than controls (mean difference = 36.12). Lastly, the Landmarks by Group interaction was significant [$F(4,72) = 2.86, p = .03, \eta^2 = .14$], with different distortion of landmarks depending on the group considered. Independent Bonferroni-corrected t-tests (p value of .01) revealed that SL participants perceived the right eye [$t(18) = 2.99, p = .008, d = 1.34$], the nose [$t(18) = 3.74, p = .001, d = 1.67$], and the mouth [$t(18) = 3.19, p = .005, d = 1.43$], significantly more accurately than controls. There were no significant differences for the left eye ($p = .08$) or between eyes area ($p = .4$).

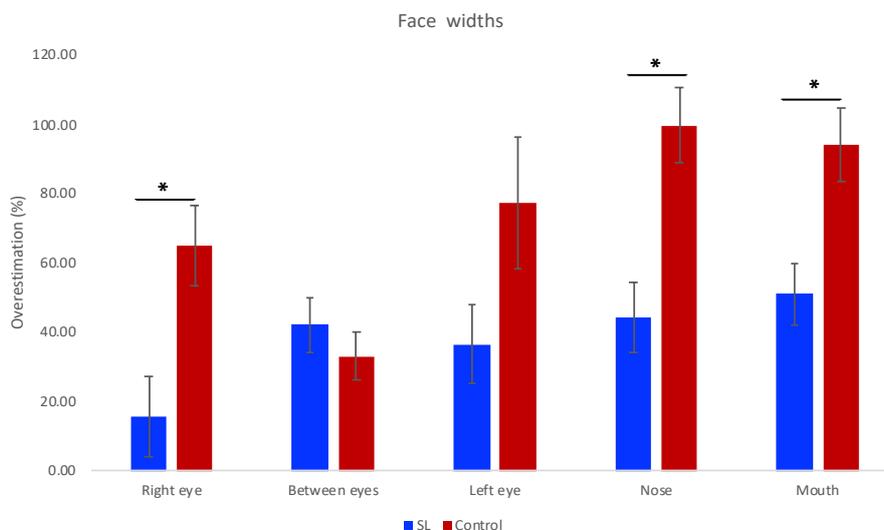


Figure 4.18. Face width distortion.

Graph depicting representation of the width of face landmarks for both groups. Error bars represent the Standard Error of the Mean. * denote significant differences.

4.4 General discussion

Previous studies have shown that metric distortions of body parts are intrinsic to healthy representation of the body, as seen in Chapter 3, and can be modulated by intensive long-term training (Coelho et al., 2019; Romano et al., 2019). Despite the interest on the representation of hands (see Longo, 2017, 2019 for recent reviews), few studies have looked at the impact of extensive tool-use on hand representation (e.g., Coelho et al., 2019), and none have explored the modulation of the representation of the face.

In Experiment 2A, SL experts considerably outperformed controls at estimating the width of their hands in near-reaching space (but not in far). However, there was no advantage in the representation of lengths. These results contrast with findings in Experiment 1, in which magicians' expertise was associated to improved finger length perception. This difference may be due to the type of expertise. Magicians are experts on the instrumental use of hands; that is, they have trained to use them when holding objects, improving their sleight of hands and, in particular, refining the representation of their fingers, which are highly trained (Cavina-Pratesi et al., 2011). Instead, SL is an embodied visual-spatial language and practitioners use hands and face for language and communication (Shield & Meier, 2018), but do not train the sleight of hand to manipulate certain objects or 'deceive', as in the case with magicians. The importance of the use of hands in SL include which handshape they adopt, where they are located in relation to other body parts, and in which direction they are moving (Mitchell, Letourneau, & Maslin, 2013; Sehyr & Cormier, 2016). This type of hand use may improve the accuracy of location judgements in comparison with controls, but this may not be evident for the finger length. Therefore, it could be argued that expertise may not necessarily cause an overall improved representation, rather,

evidence suggests that it modulates representation in the direction that is linked to the function in hand.

In Experiment 2B (study on face representation), the metric representation of the face was also explored. In line with Experiment 2A, SL users perceived the width of facial features more accurately than controls, whereas no differences were found in length perception. Hence, it is also the case that the representation of the face tends to be smaller for SL. As seen with magicians, prolonged manual practice can produce long-term changes in the representation of the body. However, the link between better representation and expertise may not be as straight forward. Instead, these results may indicate that the body distortions may be modulated in the direction that best fits each type of expertise (Coelho et al., 2019).

In SL, practitioners do not visually track the movement of their hands when signing, and vision is instead used to calibrate the signing space, relying on somatosensory, kinaesthetic and tactile feedback (Emmorey, Bosworth, et al., 2009), as in magicians (Cavina-Pratesi et al., 2011). They look at the face of the addressee (Emmorey, Thompson, & Colvin, 2009; Siple, 1978), and signs fall in the periphery or outside of the visual field (Emmorey, Bosworth, et al., 2009). Signers require advanced visuo-motor skills to process this language, as they are “faced with the dual task of spatial perception, spatial memory and spatial transformation, on the one hand, and processing grammatical structure on the other – in one and the same visual event” (Emmorey et al., 1993, p. 140). Further, SL experts show superior face recognition skills, directly linked to the expertise in signing (Bettger et al., 1997). In particular, expertise with SL fine-tunes face-processing skills, such as local facial features discrimination (Emmorey & McCullough, 2009), rather than just enhancing overall visual discrimination (McCullough & Emmorey, 1997). For example, studies have

shown processing skills that are particularly strong when identifying subtle facial feature changes in eye configuration or mouth shape (McCullough & Emmorey, 1997). This was associated with the experience with SL and lipreading skills (McCullough & Emmorey, 1997), and not with the experience of deafness (Parasnis, Samar, Bettger, & Sathe, 1996). Interestingly, this advantage disappears with inverted faces, in which signers perform as non-signers, confirming the gain directly depends on the perceptual experience with the body part (Bettger et al., 1997). Further, attention to faces in the general population is directed to the upper areas/eyes, whilst in the case of signers there is an equal distribution to upper and lower areas (Letourneau & Mitchell, 2011; Mitchell, 2017), with a preference or salience for lower ones (Mitchell et al., 2013). This may explain the general improvement in the representation of all face features. Furthermore, this highly developed skill in face processing will help construct a more robust self-face representation, with greater detailed information on spacing between features, instrumental for own face discrimination (Tsao & Livingstone, 2008).

Contributing to this combination of improved somatosensory and imagery skills, anatomical cortical changes appear due to long-term practice of SL. Indeed, fine motor control of the hands for signing causes structural differences in the volume of the hand knob (Allen, Emmorey, Bruss, & Damasio, 2013; Penhune, Cismaru, Dorsaint-Pierre, Petitto, & Zatorre, 2003), an area that includes the motor representation of the hand (Sastre-Janer, 1998). Moreover, areas involved in the representation of the size of the body, such as parietal lobes, including supramarginal gyrus, are involved in SL (Emmorey, Mehta, & Grabowski, 2007) and not in oral word production (Indefrey & Levelt, 2004). These structural and functional changes due to SL expertise may also have an effect in the metric representation of the body.

To sum up, these results confirm that an embodied visual language can influence non-linguistic cognitive processes, indicating that mechanisms related to SL are not domain-specific and, instead, interact (Bettger et al., 1997). As seen with magicians, prolonged manual practice can produce long-term changes in the representation of the body. However, these changes may not be related to actual general improvement of the representation, but appear modulated by the type of expertise (Coelho et al., 2019). Hence, the direction of distortions differs between expert groups.

Further, these two studies also help answer one of the controversies in the field. Previous research could not discern if this task was measuring a prototypical body or not, as the same distortions were found when estimating a fake leg or when imagining the body (Coelho et al., 2019). However, if the body prototype was the reason for these distortions, one would not expect a changed representation due to expertise. Instead, this body model was modulated by expertise. Along this line, if modulation is achieved through long-term use of body parts, then one must assume that impoverished somatosensory information and, hence, non-use, will then disrupt representation. Indeed, body size perception is altered in patients with amputations (Giummarra et al., 2007; Paqueron et al., 2003), deafferentation (Fuentes, Pazzaglia, Longo, Scivoletto, & Haggard, 2013), and in health can be easily manipulated, such as with anaesthesia (Gandevia & Phegan, 1999). However, not only bottom-up processes modulate the representation of the body. Indeed, top-down modulatory processes occur after damage to different areas in the brain. For example, autotopagnosia, a disorder in which patients are unable to locate their own body, appears after left posterior parietal lobe lesions (Berlucchi & Aglioti, 2010; Buxbaum & Coslett, 2001; Pick, 1922).

Hence, there is a variety of disorders associated with afferent and efferent disruptions on information processing, at different stages of a wide network of areas

that play a central role in constructing a representation of the body (Berlucchi & Aglioti, 2010; Palermo et al., 2018). Therefore, the study of disrupted body representation after brain insult could shed further light in the involvement of different cortical areas in the representation of body size. To this aim, the next chapter will present a patient with a left precentral glioblastoma in Experiment 1, to explore its effect in the representation of hands and face. In Experiment 2, evidence in the distorted representation of hands and face will be investigated for a group of patients experiencing Personal Neglect (PN).

Chapter 5: **Effects of brain damage on the size representation of the hands and face**



Josephine Cardin Photography

5.1 Introduction

The study of body representation disorders has been of interest since the early stages in body representation research, due to their complexity, variety and distinctiveness (Palermo et al., 2018), and the impairments they cause. Indeed, our understanding of the perception of the body has been promoted by studying errors (Medina & Coslett, 2016), and distortions (Longo, 2017b). Disorders of body representation are quite variable in their presentation, and range from brain damaged-related disorders, such as *Supernumerary Phantom Limbs Disorder*, where patients experience ownership of multiple limbs (Hari et al., 1998; McGonigle et al., 2002); to psychiatric conditions, such as *Body Integrity Disorder*, in which individuals have a desire to acquire a disability (First & Fisher, 2012); or body injury-derived disorders, such as *Spinal Cord Injury* (Magnani & Sedda, 2016; Sedda et al., 2019). Interestingly, in many occasions these disruptions are associated with altered size perception. For example, patients with *Anorexia Nervosa* overestimate the width of their body (Mohr et al., 2010; Mölbert et al., 2017); whereas patients with *Chronic Pain Syndrome* feel their affected limbs are overestimated (Lotze & Moseley, 2007), due to altered cortical maps (Moseley et al., 2012). This size overestimation has also been seen for the face in patients with *Chronic Orofacial Pain* (Dagsdóttir et al., 2016; Kothari et al., 2020). The study of these disorders is a major contributing factor in the development of multiple models trying to explain the different components of body representation, as seen in Chapter 1.

Moreover, the study of body disorders has helped in identifying a wide network of cortical areas that play a central role in representing the body (Berlucchi & Aglioti, 2010; Palermo et al., 2018), as seen in Chapter 2. For example, lesions to the left posterior parietal lobe are associated with *Autotopagnosia*, a disorder in which

patients are unable to locate their own body (Berlucchi & Aglioti, 2010; Buxbaum & Coslett, 2001; Pick, 1922), whereas reduced activity in the extraestiate body area (EBA) is at the core of body image disturbances observed in eating disorders (Pazzaglia & Zantedeschi, 2016; Urgesi et al., 2012).

One particular type of brain lesion is the case of brain tumours, a relatively slow and progressive form of brain damage. Brain tumours occupy cerebral space, damaging adjacent areas, causing oedema and compressing cerebral structures (Ebeling, Schmid, Ying, & Reulen, 1992), and the effects on body representation can be striking depending on their localisation. For instance, a recent case study presented a patient with a right temporoparietal tumour that caused complete bilateral loss of body ownership, feeling as if his body had been ‘lost’ (Smit, Van Stralen, Van den Munckhof, Snijders, & Dijkerman, 2018). The study on the effects of brain tumours can further help understand the involvement of different brain areas in body size perception. With this in mind, Experiment 1 in this chapter presented the case of AM, a patient with a well-defined tumour in the left precentral area, which underlies the somatosensory and motor representation of the hand. This allowed the investigation of the impact of a relatively slow-progressing lesion in body representation, and in particular, of its metrics. For this, the localisation task to measure the metrics of the hand and face were administered before and after tumour resection.

Similarly, some disorders in which patients show an impairment in the use of the body have been better explained by an underlying disordered body representation. One of these disorders is Personal Neglect (PN), in which patients show hemi-inattention towards the contralesional side of the body, failing to attend, explore, orient towards or use the affected limbs, deficit that cannot be explained by sensory or motor defects (Baas et al., 2011; Committeri et al., 2018, 2007; Heilman,

Valenstein, & Watson, 2000). Due to the multidimensionality of body representation, multiple tasks have been used to better understand the altered components in this disorder. A variety of body impairments have been identified in PN; from a distorted body perception, to altered visuospatial body map, body schema, motor control or sense of ownership (see Caggiano & Jehkonen, 2018; Committeri et al., 2018 for recent reviews). This disorder is associated with damage to parietal areas, which are also presumed to be involved in storing the metrics of the body (Committeri et al., 2018, 2007). Hence, it is possible that these patients show distortions on the perceived size of their bodies. However, no previous research has attempted to study the effects of PN in relation to body size. In order to fill this gap in research, a group of PN patients were recruited for Experiment 2, to investigate the representation of the size of their hands and faces through the body size estimation task.

5.2 Experiment 1: selective effects of a tumour in the left precentral cortex on the metric representation of the hands

5.2.1 Introduction

Brain tumours and their effects allow to investigate the involvement of particular brain areas in specific functions. Due to their singularity and uniqueness, the study of brain tumours has brought a diverse array of presentations related to the body. For example, a recent case study presented a patient with a right temporoparietal tumour that caused complete bilateral loss of a patient's body ownership, feeling as if his body had been 'lost' (Smit et al., 2018). In another study, a patient with a gliosarcoma in the right hippocampus extending to the medial regions of the right temporal gyrus and parietal regions, presented a severe case of misoplegia, with verbal and physical aggression towards her left leg despite the absence of any sensory or motor deficits (Loetscher, 2006). A disorder of body awareness has also been reported

after tumour resection located in the right anterior frontal insula and operculum, in which the deficient access to hand representation was associated with perseveration drawing six fingers in a human figure (Niki, Maruyama, Muragaki, & Kumada, 2014). Further, a recent study explored the effect of brain tumours in developing brains (children and adolescents), finding altered body representation after tumours in infratentorial areas (cerebellum) associated with problems of motor imagery and visual processing of bodies (Corti et al., 2018). Lastly, impaired mental body representation was reported in a patient after resection of a right-parietal meningioma, causing the pervasive feeling of having four legs (Vuilleumier, Reverdin, & Landis, 1997).

Here, the case of patient AM is presented. AM had a tumour located in the left precentral cortex, within the hand's motor/premotor region. Structural changes in this area are associated with extensive practice in fine motor skills, such as sign language (Allen et al., 2013; Penhune et al., 2003), linking structural changes to motor performance and body representation. Moreover, cortical non-invasive stimulation of sensorimotor areas modulates the perceived size of the hand (Giurgola et al., 2019). Hence, it would be of interest to understand if this lesion causes an impairment in the metrics of the body. For this, the localisation tasks for the hand and face introduced in Chapter 3 were used. The localisation task has only been used in a clinical population twice, firstly in a patient with congenital limb loss (Longo et al., 2012), and recently to study the representation of lower limbs in patients with *Body Integrity Disorder* (K. D. Stone et al., 2020). Interestingly, both studies reported normal metric representation. Considering the location of the lesion in the case presented here, this experiment explored if there would be an impairment specific to the represented body part (contralateral hand), or if both hands would instead be impaired. Measures for the

representations of hands were taken before and after tumour resection. Moreover, the representation of the face was also explored to compare performance after tumour resection, to understand the specificity of the disruption further.

5.2.2 Method

5.2.2.1 Participants

Patient AM was a 41 years old man from Italy. He had 18 years of formal education and was right-handed. He was an experienced body builder for the last 8 years. The first clinical signs consisted of multi-week right hemi-facial tremor of about 10s duration. The pathological diagnosis was completed after about one year from symptoms' onset at the IRCCS Neuromed, Mediterranean Neurological Institute (Pozzilli, Italy) and consisted in a left precentral glioblastoma (grade IV). Histopathological analysis showed a mutant IDH1 and ATRX, compatible with the diagnosis of secondary glioblastoma from an astrocytic lineage, and in accordance with the long radiological and clinical history.

The patient underwent conventional anatomic MRI scans with and without contrast sequences on a 3 Tesla GE scanner both before and after surgery (see Figure 5.1), as well as pre-surgical functional mapping of language and motor functions. The structural scans showed a lesion of about 13 cm³, localised in the left precentral cortex, within the hand motor cortex (Caulo et al., 2007). Pre-surgical neurological and neuropsychological examination (see results section) did not identify any deficits.

AM underwent a resection of the tumour after about 5 months from diagnosis. Subpial microsurgical (i.e. under surgical microscope magnification) resection under continuous and real-time neurophysiological monitoring was performed. The procedure was conducted under local anaesthesia (awake surgery), with the aid of a

neuronavigation system. Surface cortical stimulation mapping showed critical sites for hand and arm contralateral movements localized outside the tumour lesion, in the posterior side, and a language site eliciting dysarthria in the inferior side of the cortical boundary of the tumour. The resection was stopped when normal surrounding tissue was encountered, paying more attention when motor performance worsened, especially during fine movements evaluation.

Immediately after the surgery, AM showed dysarthria and a mild strength deficit of the right upper limb, mainly distal, but both resolved within 6 days. AM was assessed again 4 months after the surgery. No further neurological or neuropsychological deficits were identified at the time of the second assessment (see results section).

A group of 10 age-matched control participants (6 females and 4 males), with no previous history of neurological, psychiatric or physical disorders, was recruited as controls for this study. Their average age ($M = 36.3$ years, $SD = 11.16$) was not significantly different from AM's [$t(1,9) = .4$, $p = .697$] as tested by Crawford's t-test for single case (Crawford, Garthwaite, & Porter, 2010). On average, they had 15.2 years ($SD = 2.15$) of formal education, which also did not differ when compared with AM's [$t(1,9) = 1.24$, $p = .25$].

Handedness was measured with the Oldfield Questionnaire (Oldfield, 1971). The range of scores varies from -1 to +1. Left-handedness is indicated by values under -0.5, whilst scores over +0.5 indicate right-handedness. Scores in between -0.5 and +0.5 are indicative of ambidexterity. Controls were all right-handed but one. AM was also right-handed (score = .91). The handedness scores between the control group and AM did not significantly differ [$t(1,9) = .51$, $p = .62$].

All participants gave informed consent before testing in accordance with the Declaration of Helsinki.

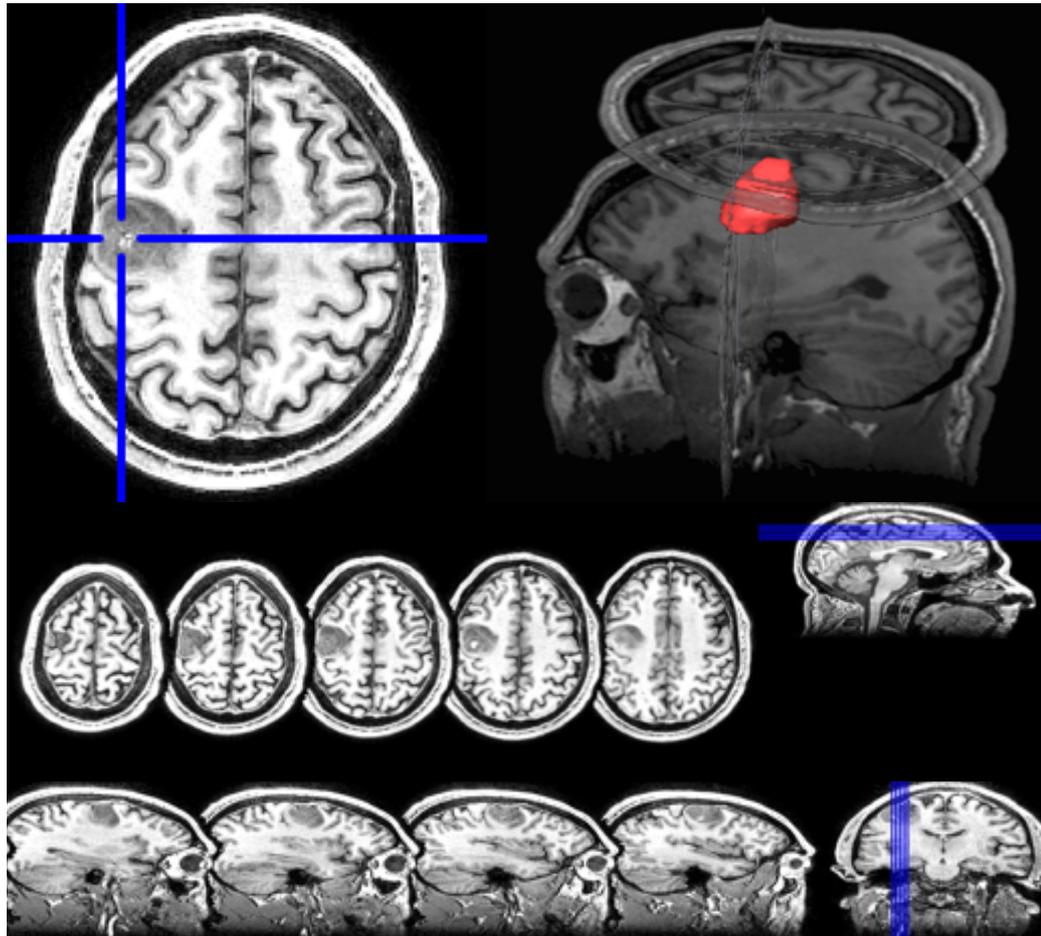


Figure 5.1. AM MRI scans.

Patient AM's T1-weighted (SPGR) magnetic resonance imaging scans in native space, showing lesion location in the left precentral cortex, within the hand motor knob (see arrows on the top left transverse slice). Top right panel shows a 3D reconstruction of the lesion volume. Middle and bottom rows show a series of transverse and sagittal slices across the lesion, respectively.

5.2.2.2 General Neuropsychological Assessment

AM was submitted to neuropsychological assessment before tumour resection and 4 months after to check for any cognitive impairments. Three tests batteries were administered: The Brief Neuropsychological Examination (Esame Neuropsicologico

Breve 2, ENB2), Mini Mental State Examination (MMSE), and Frontal Assessment Battery (FAB).

The ENB2 is a battery of 15 tests administered in between 60 to 90 minutes, to assess general cognitive function (Arcara, Bisiacchi, Mapelli, Mondini, & Vestri, 2011). 10 subtests were considered for this patient: digit span, trail making tests (A and B), memory with interference tests (working memory: 10 seconds and 30 seconds), story recall (immediate and delayed recall), overlapping figures, phonemic fluency test, and the clock test. The ENB2 allows for the combination of performance across all tests to obtain an overall score. A score below 22 indicates a pathological performance. This battery was administered before and after surgery.

The MMSE is a test administered in 10-15 minutes that assesses orientation, attention, memory, language and visuo-spatial skills (Folstein, Folstein, & McHugh, 1975). The Italian version of this test was used, with a cut-off score of 22 (Frisoni, Rozzini, Bianchetti, & Trabucchi, 1993; Magni, Binetti, Bianchetti, Rozzini, & Trabucchi, 1996). This test was administered before surgery.

The FAB is a short battery to assess executive functioning problems (Dubois, Slachevsky, Litvan, & Pillon, 2000). It includes six subtests: conceptualization, mental flexibility, motor programming, sensitivity to interference, inhibitory control and environmental autonomy. As with MME, this test was completed before surgery. An Italian version of the FAB was administered (Appollonio et al., 2005), the maximum score is 18 (better performance) and the cut-off is 12.

5.2.2.3 Motor function assessment

As discussed, the tumour in patient AM was located in an area that is involved in the sensorimotor representation of the hands. Thus, potential effects in motor

function were also explored. For this, two tests were performed: finger dexterity assessment and maximal grip strength. Both measures were taken before and after tumour resection.

5.2.2.3.1 Finger dexterity assessment

Finger dexterity was measured with the Nine-hole peg test (Kellor, Frost, Silberberg, Iversen, & Cummings, 1971; Mathiowetz, Weber, Kashman, & Volland, 1985). This test consists of a plastic board with 9 holes in it (10mm diameter, 15 mm depth) at a distance of 32mm apart, and a shallow round dish on the opposite end. It also includes a set of 9 plastic pegs (7mm diameter, 32 mm length) which are all fitted in the holes. The board is positioned on a table, aligned with the participant's body midline oriented in such a way that the dish is on the participant's dominant hand side. AM was seated positioned in front of the board and was asked to pick 1 peg at a time and put them in the shallow dish as fast as possible, only using one hand, until all pegs were removed. Standard instructions were provided (Mathiowetz et al., 1985) and AM was allowed a short practice. The procedure started with the dominant hand (right hand), followed by the non-dominant hand. AM was allowed to hold the board with the hand not being evaluated in each trial, as per instructions. AM was timed with a stopwatch.

5.2.2.3.2 Maximal grip strength

Maximal Grip strength is normally used as a functional measure of the integrity of upper extremity that quantifies weakness (Bertrand et al., 2015; El-Sais & Mohammad, 2014). AM was tested for both upper extremities with a Jamar digital dynamometer (Sammons Preston Rolyan, Bolingbrook, USA), and results were recorded in kilograms force (kgf). AM's grip strength was measured in a seated position following the American Society of Hand Therapists recommendations: elbow

flexed at 90°, forearm in neutral position, shoulder adducted and neutrally rotated and wrist between 0° and 30° of extension (El-Sais & Mohammad, 2014; Fess & Moran, 1981). The patient repeated the test twice, and the average value was considered as the result. The first rehearsal was conducted with the dominant limb.

5.2.2.4 Proprioception

To measure proprioceptive accuracy a proprioceptive contralateral concurrent matching task was used (Cioffi, Cocchini, Banissy, & Moore, 2017). This measure was taken after tumour resection.

AM was sat in front of a table and was asked to familiarise himself with the size of a sheet of A3 paper. Following this, he was asked to close his eyes and keep them closed for the whole duration of the task. A new A3 sheet was positioned where the previous sheet was (centred on participant's body midline). In this sheet, 4 different points were drawn at each side of the middle of the sheet (4 on the right, and 4 on the left) at equidistant positions. AM's right index finger was positioned on top of the first drawn dot. AM was asked to point to mirror this position with his left index finger, on the left side of the sheet. The procedure was repeated for the 8 dots, 4 per hand. The measure of accuracy was calculated as the average distance (in centimetres) from the actual accurate mirrored position and the pointing response from AM (0 = no discrepancy).

5.2.2.5 Body representation tests

Both control group and AM were assessed for the metric representation of their right hand and face. This was done by using the localisation task (e.g., Longo & Haggard, 2012) in which participants are asked to point to different body parts to discern the metric representation of their body. AM was tested before and after tumour

resection for the hands' representation, whereas face representation was only tested after surgery.

5.2.2.5.1 Hand localisation task

The modified version of the hand localisation presented in Experiment 1 in Chapter 3 was used for this experiment. A horizontal transparent Perspex board (30 x 30 cm) was positioned on top of four metal posts (10 cm high). The board was on a table, in front of the participant. A remote-controlled camera (Nikon 6000) was placed on a tripod (90 cm height), perpendicular to the centre of the board, in such a way that the camera focus was aligned with it. A small canvas (20 x 20 cm) was positioned underneath, on which participants rested the tested hand. Participants were sat in front of the table, and had their eyes closed for the whole duration of the procedure. One of their hands (counterbalanced) was positioned underneath the board, on top of the white canvas, with fingers spread comfortably. The middle finger was aligned with participant's body midline. They kept the hand still in this position for the whole duration of the task. Both hands were tested.

Participants were then asked to use the index finger of their other hand (dot drawn on their indexes fingernail for reference) to point on top of the board to different landmarks on the occluded hand. There was a total of eleven landmarks requested, one at a time (5 fingertips; 4 interspaces; and the two sides of the wrist's bones, ulna and radius). Each landmark was requested three times. Pointing adjustments were allowed (Kammers, de Vignemont, et al., 2009; Króliczak et al., 2006) as in Chapter 3. A picture (5184 x 3456 pixels) of each pointing response was taken, and these were used to measure the accuracy of the metric representation of the hand. A measuring tape was placed on the borders of the board to allow conversion of pixels into centimetres.

5.2.2.5.2 Face localisation task

The face localisation task was identical to the one used in Experiment 2 in Chapter 3. As with the hand, this task consisted in localising different facial landmarks by pointing with the right or left index finger. In this case, the Perspex board (30 x 30 cm) was positioned on top of two metal posts (20 cm) placed in front of the participant. Their head rested on a chin rest, which was on the edge of the table. The Perspex board was positioned very close to the face (around 1 cm from the tip of the nose). The camera (Nikon 6000) was on a tripod on the other side of the board, at around 1 meter from it, with the focus centred in the centre of the board.

Participants were asked to remain still, without moving their face or head. They had their eyes closed for the whole procedure. They were given instructions to point to eleven face landmarks (middle of the hairline; exterior side of the right eye; interior side of the right eye; interior side of the left eye; exterior side of the left eye; right side of the nose; tip of the nose; left side of the nose; right side of the mouth; left side of the mouth; and chin), one at a time, across the board; that is, towards their face (see Chapter 3). Each landmark was requested three times, in random order. Controls performed the task once, pointing with their right index finger. AM performed this task twice; once, pointing with his right index, and the next, with the left index finger. A picture (5184 x 3456 pixels) was taken of each pointing response. A measuring tape was placed on the board to allow conversion of pixel units into centimetres during image analyses.

5.2.2.6 General analyses

5.2.2.6.1 Image processing

The pictures were analysed with a bespoke-made image analysis programme using Borland C++ Builder (2007) that allowed conversion of pixel units into

centimetres. The x and y coordinates for the real and perceived locations were obtained for each landmark (the origin was at the bottom right corner of each picture). With the coordinate data, distances (in centimetres) between pairs of landmarks were calculated. For the hands, these were: length of fingers (distance between each fingertip and adjacent interspace); length of the hand's dorsum (distance between the interspace between the ring and little fingers, and the exterior side of the wrist); width of the hand (distance from the interspace between the index and middle fingers, and the interspace between the ring and little fingers); and width of the wrists (distance between the two sides of the wrists) (see Figure 5.2A for all the distances). For the face, the width of face landmarks (i.e., right eye, left eye, nose and mouth) and face length (distance from the top of the forehead to the tip of the chin) were calculated (see Figure 5.2B).

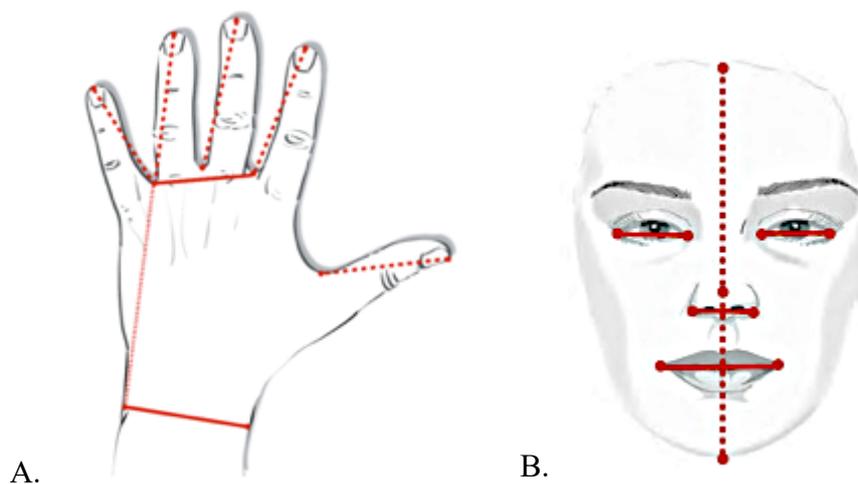


Figure 5.2. Distances considered for hand and face.

Representation of finger lengths (five fingers), hand width, wrist width and dorsum length for the hand (A), and representation of the length of the face and the width of face landmarks (right eye, left eye, nose and mouth) for the face, with schema of the shifts considered (B).

Further, percentages of over/underestimation for length and width perception were obtained by comparing the perceived size against the real size: $[(\text{perceived size} - \text{real size})/\text{real size}] \times 100$. Negative values denoted underestimation; positive values, overestimation, whilst zero denoted perfect performance.

5.2.2.6.2 Statistical analyses

The results were analysed in two steps: firstly, patient's results were considered by running one-sample t-tests to assess if the distortions were significantly different from zero. Paired-samples t-tests were used to assess differences between hands and assessment time (before and after surgery were data from both sessions was available).

Secondly, AM's representations were compared against the representations for the control group. For this, Crawford's t-tests were run for single case analyses with SINGLIMS.ES.exe software (Crawford et al., 2010).

5.2.3 Results

5.2.3.1 General neuropsychological assessment

Scores for AM's performance in all neuropsychological tests and cut-off scores are presented in Table 5.1. In the ENB2, AM's performance before the surgery and on the 4-month follow-up was within normal range for all subtests. In the MMSE, AM obtained the maximum score of 30 before surgery, hence indicating no disrupted performance. Similarly, in the FAB, AM obtained the highest score before surgery after correction for age and education (i.e., 18), hence, not showing executive functioning problems.

Table 5.1. Neuropsychological, motor and proprioceptive assessment tests results.

Results for ENB2, MMSE, FAB, nine-hole peg test, maximal grip strength and proprioceptive pointing for AM.

Subtests		Pre-surgery	Post-surgery	Cut-off
ENB2				
Digit Span		7	7	5
Story recall - immediate		18	16	8
Story recall - delayed		19	19	11
Memory with interference – 10 sec		9	9	6
Memory with interference – 30 sec		8	9	4
Trail making test - A		32	36	55*
Trail making test - B		91	92	142*
Phonemic fluency test		12	10	10
Overlapping figures test		38	N/A	32
Clock test		9	9	8
MMSE		30	NA	22
FAB		18	NA	13.5
Motor assessment				Mean (SD)
Nine-hole peg test (sec)	RH	19.9	20.7	18.54 (2.88)
	LH	19.6	20	18.49 (2.42)
Maximal grip strength (Kgf)	RH	42.9	41.8	35.5 – 55.3
	LH	37.25	37.5	35.5 – 55.3
Proprioceptive assessment			Mean (SD)	Mean (SD)
	RH (cm)	NA	3.25 (2.11)	4.28 (1.33)
	LH (cm)	NA	4.81 (2.47)	3.16 (1.01)
<i>NA = not available</i>		<i>* Cut-off in seconds - normal performance should be below cut-off</i>		
<i>RH = right hand; LH = left hand</i>		<i>off</i>		

5.2.3.1 Motor function results

5.2.3.1.1 Finger dexterity results

AM performed in a similar way for both hands before surgery, needing 19.9 seconds to complete the task with the right hand, and 19.6 seconds with the left. Post-surgery, he needed 20.7 seconds with the right hand, and 20 seconds with the left. Considering normative data from a recent study (Oxford Grice et al., 2003), Crawford t-tests for single case were run for both hands, before and after. Results did not reach significance for any (all ps. > .05), confirming AM performed within norms.

5.2.3.1.2 Maximal grip strength results

AM's results for grip strength before and after surgery are reported in Table 5.1. These scores are within the normal range for participants in his age range.

5.2.3.2 Proprioception

AM was more accurate pointing with his left hand ($M = 3.25\text{cm}$, $SD = 2.11$), which was close to significance but did not reach it [$t(3) = 3.08$, $p = .05$, $d = 1.54$]. Larger proprioceptive drift was found for the right hand ($M = 4.81\text{cm}$, $SD = 2.47$), being significant [$t(3) = 3.9$, $p = .03$, $d = 1.95$]. Thus, proprioceptive judgements with the right hand showed more shift from real location, even though differences between hands were not significant [$t(2) = 1.38$, $p = .26$, $d = .69$]. Results from Cioffi et al. (2017) were considered in order to compare AM's performance against available norms ($M = 4.28\text{cm}$, $SD = 1.33$) via single case Crawford's t-tests. No significant differences were found in performance for any hand (right hand [$t(1,14) = .39$, $p = .71$]; left hand [$t(1,14) = -.75$, $p = .47$]), confirming the performance of AM was within norms.

5.2.3.3 Representation of the hands

The perceived size of the length of fingers, length of the dorsum of the hands, width of the hands and width of the wrists were obtained.

5.2.3.3.1 Finger lengths

Patient's performance

Overall, AM perceived the length of his fingers underestimated. Before surgery, there was a -25.79% ($SD = 15.06$) underestimation for the right hand, which did not reach significance [$t(2) = -2.97$, $p = .097$, $d = -1.71$]; and a -33.25% ($SD = 8.17$) for the left, distortion that was significant [$t(2) = -7.05$, $p = .02$, $d = -4.07$].

Differences between hands were not significant [$t(2) = .595, p = .61, d = .34$], confirming a similar pattern of distortion between hands for finger lengths.

After surgery, the finger length underestimation of the right hand was of -19.23% (SD = 16.68), and the distortion was not significantly different from zero [$t(2) = -1.99, p = .18, d = -1.15$]. The underestimation for the left hand was larger than before (M = -40.74%, SD = 15.88) and close to significance [$t(2) = -4.44, p = .047, d = -2.57$]. Despite the differences in the distortion between hands, these did not reach significance [$t(2) = 1.17, p = .36, d = .68$] (see Figure 5.3).

Further, significant differences were not found before and after surgery for the right hand [$t(2) = -.39, p = .73, d = -.23$] or the left hand [$t(2) = .91, p = .46, d = .53$]. These results indicated that there were no significant differences in the perception of finger length between hands, and no significant changes after tumour resection in their representation.

Group comparisons

Underestimation of finger lengths was also found in controls (see Figure 5.3), with overall distortion of -13.44% (SD = 14.81) for the right hand, and -11.62% (SD = 14.06) for the left hand. AM's length perception was well within the 'normal' range for the right [$t(1,9) = -.79, p = .45$] and left hands [$t(1,9) = -1.29, p = .23$] before surgery. Similarly, no differences were found after surgery for either hand (right hand: [$t(1,9) = -.37, p = .72$]; left hand: [$t(1,9) = -1.75, p = .11$]). These results confirm AM represented the length of his fingers within 'healthy' range.

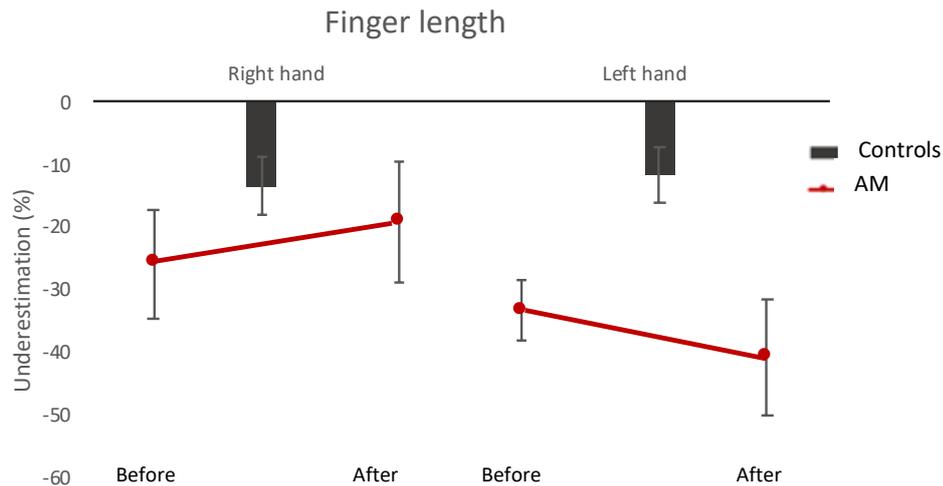


Figure 5.3. Finger length distortion.

Representation of perceived underestimation (%) averaged across all fingers, for both hands. Error bars represent the Standard Error of the Mean.

5.2.3.3.2 Hands' dorsum

Patient's performance

AM's right hand's dorsum was overestimated before surgery ($M = 19.55\%$, $SD = 14.78$), but not significantly so [$t(2) = 2.29$, $p = .15$, $d = 1.32$]. The left hand was also overestimated ($M = 41.59\%$, $SD = 13.18$), distortion that was significant [$t(2) = 5.46$, $p = .03$, $d = 3.15$]. Differences between hands were not significant [$t(2) = -1.46$, $p = .28$, $d = .84$].

After surgery, AM underestimated the length of the right hand's dorsum ($M = -6.12\%$, $SD = 11.39$), but this distortion was not significant [$t(2) = -.93$, $p = .45$, $d = -.54$]. The left hand's dorsum was also underestimated ($M = -.26\%$, $SD = 15.61$), again, not significantly different from zero [$t(2) = -.03$, $p = .98$, $d = -.02$]. Differences between hands were not significant [$t(2) = -.43$, $p = .71$, $d = -.25$].

Further, there were significant differences for the right hand between sessions (i.e., before and after surgery) [$t(2) = 4.83$, $p = .04$, $d = 2.79$], as there was a reduction

of the distortion after tumour resection. There were no significant differences for the left hand [$t(2) = 2.67, p = .12, d = 1.54$]. In summary, the distortion of the dorsum was reduced after surgery for both hands, but more so for the right, suggesting some modulation due to tumour resection (see Figure 5.4).

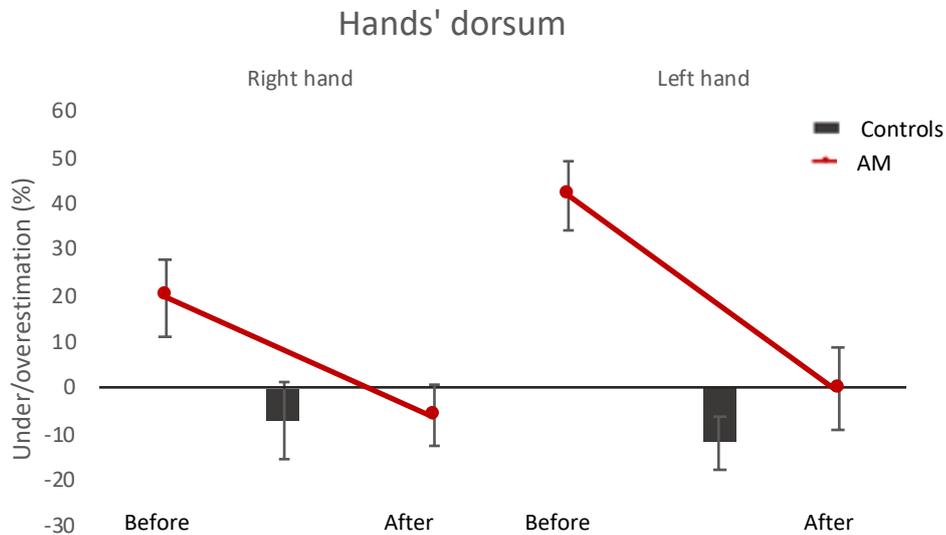


Figure 5.4. Distortion of hands' dorsum.

Representation of the percentage of under/overestimation (%) for the averaged perceived size of the dorsum's length for both hands. Error bars represent the Standard Error of the Mean.

Group comparisons

Controls underestimated the length of their hands' dorsum (right hand: $M = -7.14\%$, $SD = 26.1$; left hand: $M = -11.98\%$, $SD = 17.7$). When compared with AM, there were no significant differences for the right hand's dorsum before [$t(1,9) = .98, p = .36$], or after surgery [$t(1,9) = .037, p = .97$]. In contrast, AM perceived the length of his left hand's dorsum significantly more overestimated prior surgery than controls [$t(1,9) = 2.89, p = .02$]. The significance is lost after surgery [$t(1,9) = .63, p = .54$] (see Figure 5.4).

5.2.3.3.3 Hand width

Patient's performance

Overall overestimation of hand width was present in all conditions (see Figure 5.5). In detail, the right hand was overestimated before surgery by a 71.38% (SD = 9.89), distortion that was significant [$t(2) = 12.49, p = .006, d = 7.21$]. Similarly, there was overall overestimation of the left hand (M = 146%, SD = 49.13), which was also significant [$t(2) = 5.15, p = .04, d = 2.97$]. The distortion between hands was not significantly different [$t(2) = -2.19, p = .16, d = -1.27$].

After tumour resection, there was significant width overestimation of 28.59% (SD = .36) for the right hand [$t(2) = 194.2, p < .001, d = 112.12$]. The width of the left hand was also overestimated, but in larger magnitude (M = 93.23%, SD = 8.47), distortion that was significantly different from zero [$t(2) = 19.06, p = .003, d = 11.01$]. In this case, a significant difference in width perception between hands was found [$t(2) = -13.46, p = .005, d = -7.72$], confirming the left hand was more distorted.

Between surgeries, significant results were found for the right hand [$t(2) = 7.49, p = .02, d = 4.33$], confirming there was a significant reduction of the perceived width of this hand after surgery and providing evidence of an improvement on its representation. In contrast, there were no significant differences for the left hand between surgeries [$t(2) = 52.81, p = .17, d = 1.21$].

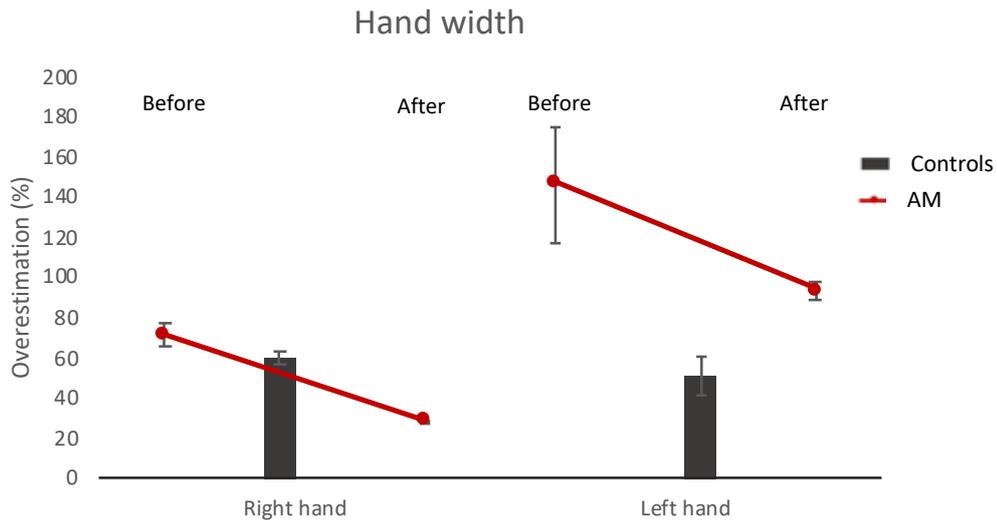


Figure 5.5. Hand width distortion.

Representation of the percentage of overestimation (%) for the averaged perceived size of the width of the hand, for both hands. Error bars represent the Standard Error of the Mean.

Group comparisons

No significant differences were found when comparing the width of the right hand prior to surgery between groups [$t(1,9) = 1.11, p = .29$], indicating AM perceived the width of his hand in line with controls ($M = 59.61\%$, $SD = 10.12$). For the left hand, controls showed a 51.4% ($SD = 30.64$) distortion. Crawford's t-test showed differences were significant when comparing AM to controls' performance [$t(1,9) = 2.95, p = .016$], confirming the left hand was far more distorted for AM than controls.

After surgery, the left hand was more distorted than the right hand for AM. When compared with controls, significant differences were found for the right hand after surgery [$t(1,9) = -2.92, p = .017$]. Interestingly, AM showed better representation of the width of the right hand than controls. For the left hand, there were not significant differences when compared with controls [$t(1,9) = 1.3, p = .23$].

5.2.3.3.4 Width of the wrists

Patient's performance

Lastly, the percentage of over/underestimation for the width of the wrists was considered. AM's right wrist was overestimated before surgery by a 101.22% (SD = 20.47), distortion that was significant [$t(2) = 8.57, p = .01, d = 4.95$]. The left wrist was also overestimated in size (M = 84.19%, SD = 13.07) and also significantly so [$t(2) = 11.15, p = .008, d = 6.44$]. Differences between hands did not reach significance [$t(2) = 3.99, p = .06, d = 2.3$].

In contrast, the distortion for the right wrist after surgery appeared much reduced (M = 25.03%, SD = 35.81), not being significant [$t(2) = 1.21, p = .35, d = .7$]. The left wrist, instead, showed larger overestimation (M = 103.32%, SD = 6.21), and the distortion remained significantly different from zero [$t(2) = 28.84, p = .001, d = 16.65$]. In this case, there were significant differences between hands for the perception of the wrists after surgery [$t(2) = -4.58, p = .045, d = -2.64$], confirming the left wrist was more disrupted than the right.

Lastly, differences before and after surgery were compared, and a trend was found for the right wrist [$t(2) = 3.39, p = .077, d = 1.96$]; whilst no differences were found for the left [$t(2) = -2.34, p = .14, d = -1.35$]. Again, there was some modulation on the perceived size of the right wrist after tumour resection, whilst the left wrist was the most distorted at both times (see Figure 5.6).

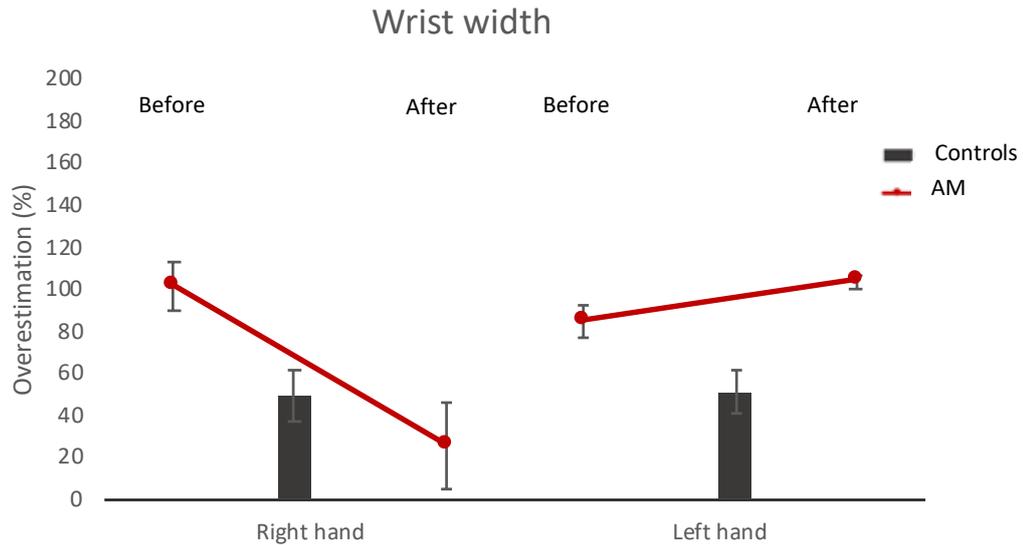


Figure 5.6. Wrist width distortion.

Representation of the percentage of overestimation (%) for the averaged perceived size of the width of both hands. Error bars represent the Standard Error of the Mean.

Group comparisons

AM's perception followed the pattern from controls for the wrists, that also overestimated their width, with an average of 48.86% (SD = 38.91) for the right, and a 50.81% for the left (SD= 32.54). Differences with AM for the right wrist were not significant prior surgery [$t(1,9) = 1.28, p = .23$] or after [$t(1,9) = -.58, p = .57$], confirming similar width perception of the right wrist. Similarly, differences for the left wrist prior surgery did not reach significance [$t(1,9) = .98, p = .35$], nor after [$t(1,9) = 1.54, p = .16$].

5.2.3.3.5 Summary hand results

These results confirm different size distortions depending on the hand considered, but also variability between surgeries. A summary table of the results of all analyses in this section can be found in Table 5.2, whereas hand maps for all conditions are presented in Figure 5.7. The right hand displayed more variation before

and after tumour resection, being perceived more accurately in width, dorsum length and wrist width afterwards. In contrast, when comparing performance between hands, the left hand was represented ‘worst’. This hand was more overestimated in width, dorsum length and wrist width, and the size representation did not appear to be modulated between sessions. These results can be interpreted in two ways: on one hand, the findings may support the idea of altered representation of the ipsilesional hand due to the location of the tumour holding a more bilateral representation; on the other, it could be that motor control of the right affects the performance in the pointing task, and in turn, the representation of the left. However, the initial proprioceptive task did not show an impairment in pointing or motor control of the right hand, even though the proprioceptive shift was larger than when pointing with the left.

Table 5.2. Performance of AM and controls in the hand localisation task.

Percentage of over/underestimation (with standard deviation) for all areas and significance values for all comparisons. A significant p value ($p < .05$) is marked with *.

Areas	Hand	AM		Significance test one sample (p values)		Significance test paired-samples t-tests (p values)		Control group	Significance test Crawford's t-test (p values)		
		Before Mean (SD)	After Mean (SD)	Distortion		Between hands			Before/after	Mean (SD)	Before
				Before	After	Before	After				
Length of fingers (%)	Right	-25.79 (15.06)	-19.23 (16.68)	.09	.18	.61	.36	.73	-13.44 (14.81)	.45	.72
	Left	-33.24 (8.17)	-40.74 (15.88)	.02*	.047			.46	-11.62 (14.06)	.23	.11
Dorsum length (%)	Right	19.55 (14.78)	-6.12 (11.39)	.15	.45	.28	.71	.04*	-7.14 (26.1)	.36	.97
	Left	41.59 (13.18)	-2.26 (15.61)	.03*	.98			.12	-11.98 (17.7)	.02*	.54
Hand width (%)	Right	71.38 (9.89)	28.59 (.26)	.006*	.000*	.16	.005*	.02*	59.61 (10.12)	.29	.02*
	Left	146.05 (49.13)	93.23 (8.47)	.04*	.003*			.17	51.4 (30.64)	.02*	.23
Wrist width (%)	Right	101.22 (20.47)	25.03 (35.81)	.01*	.35	.06	.04*	.08	48.86 (38.91)	.23	.57
	Left	84.19 (13.07)	103.32 (6.21)	.008*	.001*			.14	50.81 (32.54)	.35	.16

With this in mind, the study of the representation of the face was carried out after tumour resection to investigate the specificity of the altered representation. As this tumour was circumscribed to the hand representation area, no distortions were expected for the face. Hence, AM was tested in his performance on the face localisation task by using his right and left hands. If there was an impairment in motor control of the right, affecting pointing, more distortion would be expected in the face representation to appear in this condition. If, instead, the differences are due to representational components, distortion of the face representation should not be found with any pointing hand.

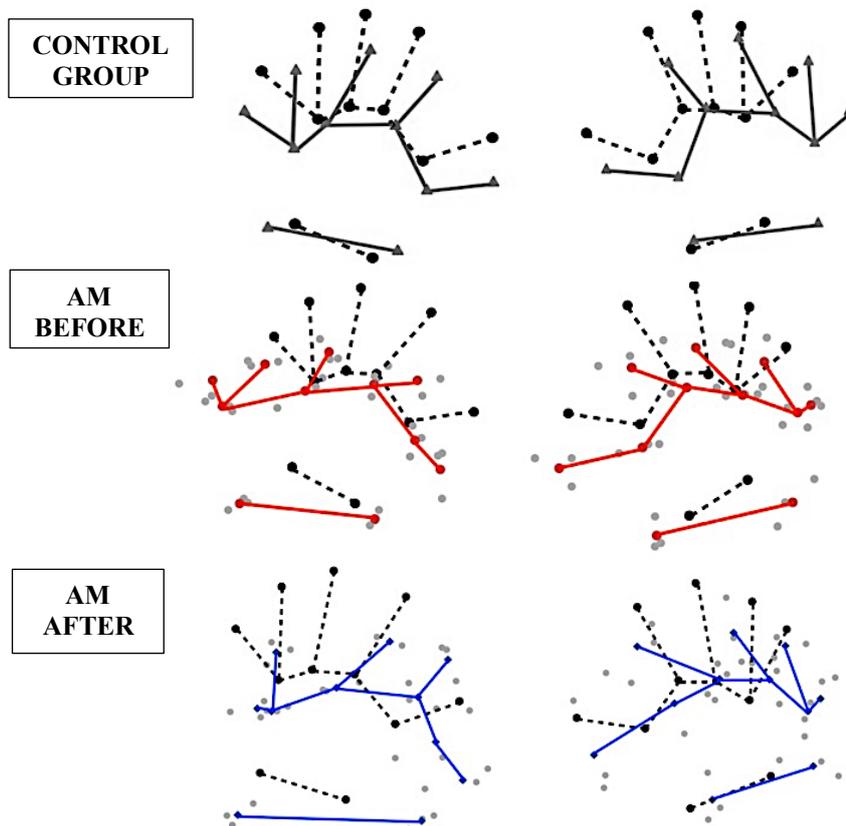


Figure 5.7. Cartographic maps for the real and perceived representation of the hands.

Black dotted lines represent the real size of the hands. Results for control group are presented at the top, with grey continuous lines for their perceived representation. Red continuous lines denote AM perception before surgery, and blue after surgery. The grey dots (in AM before and AM after) represent all pointing responses for AM from which averaged representation is calculated.

5.2.3.4 Representation of the face

The representation of the face was assessed after tumour resection. As differences in the distortion of hands had been found previously, the study of the distortions of the face could elucidate if these are associated just to disrupted hand representation or to a more general pointing bias that would also affect the pointing task for the face.

5.2.3.4.1 Patient's performance

Face length

The face was, overall, underestimated in length when AM pointed with the right hand ($M = -6.78\%$, $SD = 8.45$), but this distortion did not reach significance [$t(2) = -1.39$, $p = .299$, $d = -.8$]. The distortion was on the same direction with left-hand pointing ($M = -11.05\%$, $SD = 13.61$) and not significant [$t(2) = -1.41$, $p = .295$, $d = -.81$]. Differences between representations did not significantly differ [$t(2) = .53$, $p = .65$, $d = .31$] (see Figure 5.8).

Width of facial features

AM perceived, overall, the width of the face landmarks overestimated by a 67.41% ($SD = 24.85$) when pointing with the right hand, whilst the overestimation was 42.06% ($SD = 18.11$) with left hand pointing. The distortion with right-hand pointing was significantly different from zero [$t(2) = 4.69$, $p = .04$, $d = 2.71$], whilst it did not reach it with left-hand pointing [$t(2) = 4.02$, $p = .06$, $d = 2.32$]. Differences between representations were not different in any case [$t(2) = 1.26$, $p = .33$, $d = .73$] (see Figure 5.8).

5.2.3.4.2 Group comparisons

Comparisons for the perceived length of the face against controls were run. Controls overestimated its length by a 5.39% (SD = 16.52) on average. Differences were not found when compared with AM's performance for the right-hand pointing condition [$t(1,9) = -.7, p = .5$], nor the left [$t(1,9) = -.95, p = .37$].

The averaged width of face landmarks for AM was compared against the results for the control group. On average, controls perceived all overestimated in width by an 83.94% (SD = 26.71). Crawford's t-tests were run to compare AM's performance against controls results. Differences were not significant when pointing with the right hand [$t(1,9) = -.59, p = .57$], or the left [$t(1,9) = -1.49, p = .17$] (see Figure 5.8). These results confirmed that the size perception of the face was within healthy population's range.

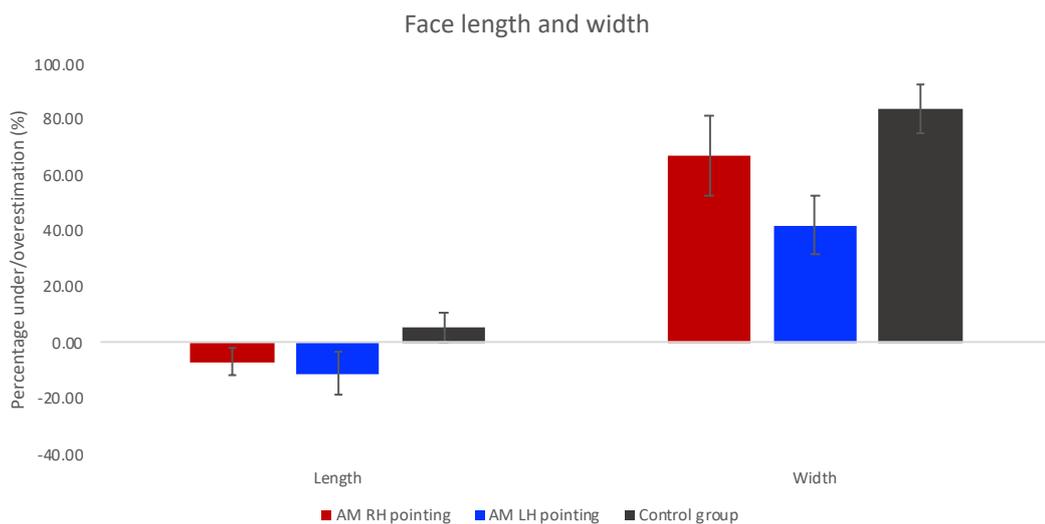


Figure 5.8. Percentage of distortion of the size of the face.

Averaged under/overestimation of the length and width of the face for AM pointing with right hand, left hand and for controls. Error bars represent the Standard Error of the Mean.

5.2.3.4.3 Summary face results

A summary of all analyses is included in Table 5.3. Overall, AM did not show any differences in the representation of the face in any condition when compared to controls. This indicated that aforementioned differences in the perception of the hand are specific to the body part and cannot be explained due to misallocation of pointing responses due to right (contralesional) hand motor performance.

Table 5.3. Performance of AM and controls in the face localisation task.

Percentage of over/underestimation for the face length and width for AM and controls (with standard deviation), and significance values for all comparisons. A significant p value ($p < .05$) is marked with *.

Face		AM	Significance test one sample (p values)	Significance test paired-samples t-tests (p values)	Control group	Significance test Crawford t-test (p values)
		Mean (SD)	Distortion	Between hands	Mean (SD)	
Length (%)	Right	-6.78 (8.45)	.299	.65	5.39 (16.52)	.5
	Left	-11.05 (13.61)	.295		-	.37
Width (%)	Right	67.41 (24.85)	.04*	.33	83.94 (26.71)	.57
	Left	42.06 (18.11)	.06		-	.17

The coordinate data were used to produce maps of the representation of the face for AM after surgery, pointing with the right hand, left hand; and averaged representation for controls (see Figure 5.9).

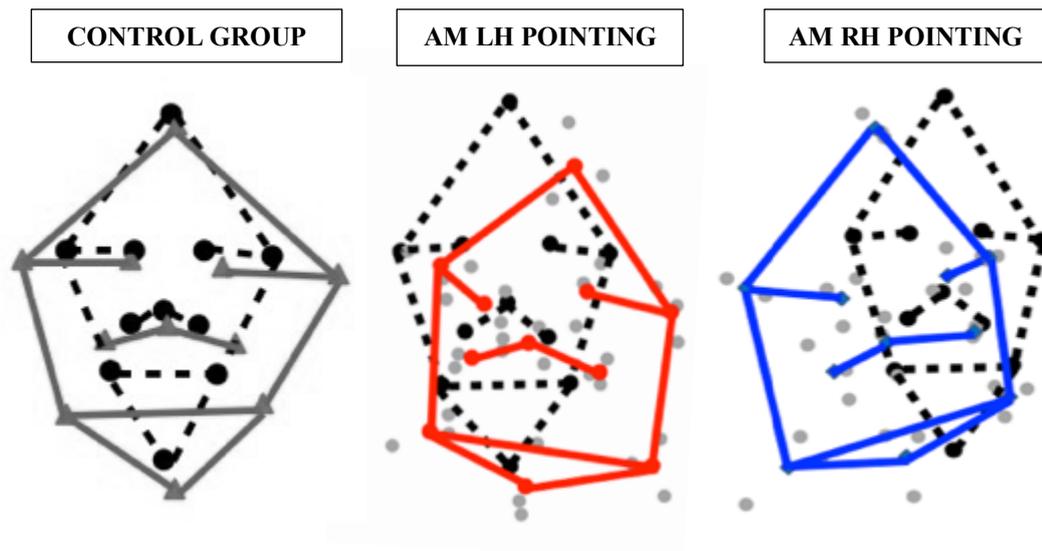


Figure 5.9. Face maps.

Representation of the real face (dotted lines) and perceived face representation for controls (grey continuous line); AM with left hand (LH) pointing (red continuous lines), and AM with right hand (RH) pointing (blue continuous lines).

5.2.4 Discussion

In this study, the representation of hands and face were explored in a patient with a left precentral glioblastoma. The association between sensorimotor areas and the metric representation of the hands are linked. In particular, overestimation of the width of hands and underestimation of the length fingers has been associated to the size of the receptive fields and the cortical representation for these areas (Longo & Haggard, 2010, 2012a). Further, improvements in motor function and representational components are associated with an increase of the size of the hand knob, as seen in sign language experts (Allen et al., 2013; Penhune et al., 2003). Hence, disruption of these areas should be linked with distortions in the underlying body model. AM's performance followed the pattern found in the healthy population; that is, underestimation of length and overestimation of width (as in Chapter 3) (Longo & Haggard, 2012a), with no other relevant impairments in motor control. In fact, no actual differences in perceived size were found for the right hand and face against

controls. Instead, the hand that showed most impairment was the left. Interestingly, this significance was lost after surgery, due to an amelioration of the distortion. Similarly, the distortions found for the right hand before surgery were significantly reduced afterwards.

One potential explanation for the lack of significant disruption in the contralesional hand may be due to brain plasticity that diminishes the potential damage caused by slow-developing tumours, which may not become symptomatic, in contrast with acute lesions in same areas (Wunderlich et al., 1998). In fact, the cortical areas around the mass of the tumours are electrically excitable, but not the mass of the tumour itself; hence, remaining functions cannot be mediated by the neurons within it, but by the tissue around it (Wunderlich et al., 1998). In other words, in order to preserve an accurate representation of the hand, with normal motor performance, topographical reorganization of sensorimotor areas must have happened (Ebeling et al., 1992), as also seen in neural damage after stroke (Medina & Rapp, 2014).

In contrast, AM's left-hand representation was more distorted than in healthy population, in particular for the length of the dorsum and width of the hand before surgery. This was unexpected, as more distortion was predicted for the contralesional right hand due to the location of the tumour. However, there may be influences from bilateral representation of the hands in the damaged area or interhemispheric connections (Borchers, Hauser, & Himmelbach, 2011). This type of effect has already been reported in previous studies. Indeed, ipsilesional impairment has been shown after stroke for sensory (Brasil-Neto & de Lima, 2008), proprioceptive (Buxbaum & Coslett, 2001), and motor deficits (Schaefer, Haaland, & Sainburg, 2007). Moreover, left-hemisphere lesions affect the whole body more than right-sided lesions, as the left hemisphere may contain the structural description of the body (Buxbaum & Coslett,

2001). Supporting this, there was an overall reduction of the distortion of width for both hands after surgery. Further, handedness cannot fully explain this distortion, as otherwise more distortion on the right hand would have been found, as when judging the length of arms (Linkenauger et al., 2009) or the width of the body (Hach & Schütz-Bosbach, 2010).

Modulation following surgery on size perception due to tumour resection was found for both hands (52.83% reduction of the width distortion for the left hand, 42.79% for the right), with overall amelioration. Indeed, differences in hand width perception for the left hand against controls were not significant after surgery, whereas these were before. The right hand was instead perceived within norms to start with, being also the dominant hand. Thus, differences against controls were not seen prior to surgery. However, the amelioration after surgery was significant. In other words, the overall dominant hand representation also improved after tumour resection. Improvement of sensorimotor functions after tumour resection has already been reported in a previous study. In particular, patients with meningiomas in the parietal-occipital areas that showed impairments in body related tasks, such as left-right orientation, recovered in their functions once the tumour was removed (Nikishina et al., 2016). Indeed, the consequences of brain tumours may not always be explicit due to topological displacement of cerebral functions to adjacent undamaged cortical areas (Ebeling et al., 1992; Wunderlich et al., 1998). Seitz et al. (1995) reported the case of six patients with slow-developing tumours located in the precentral cortex, and in particular, located in the hand/arm area, that showed preserved motor functions due to remapping of the sensorimotor cortex to healthy adjacent cortical areas.

An alternative explanation to these findings that could be merely assumed focuses on motor control. In other words, following these results and tumour location,

poor motor control of the right hand could have affected the localisation of the left. Motor control or proprioceptive difficulties were not identified for either hand in preliminary tests, but these were only administered after surgery. Hence, potentially motor control difficulties could have been present in the first time AM was tested with the localisation task. However, previous studies have not found significant differences in the perceived body model when location of landmarks is done through verbal command (Longo, 2018), meaning that the motor control of the pointing hand is not biasing this model (Haggard, Newman, Blundell, & Andrew, 2000; Peviani & Bottini, 2018). Moreover, motor control of the right hand did not affect the representation of the face. Still, there were different shifts directions when pointing with each different hand, as see in the face maps (Figure 5.9). To further understand the effects of the location of this tumour and remove potential motor control effects, localisation through verbal command could be considered for further studies.

To sum up, the results reported in this study support the involvement, at some level, of sensorimotor areas in the representation of the body size. Indeed, the distortions of body size found in healthy participants preserve the characteristics of the homuncular representation. In detail, areas that occupy a larger area in the cortex are, in turn, perceived as larger (Miller, Longo, & Saygin, 2016). It is then logical to assume that disruption or increase of the activity in these cortical areas may, in turn, affect the perceived size of the body. Indeed, this appears to be the case. For instance, increasing the size of a body part does enhance the activation of the somatosensory cortex (D'Amour & Harris, 2017), in the same way that direct cortical activation of these areas through repetitive Transcranial Magnetic Current stimulation (rTMS) increase the perceived size of the hand (Giurgola et al., 2019). Here, specific modulation of hand size representation was found, supporting this interrelationship.

However, these effects may not only be seen when investigating somatosensory areas, as others have also found modulation of size perception when other cortical areas are involved. As discussed above, right parietal areas are involved in the metric representation of the body (Nico et al., 2010; Spitoni et al., 2013). These are thought to hold the body image (Longo et al., 2010), and are instrumental for configural processing of the body (Urgesi et al., 2007). For example, a recent study found disrupted body size image representation in patients with meningiomas in the parieto-occipital areas (Nikishina et al., 2016). Moreover, in healthy adults, brain stimulation of the right angular gyrus modulates the perceived size of the contralateral arm (Spitoni et al., 2013). Further, parietal areas are critical to integrate inputs from vision and somatosensation in a coherent body representation (Avillac, Denève, Olivier, Pouget, & Duhamel, 2005; Lewis & Van Essen, 2000). In fact, lesions of the posterior parietal cortex (PPC) cause changes in body image, such as after resection in parietal lobe epilepsy (Salanova, Andermann, Rasmussen, Olivier, & Quesney, 1995). Further, phenomena such as telescoping or phantom limbs after amputation are associated with activation changes in the PPC (Flor et al., 2000), which can be suppressed by lesions in these areas (Berlucchi & Aglioti, 1997). Hence, it is of relevance to study the involvement of parieto-occipital areas in the metric representation of the body, which was the focus of the next study.

In light of this, the aim of Experiment 2 was to investigate the metric representation of the body in patients that experienced lesions in parietal areas, resulting in Personal Neglect (PN). This hemi-inattention disorder is characterised for lack of awareness, exploration, use, orientation or response to the contralesional side of the body, not explained by other motor or sensory problems (Baas et al., 2011; Bisiach & Vallar, 2000; Heilman et al., 2000).

5.3 Experiment 2: effects of Personal Neglect on the size representation of the hands and face

5.3.1 Introduction

A wide-array of body representational disorders are found in patients after brain injury, sometimes associated with motor impairment (Berlucchi & Aglioti, 1997; Llorens et al., 2017; Razmus, 2017; Rousseaux, Honoré, & Saj, 2014), severely disrupting daily living activities and independence (Committeri et al., 2018). One of these is PN, a particularly pervasive disorder that affects their ability to interact with their own bodies, associated with longer recovery and poorer outcomes (Buxbaum et al., 2004; Chen-Sea, 2000; Iosa, Guariglia, Matano, Paolucci, & Pizzamiglio, 2016). Efforts have been made to understand its complex nature. The current predominant view is that a defective contralesional body representation underlies this disorder (Coslett, 1998; Guariglia & Antonucci, 1992), intertwined with hemi-spatial inattention (Committeri et al., 2018). Lesions to parietal areas underly this disorder (Bisiach, Perani, Vallar, & Berti, 1986; Committeri et al., 2007; Heilman et al., 2000). Hence, it is not unexpected that lesions causing PN also lead to body related difficulties, including size misrepresentation (Committeri et al., 2018).

PN is a distinct syndrome from the Unilateral Neglect spectrum, which includes an array of disorders (i.e., Extrapersonal Neglect (EN) (Bisiach et al., 1986; Guariglia & Antonucci, 1992); Motor Neglect (Kerkhoff, 2001); Perceptual Neglect (Heilman et al., 2000); Representational Neglect (Bisiach & Luzzatti, 1978; Guariglia, Padovani, Pantano, & Pizzamiglio, 1993)). The differentiation between these is based on the spatial domains each disorder disrupts, as space processing is multifaceted with different underlying neural correlates (Bisiach et al., 1986; Kerkhoff, 2001; Vallar, 1998). In particular, PN is an egocentric disorder in which the personal body space is

affected (Caggiano & Jehkonen, 2018; Committeri et al., 2018; Kerkhoff, 2001). This is caused by injury to inferior parietal areas (Bisiach et al., 1986; Heilman et al., 2000); temporo-parietal junction (Baas et al., 2011); the postcentral and supramarginal gyri in the parietal lobe (Committeri et al., 2007), and white matter connections to fronto-parietal areas, causing a “within-parietal disconnection” (Committeri et al., 2018, p. 274, 2007). Interestingly, PN is normally associated with right hemisphere damage, but can also appear after left hemisphere lesions (Caggiano, Beschin, & Cocchini, 2014; Heilman et al., 2000); however, more severity and least recovery is associated with right brain damage (Kerkhoff, 2001; S. P. Stone et al., 1991). Given that personal body space is disrupted in PN, the main diagnostic tools of PN are centred on assessing interactions with one’s own body. These are the Comb and Razor test (Beschin & Robertson, 1997), the Fluff test (Cocchini et al., 2001) and the One Item test (Bisiach et al., 1986).

A variety of body impairments have been identified in PN; from a distorted body perception, to altered visuospatial body map, body schema, motor control or sense of ownership (see Caggiano & Jehkonen, 2018; Committeri et al., 2018 for recent reviews in this matter). Consequently, several studies have tried to disentangle the different components of the multidimensional body representation that are affected in PN. For instance, in one of the first studies exploring the characteristics of the body representation in PN, authors found that an impaired mental body representation caused constructional problems of the body and face, at the same time as impaired localisation of body parts on the left side of the patient’s body (Guariglia & Antonucci, 1992). Coslett (1998) described a selective impairment of body schema in the hand laterality task. Further, Baas et al. (2011) identified specific difficulties in recognizing left sided hands and rear-view mirrors, but only body related errors predicted PN,

pinpointing body representation as the critical mechanism (Johnson, Sprehn, & Saykin, 2002). Likewise, the Frontal Body Evocation subtest identifies impaired visuo-spatial mental representation in PN, as patients are unable to construct a coherent body (Di Vita et al., 2019; Palermo, Di Vita, Piccardi, Traballes, & Guariglia, 2014). However, the understanding of how these patients represent their own bodies is still limited, and more knowledge is required to provide specific rehabilitation programmes targeting body representation rather than EN (Committeri et al., 2018). Indeed, despite previous studies showing the involvement of parietal areas in the metric representation of the body (Nico et al., 2010; Spitoni et al., 2013) and these areas being highly associated with PN (Committeri et al., 2018, 2007), no studies have tried to elucidate any potential distortions in size representation in this disorder. Hence, the main aim is to study the metric representation of the body in patients with PN, and in particular, the size estimation of specific body parts relevant for its diagnosis (i.e., hands and face). Unlike previous study with tumour patient, the focus here is to explore the body distortion in a group of patients that experience an attentional disorder, rather than a pure sensorimotor impairment.

In this experiment, the size representation of the hands and face was explored in patients with PN by the body size estimation task, using distorted pictures. PN patients and patients after stroke may present with contralateral motor impairment; hence, this task was considered more appropriate than pointing tasks. Depictive methods have been used in numerous studies to assess the body image, the explicit component of body representation (Azañón, Tamè, Maravita, Linkenauger, Ferrè, Tajadura-Jiménez, Linkenauger, et al., 2016; Mölbert et al., 2017). In general, pictures of the body are distorted (mainly in the horizontal dimension) and participants are required to choose the one that most closely match their perceived body size.

Interestingly, there is a dissociation between more implicit tasks (such as location task) and explicit task (such as depictive ones) in healthy adults. In detail, size distortions on the metric representation of hands are found when using the location task; whereas these did not show when using the template matching task (Longo & Haggard, 2012b). Instead, visual estimations of body size do show distortions in clinical populations. For example, patients with anorexia and bulimia nervosa overestimate the size of their bodies when making explicit judgements through distorted pictures (Mohr et al., 2010; Mölbert et al., 2017). Further, the visuospatial transformation between one own's body and the presented image requires activation of the parietal cortex (Peltz, Seifert, Lanz, Müller, & Maihöfner, 2011), and the task requires retrieving the internal mental representation of one's own body (Mohr et al., 2010; Spitoni et al., 2013). This process may then be impaired in patients with PN. Thus, it was hypothesized that patients with PN will show a more distorted representation of the body in comparison with a control group of healthy subjects and patients without PN (PN-).

5.3.2 Method

5.3.2.1 Participants

A group of 9 right brain-damaged patients (7 males and 2 females) was recruited from 'Centro Referencia Estatal de Atención al Daño Cerebral' (CEADAC), in Madrid, Spain. All patients suffered right hemisphere strokes (2 ischemic, 5 haemorrhagic and 2 ischemic with haemorrhagic infarction). They were all Spanish speakers and testing took place in Spain. The mean time from injury onset was 256.33 days (SD = 91.5) and all had been in intensive rehabilitation for an average of 111.89 days (SD = 59.05). The exclusion criteria for this group were: history of neurological or psychiatric disease, substance abuse, previous cerebrovascular accident (CVA),

neoplastic aetiology and inability to provide informed consent or perform the experimental tasks. They were all right handed except one, who was left handed (P04), as measured by the Oldfield Questionnaire (Oldfield, 1971). Demographic data is presented in Table 5.4.

A group of 16 right-handed healthy participants was recruited as the control group (mean age = 38.81 years, SD = 11.71; mean education = 10.31 years, SD = 2.12). This group was matched with the patients' group in Age [$t(23) = -1.66, p = .11$], Gender [$t(23) = 2.01, p = .06$] and Education [$t(23) = .56, p = .58$]. The individuals in the control group did not have any neurological or psychiatric impairments.

Table 5.4. Demographic data.

Demographic information for all 9 patients.

	Gender (0= male)	Age (years)	Education (years)	Aetiology	Lesion site	Time from injury (days)	Time at CEADAC (days)
P01	0	44	8	I, H	T, P, O	326	29
P06	0	54	14	H	Bg, t, Ins	239	120
P07	1	39	8	H	//	423	217
P08	0	52	10	H	Bg, t, Ins	283	149
P09	0	40	8	H	Bg, t,	150	73
P02	0	38	14	I	Bg, t, Ins, P, T	144	65
P03	0	53	8	H	O, c	276	168
P04	1	39	10	I, H	O, Bg,	296	115
P05	0	53	8	I	ic, Bg	170	71

Note: I/H: ischemic/haemorrhagic lesion.

Lesion site: F = frontal; P = parietal; T = temporal; O = occipital; Ins = insula; ic = internal capsule; Bg = basal ganglia; t = thalamus; c = cerebellum; ic = internal capsule; // = neuroradiological examination not available.

The study was approved by Goldsmiths Research Committee in line with the principles of the Helsinki Declaration. All participants provided informed consent.

5.3.2.2 Personal and Extrapersonal Neglect examination

The presence of PN was assessed by three different tests to account for its multidimensionality (Committeri et al., 2018; Guariglia & Antonucci, 1992). These were the Comb and Razor test (Beschin & Robertson, 1997), the Fluff test (Cocchini et al., 2001) and the One Item test (Bisiach et al., 1986).

The Comb and Razor test is a semi-structured test in which patients are required to perform actions on their own body by using common objects (Beschin & Robertson, 1997). Patients were provided a comb and a razor/compact powder case (male/females) and were asked to use each object for 30 seconds. The experimenter counted the number of strokes the patient performed on each side of the head/face, and also in the middle. The bias index proposed by McIntosh, Brodie, Beschin, & Robertson (2000) was used to identify patients that will show PN (cut-off score of +11 for left PN, and -11 for right PN).

The Fluff test (Cocchini et al., 2001) was also used to assess PN. The test consists of 24 identical circles (2 cm in diameter), which were made out of Velcro. The circles were attached on the patients' clothes, at specific locations (6 stickers on left arm, 6 on the trunk, 6 on the right leg and 6 on the left leg). Patients were blindfolded to prevent them from looking involuntary and were sat down for the whole duration of the task. Experimenter positioned all the stickers carefully to avoid tactile feedback whilst keeping patients distracted in conversation. Patients were required to remove all stickers from their body by using the right hand. The task finished when patients declared they had located all stickers. The cut-off score for this test is 86.7% contralesional targets detached (i.e., more than 2 targets missed on the contralesional side of the body).

PN was further assessed by using the One Item test (Bisiach et al., 1986). In this test, patients are requested to touch their left hand using their right. Specifically, both hands are lying on the table, and the experimenter points to the right hand, and instructs: ‘with this hand, touch your other hand’. There are four different scores for this task: 0 indicates no difficulties; 1 indicates slight difficulties (hesitation and search); 2 is awarded for interrupted search (before target is reached); and 3 indicates lack of movement towards the target hand.

EN was assessed by means of the Behavioural Inattention Test (BIT), a widely-used test to assess visual neglect (Wilson, Cockburn, & Haligan, 1987). The conventional subtests were administered, which are: line crossing, letter cancellation, star cancellation, figure and shape copying, line bisection, and representational drawing. Patients who scored below the total aggregated cut-off score of 129 out of 146 were classed as having EN.

5.3.2.3 General neuropsychological assessment

Patients were also subjected to an extensive assessment of cognitive functions for abstract and verbal reasoning, short term memory, executive functioning, activities of daily living, and awareness. These measures were considered to identify potential differences between both patients’ groups.

The Digit span test was administered to measure short-term memory. In this test, a list of numbers is read aloud, and participants are required to recall it, either in direct order (forwards) or reverse (backwards). The testing stops once the participant cannot recall a full list or reaches the maximum list length (starting from 2 digits up to 9 in forward condition, and up to 8 in backwards condition). Two trials for each span were administered, even if there were no errors in the first trial; hence, there were a total of 16 trials for direct presentation, and 14 in reverse. The highest number of

digits recalled (span) for each presentation order was recorded. The average span for Spanish population is 6 ± 1 digits in direct order, whereas this was 5 ± 2 in reverse order (Tamayo et al., 2012). A span of 4 or less was considered pathological.

Verbal learning and memory was assessed by the Hopkins Verbal Learning Test revised (HVLT-R) (Benedict, Schretlen, Groninger, & Brandt, 1998). It includes three learning trials, in which patients are read 12 words from a list and are asked to remember as many words as possible, in any order. The sequence of words remembered is recorded. Patients are told they may be asked the list at a later stage. After 20 minutes, they are asked to recall the list again. Lastly, a list of 24 words is presented, that includes the 12 target words from the previous list plus 12 nontarget words (6 are semantically related to targets). Patients have to report which words were present in the previous list, and false and true answers are recorded. The total recall score is calculated as the total number of correct words remembered in the first three trials (maximum score is 36). The delayed recall is the total number of words remembered in trial 4 (maximum score of 12) (Cherner et al., 2007). The cut off for the total recall to detect memory impairment in Spanish population is < 13 , whereas it is < 4 for the delayed recall (González-Palau et al., 2013).

Phonemic and semantic fluency was also measured. The FAS or Controlled Oral Word Association (COWA) test was used to assess phonemic fluency (Barry, Bates, & Labouvie, 2008; Strauss, Sherman, & Spreen, 1998), in which patients were required to produce as many words as they could beginning by each letter (F, A, and S) in one minute. Proper names and repetitions are not scored. The total score is the total number of words produced for the three letters (Strauss et al., 1998). Normative scores in a Spanish speaking sample determined a cut-off of 7.6 words for F category, 7.2 in A category, and 7.6 for S category (Rosselli et al., 2002). Scores under

normative performance were considered pathological. The Animal verbal fluency test was used to measure semantic fluency. In this test, patients are asked to generate as many words as possible pertaining to the semantic category of animals, within 1 minute (Benton, 1968). Only correct answers are recorded, whilst perseverations (repeated words) or intrusions (words from another category) are not considered. Normative values for Spanish speakers were considered, with a cut-off score of 12.9 words (Rosselli et al., 2002).

The Wisconsin Card Sorting task (WCST) was used to measure executive functioning (Bowden et al., 1998). Patients were asked to classify 60 cards according to different criteria: colour of the symbols (red, yellow, blue and green), their shape (stars, crosses, triangles and circles), or the number of shapes on each card (1 to 4). The rule for the classification changes every 10 cards. The task measures how people adapt to the change of rules. The number of correct matches, errors (perseverative and non-perseverative) and categories completed are recorded. The total number of errors and perseverative errors are used in the formula following Nelson (1976) to calculate the final score $[(\text{perseverative errors} / \text{total errors}) \times 100]$. The cut off score is 50.

The Galveston Orientation and Amnesia Test (GOAT) was administered to measure orientation to person, place and time, and memory for events preceding and following the injury. Thus, this test assesses post-traumatic amnesia (PTA) and retrograde amnesia (RA) after severe brain injury (Levin, O'Donnell, & Grossman, 1979). It includes 10 items that are verbally asked to patients (e.g., what is your name?). The number of errors in each question is recorded and subtracted from the total score (maximum score = 100 points). Scores lower than 66 indicate impaired performance; scores between 66-75 indicate borderline performance, whilst scores over 75 indicate normal performance.

The Awareness of Deficit Scale is a semi-structured scale developed to measure the level of awareness of deficit for a group of patients with acquired brain injury (Villalobos, Bilbao, Espejo, & García-Pacios, 2018). The scale considers three main areas of awareness: awareness of injury, awareness of deficit and awareness of disability. The level of awareness in each area is measured, with a range 0-6 for the awareness of injury, 0-12 for the awareness of deficit, and 0-12 for awareness of disability. The total maximum score is 30.

The Barthel Index (BI) was administered to measure functional performance in activities of daily living (Mahoney & Barthel, 1965). Ten different items are scored based on the ability of the patient to perform the activity. A score of 0 is given if the patient cannot perform the activities as described in the criteria. Other scores are provided for different areas, such as continence, dressing or feeding. A score of 100 indicates independence in all the areas. Most studies consider a cut-off score of 60/61 (moderate dependency) (Shah, Vanclay, & Cooper, 1989).

Functional performance was also evaluated via the Functional Independence Measure (FIM) (Keith, Granger, Hamilton, & Sherwin, 1987). This scale consists of 18 different items that measure the level of independence in different areas, with an ordinal scale (1 = total assist and 7 = complete independence). Scores range between a minimum of 18 to a maximum of 126, any score below 6 in any given item would indicate supervision or assistance. Hence, a total score under 90 will be a sign of dependency.

5.3.2.4 Motor assessment

Patients' upper and lower extremity functioning was assessed for contralesional and ipsilesional limbs via the Motricity Index questionnaire (Demeurisse, Demol, & Robaye, 1980). This is a simple test of motor function that

allows quick, valid and reliable assessment (Collin & Wade, 1990). Patients were required to perform three different task: pinch grip, in which they had to try to grip a 2.5cm tube using their thumb and index fingers; elbow flexion, in which patients were required to flex the elbow in 90°, and try to touch their shoulder with the hand whilst experimenter opposes some resistance at the wrist; and shoulder abduction, in which the elbow is flexed and placed against the chest, and patient is required to abduct the arm. Scores for the pinch grip are between 0 (no movement) to 33 (normal pinch grip). For elbow flexion and shoulder abduction, scores go between 0 (no movement) to 33 (normal power). The total score is calculated by adding up all scores +1 and it ranges from 1 (no movement) to 100 (normal power) (Collin & Wade, 1990).

5.3.2.5 Body size estimation task

The body size estimation task has been inspired by tasks in previous research (Gandevia & Phegan, 1999; Longo & Haggard, 2012b; Mohr et al., 2010; Türker, Yeo, & Gandevia, 2005), where participants are presented with distorted pictures of body parts and asked to assess which one would subjectively match their perceived body size (Gardner & Boice, 2004). Image distortion tasks are thought to measure the cognitive component of the body image (Slade & Brodie, 1994). In this study, single body parts were presented to avoid comparative judgements (Fuentes, Longo, et al., 2013). Moreover, real sized pictures were used as results are susceptible to less distortion due to procedural confounds (Holder & Keates, 2006).

5.3.2.5.1 Stimuli

Real pictures of each participant's face and right hand (dorsal and palmar views) were taken with a Nikon 3200D camera, all at the same distance and position. By using Paint S (version 5.6.9), the background was removed from the pictures to make it standard white. Adjacent body areas (i.e., wrist for arm or neck for face) were

also removed from the pictures in order to prevent providing any cues (Gardner & Boice, 2004). The mirrored image of the right hand was used as stimuli for the left hand, as patients could not open their hand to take a picture due to motor problems (e.g., hemiplegia). Thus, the same was done for healthy controls. The face image was also mirrored to present it in typical view, as seen when reflected (D'Amour & Harris, 2017). The images were then resized, for width and length (one dimension at a time), by using a bespoke-made programme (Borland C++ Builder, 2007). Size increases and decrements were of 5% to ensure these were not obvious and were symmetrical from the midline of each body part. The minimum size decrement was of 50% (smallest picture), and the maximum increment was of 150% (largest picture). There was a total of 21 pictures per each body part (face, right hand and left hand) and hand view (dorsal/palmar), that is a total of 105 images where only one per body part was shown in the correct real size (100% size) (see Figure 5.10A).

5.3.2.5.2 Experimental procedure

Participants sat in front of a wall with a white screen, half a meter away from it, where the pictures were presented using LCD video projector (full HD, 1080 pixels, 2400 lumens) connected to a windows laptop. The projector was at a distance of 1.8 metres from the wall and was positioned on a table behind the participant (1 metre of height) (see Figure 5.10B). Images were initially adjusted in size, in such a way that the 100% picture (no distortion) matched the real size of the participant's body part when projected onto the wall. For this, a tape measure was used to size the real and projected body parts.

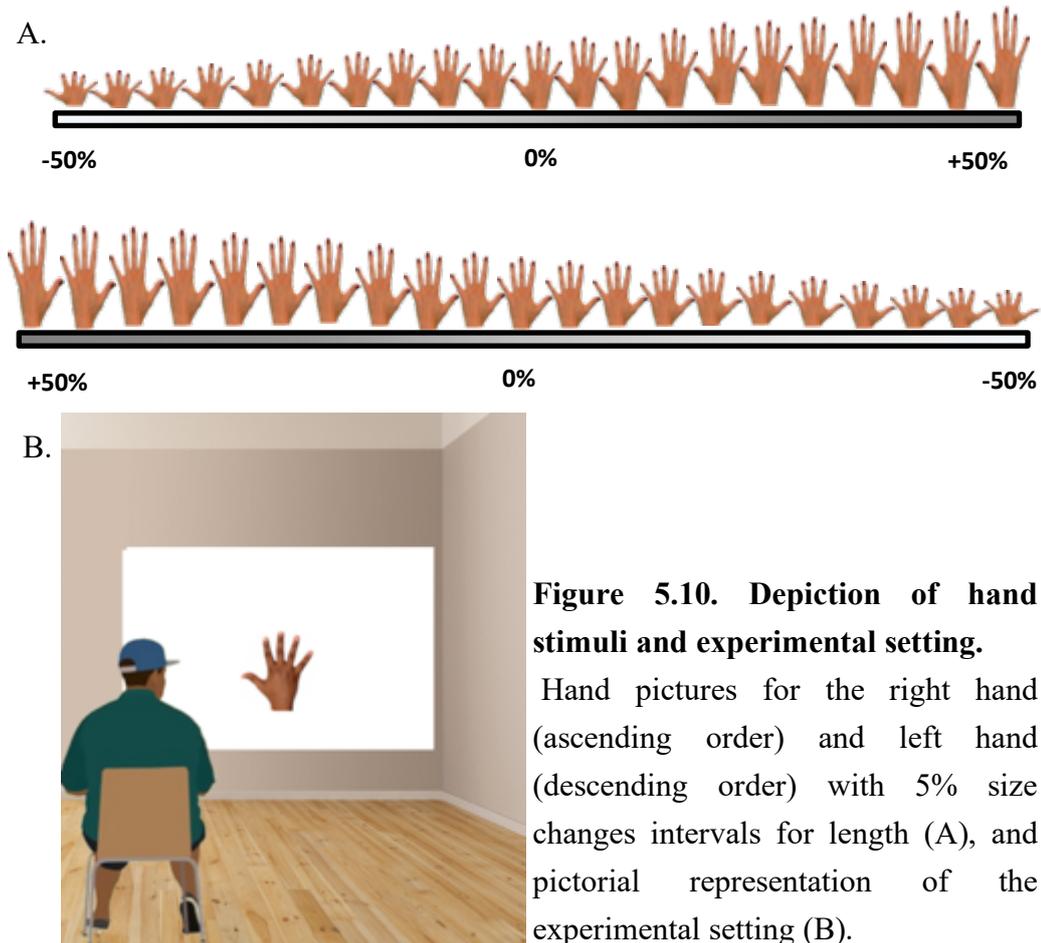


Figure 5.10. Depiction of hand stimuli and experimental setting.

Hand pictures for the right hand (ascending order) and left hand (descending order) with 5% size changes intervals for length (A), and pictorial representation of the experimental setting (B).

The images were projected in the right hemispace from participants' body midline, in order to avoid potential difficulties due to EN. Pictures were presented in ascending (from small to big) and descending (from big to small) order, one picture at a time, repeated in two rounds for each order. Presentation was counterbalanced for order (ascending and descending); dimensions (length and width); hand view (palmar dorsal), and body part (face, right hand, left hand), with a total of 8 trials for the face, and 12 trials for each hand. This method was used as other type of procedures, such as constant stimuli, require a large number of trials to ascertain the point of subjective equality (PSE) as a measure of body size estimation, which could be cumbersome for patients and increase fatigue (Gardner & Boice, 2004). For these same reasons, pictures were presented consecutively and one at a time, rather than a randomised

presentation of multiple images as per previous research (Gandevia & Phegan, 1999; Kammers, Longo, Tsakiris, Chris Dijkerman, & Haggard, 2009; Longo & Haggard, 2012b). Single picture presentation has already been reliably used in previous studies (e.g., Gardner & Boice (2004); Mohr et al. (2010)).

Participants were required to decide if the presented image corresponded with the veridical size of each body part. If they decided a certain picture was not their actual body part size (non-veridical), the experimenter presented another picture with the 5% increment or decrement in size, depending on the presentation order. The stimuli presentation continued until the participants' response changed (i.e., changed from non-veridical to veridical).

5.3.2.6 General analyses

The perceived size of the body parts was analysed in two ways. Firstly, the overall *Representational Range* was calculated for all body parts as a measure of the uncertainty of the representation. For this, the absolute difference between the averaged percentage of distortion in the ascending and descending trials per participant was obtained, getting an overall measure of variability of the distortion. For example, if a participant chose an image as veridical that was 70% the size of the original one in the ascending trial, and a picture that was 125% the size of the real sized picture in the descending, the average absolute representational range was 55%. Prior preliminary paired t-tests analyses did not identify differences in the distortion of body parts depending on the dimensions (length and width) or views for the hands (dorsal and palmar). Thus, results were averaged across dimensions for the face, and dimensions and views for the hands, as a general measure of the representation of the body parts.

Secondly, the *Body size distortion* or threshold estimates per series (ascending and descending) was computed by calculating the percentage of under/overestimation per body part (face, left hand and right hand). Previous studies have shown an influence of presentation order in size estimation of one's own body, advising against averaging size between ascending and descending conditions (Gardner & Boice, 2004; Gardner & Bokenkamp, 1996). Thus, the distortion of the size of each body part was considered in each presentation order. In this case, data was averaged across length and width dimensions to obtain overall distortion per body part.

Lastly, the cut-off value for the averaged absolute distortion per body part was obtained in order to assess pathological performance for individual patients.

5.3.3 Results

5.3.3.1 Personal and Extrapersonal Neglect examination results

Two patients (P06 and P09) showed PN with the Comb and Razor test, whilst four showed PN with the Fluff test (P06, P07, P08 and P09). None showed any difficulty in the One Item test, all scoring 0. Hence, a total of five patients showed PN at least on one task and were classed as having PN (PN+ group), whilst the other four did not show this disorder (PN- group). Two patients out of the nine showed EN, as assessed by the BIT battery, one in each group (P01 in PN+, and P04 in PN- group). Final patients' groups did not differ in Age [$t(7) = .09, p = .93$], Gender [$t(7) = -.16, p = .88$], Education [$t(7) = -.22, p = .83$], Time from injury [$t(7) = 1.03, p = .34$], or Time at CEADAC from admission [$t(7) = .31, p = .77$]. See test results Table 5.5.

5.3.3.2 General neuropsychological assessment results

Results for all neuropsychological tests are presented in Table 5.6. The scores between groups were compared in order to assess for potential differences.

In the Digit test all patients performed within the normal range in direct order, showing no impairment. In contrast all patients displayed impaired performance (<4 span) in reverse order. Specifically, PN+ patients were able to recall 7 digits (SD = 1.58) in direct order, and 2.8 digits (SD = .84) in reserve. PN- patients recalled 6.25 (SD = 1.5) in direct presentation, and 3.25 digits (SD = .5) in reverse. Both groups performed equally in this test in direct [$t(7) = .72, p = .49, d = .49$], and reverse [$t(7) = -.94, p = .38, d = .65$] presentations.

Scores in the HVLТ were considered for all patients but one (P05 in PN- group) who did not complete the test. In total recall, all patients performed over cut-off (score > 13). In delayed recall, two patients were identified as having impaired performance in PN- group (P04 and P05). Average performance was then considered to investigate differences between groups. PN+ patients were able to recall 20.6 words (SD = 6.07), whilst the PN- patients recalled 16.67 (SD = 4.62). Differences between groups did not reach significance [$t(6) = .96, p = .38, d = .73$]. Delayed recall did not differ between groups either (PN+: M = 6.4 words, SD = 2.3; PN-: M = 3.33 words, SD = 4.16; $t(6) = 1.38, p = .22, d = .91$).

Further, the scores in the phonemic fluency test (FAS) and semantic fluency test (Animal test) were considered. Single patients' performance is included in Table 5.6, and pathological scores are denoted in bold. On average, PN+ patients produced 6.6 words for category F (SD = 3.71), 5.2 for A (SD = 3.11), and 8 for S (SD = 3.08). In PN- group, patients generated 9.25 category F words (SD = 3.86), 6.75 for category A (SD = 4.92), and 9.25 for category S (SD = 5.19). Scores between patients' groups were compared via independent t-tests. PN+ and PN- patients did not differ in any of the scores in the different categories for FAS (F category: [$t(7) = -.58, p = .58, d = .38$]; A category: [$t(7) = -.45, p = .67, d = .29$], and S category: [$t(7) = -1.05, p = .33,$

$d = .7]$. Further, on the Animal semantic fluency test, PN+ participants produced, on average, 12 words ($SD = 5.24$), whereas PN- patients produced 15 ($SD = 4$). There were no significant differences in the Animal test between groups [$t(7) = -.94$, $p = .38$, $d = .64$] (see Table 5.6).

The scores in the WSCT were then calculated. Patient P01 was unable to complete this test, whilst data for P09 was not available (both in PN+ group). Thus, the data considered was from a total of seven patients (see Table 5.6 for scores in this test). Considering the cut off score of 50, two patients showed impaired performance (P06 and P08), both in PN+ group. On average, patients in PN+ group were able to complete 1.67 categories in the WCST ($SD = .58$) whilst PN- patients completed 2.75 ($SD = .96$). Differences between groups were not significant [$t(5) = -1.72$, $p = .14$, $d = 1.37$]. Further, the patients' scores in the percentage of errors formula (Nelson, 1976) was of 51.46% ($SD = 14.26$) in PN+ group, whilst it was of 60.45% ($SD = 5.65$) in PN-. Differences were again not significant [$t(5) = -1.17$, $p = .29$, $d = .83$].

Two out of nine patients showed impaired performance on the GOAT (P03 in PN- group and P09 in PN+). Performance in this test did not differ between groups [$t(7) = .53$, $p = .62$, $d = .34$].

Similarly to previous studies using the Awareness of Deficit scale (Villalobos et al., 2018), patients in both groups showed reduced awareness (PN+ group: $M = 15.6$, $SD = 4.34$; PN- group: $M = 19.5$, $SD = 1$); however, there is no normative data for this scale. Differences between groups were not significant [$t(7) = -1.74$, $p = .13$, $d = 1.24$].

The level of independence in activities of daily living as measured by the BI showed that five patients (4 in PN+ and 1 in PN-) had a score lower than 60, indicating

more dependency. Again, average scores were compared between groups, and were equivalent [$t(7) = -.8, p = .45, d = .52$]. Both groups showed partial dependency, with PN+ group obtaining, on average, a score of 46 (SD = 18.84), whilst the PN- group averaged a score of 60 (SD = 33.42). Consistently, the same patients were identified as dependent with the FIM. When group scores were compared, no significant differences were identified between groups [$t(7) = -1.17, p = .28, d = .76$], confirming their functionality level was equivalent (see Table 5.6 for scores).

5.3.3.3 Motor assessment results

Patients' scores in the Motricity Index are presented in Table 5.6. As in previous studies (Sunderland, Tinson, Bradley, & Hewer, 1989), patients with 'normal' scores (full marks) were identified. All patients but one (P03 in PN- group) were impaired in motor performance with their contralesional upper left limb. Scores ranged from 1 to 100 in the Motricity index test. On average, PN+ patients obtained a motricity score for the left upper limb of 29.8 (SD = 36.95) whilst the PN- group scored 58.75 (SD = 42.03). Differences between groups did not reach significance [$t(7) = -1.22, p = .26, d = .8$].

Impairments in the mobility of the contralesional lower limb were also identified for all patients but one (P03 in PN- group). The average score for the PN+ group was 45.8 (SD = 30.98), whilst the score for PN- group was 67 (SD = 28.23). Groups did not differ in the scores in the motricity index for this limb [$t(7) = -1.06, p = .33, d = .72$].

Table 5.6. Motor and neuropsychological assessment results.

Shaded rows indicate patients in PN+ group. Scores in **bold** indicate impaired performance.

Group	Participant	Motricity index		Awareness of Deficit Scale			Digit span		HVLIT		FAS			Animal	WSCT (% errors)	GOAT	Barthel	FIM
		UL	LL	Awareness of injury	Awareness of deficit	Awareness of disability	Total	D	R	Total recall (number)	Delayed recall (number)	F	A					
PN+	P01	53	70	6	8	0	14	5	2	16	4	3	8	2	NA	90	55	64
PN+	P06	29	53	6	4	6	16	9	3	29	8	10	11	12	41.18	98	50	68
PN+	P07	1	29	6	4	6	16	8	3	24	9	6	11	8	67.74	90	45	65
PN+	P08	1	1	6	6	10	22	6	4	20	7	5	6	6	45.45	90	15	44
PN+	P09	65	76	6	4	0	10	7	2	14	4	2	4	5	NA	59	65	90
PN-	P02	75	76	6	8	6	20	8	3	22	8	5	7	8	61.53	99	80	98
PN-	P03	100	100	6	8	4	18	5	3	14	0	3	7	7	56.25	16	75	90
PN-	P04	1	33	6	6	8	20	5	4	14	2	5	6	7	56	95	10	43
PN-	P05	59	59	6	4	10	20	7	3	NA	NA	14	17	15	68	97	75	102

Note: UL = upper left; LL = lower left. D = direct; R = reverse
NA = not available

5.3.3.4 Body size estimation task

5.3.3.4.1 Representational range

The representational range was the absolute difference between the average percentage of distortion in the ascending and descending trials. PN+ group showed the largest representational range ($M = 64.58\%$, $SD = 12.44$) followed by PN- group ($M = 35.11\%$, $SD = 13.17$) and the control group ($M = 20.49\%$, $SD = 7.45$) (see Figure 5.11).

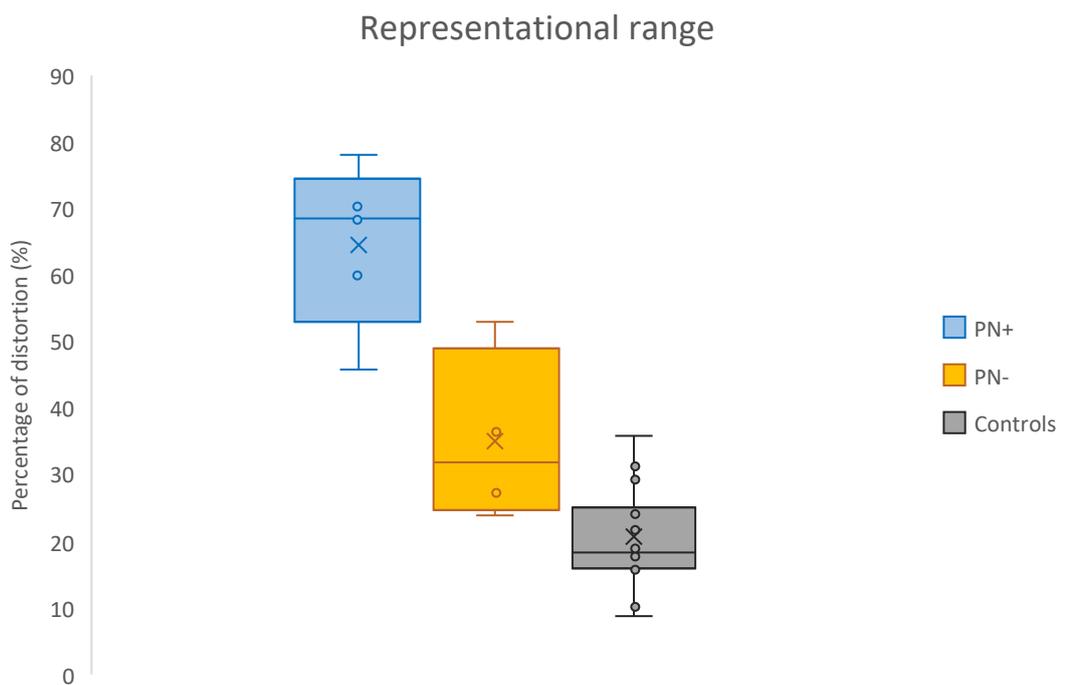


Figure 5.11. Box and whiskers plot with the data distributions for the representational range (%).

Representational range averaged across body parts for PN+, PN- and Control groups. The top of the rectangular box represents the 75th percentile of the sample, whilst the bottom represents the 25th percentile. The top upper whisker represents the maximum value of the sample, the bottom of the lower whisker represents the minimum value of the sample. Circles represent individual scores; x represents the sample mean and the line through the box is the median.

A mixed-model ANOVA was run with two factors: Body Part as repeated measures factor (face, right hand and left hand), and Group as between measures factor

(PN+, PN- and Controls). The main effect Body Part was not significant [$F(2,44) = .97, p = .38, \eta^2 = .04$], nor was the interaction between Body Part and Group [$F(4,44) = .87, p = .49, \eta^2 = .07$], indicating there were no differences in size estimation across groups depending on the body part considered. In contrast, there were significant differences when considering the Group factor [$F(2,22) = 41.65, p < .001, \eta^2 = .79$]. Bonferroni-corrected pairwise comparisons (corrected cut-off p value of .02) identified significant differences between PN+ and PN- groups [$t(7) = 3.45, p = .01, d = 2.3$], as they did between PN+ and Controls [$t(19) = 9.85, p < .001, d = 4.3$]; and between PN- and Controls [$t(18) = 3.02, p = .01, d = 1.37$]. These results confirmed there were distortions in the perceived size of all body parts in all groups, being of larger size for PN+ patients.

5.3.3.4.2 Body size distortion

Left hand

In the ascending presentation, participants showed a general tendency to underestimate the size of their hand, but in different magnitudes. In particular, larger underestimation was found on perceived size for the PN+ group ($M = -28.88\%$, $SD = 10.76$), followed by the PN- patients ($M = -19.22\%$, $SD = 7.44$). Controls also underestimated the size of the left hand but were more accurate ($M = -5\%$, $SD = 5.42$) (see Figure 5.12). A one-way ANOVA was run to investigate differences in the perceived size of the left hand between groups. Significant differences were found between Groups [$F(2,22) = 24.85, p < .001, \eta^2 = 1.25$]. Post-hoc Bonferroni corrected multiple comparisons identified significant differences between the size of the left hand in the PN+ group and Controls [$t(19) = -6.68, p < .001, d = 2.8$], and between PN- and Controls [$t(18) = -3.65, p = .004, d = 2.19$]. However, differences between PN+ and PN- did not reach significance [$t(7) = -2.06, p = .15, d = 1.04$].

In the descending condition there was, instead, overall overestimation of size, supporting the decision not to average across order conditions. Specifically, PN+ patients showed larger overestimation (M = 36.88%, SD = 5.36) than PN- patients (M = 15.31%, SD = 13.47), whilst Controls showed 14.45% overestimation of size (SD = 9.15). Significant differences in size perception were also discovered when running a one-way ANOVA [$F(2,22) = 11.38, p < .001, \eta^2 = 1.97$]. Multiple post hoc comparisons revealed these differences appeared between PN+ and PN- groups [$t(7) = 3.44, p = .007, d = 2.1$]. Differences were also significant when comparing PN+ patients to Controls [$t(19) = 4.69, p < .001, d = 2.99$], as Controls were far more accurate. Lastly, differences between PN- and Controls did not reach significance [$t(18) = .15, p = 1, d = .07$].

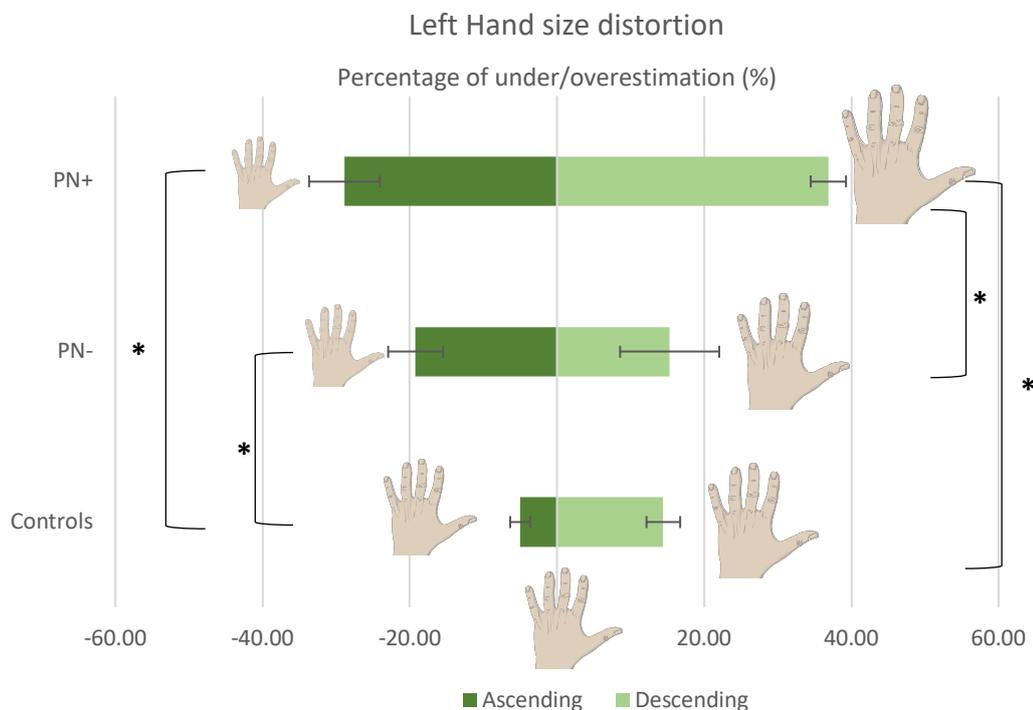


Figure 5.12. Left hand distortion.

Percentage of under/overestimation (%) of the perceived size of the left hand for all groups (PN+, PN- and Controls), for ascending and descending conditions. Hands depict the pictorial size distortion. * denote significant differences.

Right hand

In the ascending condition there was, again, overall tendency to underestimate the size of the hand in all groups (see Figure 5.13). In this case, PN+ underestimated the size of their right hand by -25.75% (SD = 10.86), followed by PN- (M = -16.41%, SD = 10.82), and controls (M = -5.2%, SD = 6.45). A one-way ANOVA yielded significant results [$F(2,22) = 13.27, p < .001, \eta^2 = 1.83$], indicating these differences in size perception were significantly different between groups. In ascending condition, there were not significant differences between PN+ and PN- patients [$t(7) = -1.72, p = .3, d = .86$], as both groups did underestimate the size of their right hand. In contrast, differences between PN+ and Controls were significant [$t(19) = -4.95, p < .001, d = -2.3$], as Controls showed smaller underestimation of size. Lastly, differences between PN- and Controls were not significant [$t(18) = -2.47, p = .07, d = 1.26$].

For the descending condition, there was again overall overestimation of size. In particular, PN+ showed larger overestimation (M = 34%, SD = 5.53) than PN- (M = 18.44%, SD = 11.21), whilst Controls were slightly more accurate (M = 15.47%, SD = 9.35). These differences in size perception between groups were significant [$F(2,22) = 7.99, p = .002, \eta^2 = 2.38$]. Bonferroni corrected post-hoc tests showed significant differences between patients' groups [$t(7) = 2.56, p = .05, d = 1.76$], and between PN+ and Controls [$t(19) = 3.99, p = .002, d = 2.41$], confirming the distortion for PN+ was much larger than the other two groups. Lastly, no differences were found between PN- and Controls [$t(18) = .59, p = .1, d = .29$].

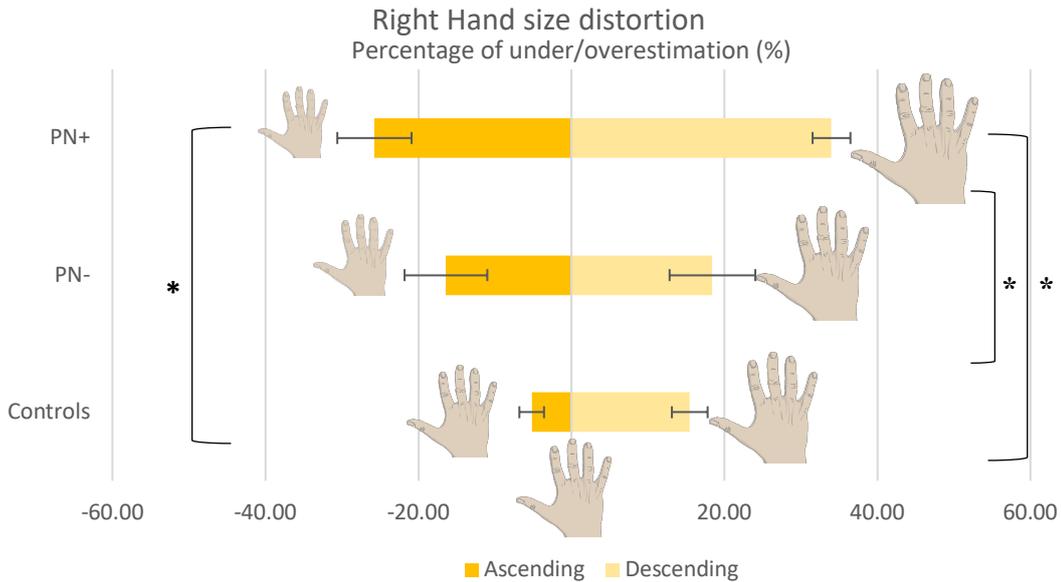


Figure 5.13. Right hand distortion.

Percentage of under/overestimation (%) of the perceived size of the right hand for all groups (PN+, PN- and Controls), for ascending and descending conditions. Hands depict the pictorial size distortion. * denote significant differences.

Face

Size distortion for the face followed the same pattern as the hands. That is, there was perceived underestimation of size in the ascending condition, and underestimation in descending (see Figure 5.14). In particular, PN+ patients underestimated the size of their face more ($M = -33.75\%$, $SD = 7.02$) than PN- ($M = -10.94\%$, $SD = 7.09$) or Controls ($M = -3.13\%$, $SD = 6.06$). A one-way ANOVA confirmed significant differences in size estimation for the ascending condition [$F(2,22) = 43.78$, $p < .001$, $\eta^2 = 1.25$]. Post-hoc comparisons revealed differences between PN+ and PN- were significant [$t(7) = -5.32$, $p < .001$, $d = 3.23$]. Similarly, PN+ showed significantly larger underestimation than Controls [$t(19) = -9.36$, $p < .001$, $d = 4.67$]. PN- and Controls similarly distorted their face [$t(18) = 2.19$, $p = .12$, $d = 1.18$].

In the descending condition, differences were identified between groups in the overall ANOVA [$F(2,22) = 13.73, p < .011, \eta^2 = 1.8$]. Post-hoc analyses revealed significant differences between PN+ and PN- patients [$t(7) = 2.69, p = .04, d = 1.62$], as PN+ patients showed larger overestimation of size (PN+: $M = 34.25\%$, $SD = 7.43$; PN-: $M = 23.13\%$, $SD = 6.25$). When compared with Controls, PN+ performed significantly worse [$t(19) = 4.58, p < .001, d = 2.48$], since Controls overestimated in less magnitude ($M = 17.73\%$, $SD = 5.78$). Differences between PN- and Controls did not reach significance [$t(18) = 2.06, p = .4, d = .9$].

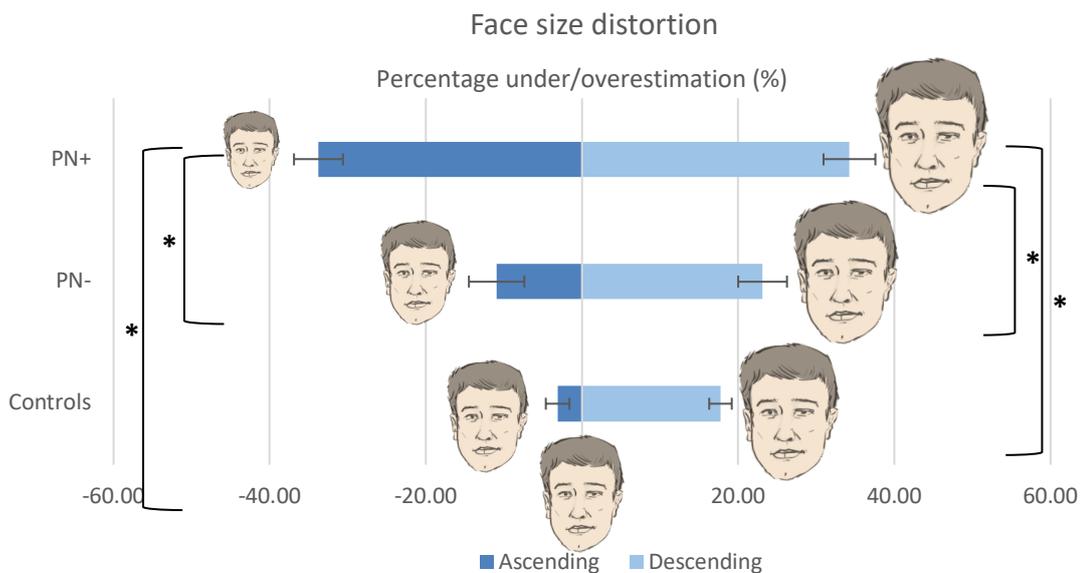


Figure 5.14. Face distortion.

Percentage of under/overestimation (%) of the perceived size of face for all groups (PN+, PN- and Controls), in ascending and descending conditions. Faces depict the pictorial size distortion. * denote significant differences between groups.

5.3.3.5 Cut-off scores and individual performances

Further analyses were run to calculate the critical cut-off scores that would indicate impaired performance for each body part as done in previous studies (e.g., Cocchini, Beschin, & Della Sala, 2018). For this, the scores for ascending and descending conditions were averaged for each body part (left hand, right hand, and

face) in the control group, to obtain a final absolute average of their performance (percentage of distortion). With this information, the highest value for each condition (body part) above which performance would be considered pathological was computed, by means of Crawford's single t-test case analyses equation (Crawford & Garthwaite, 2002; Crawford & Howell, 1998). The critical value that indicated impaired performance was 19.38% for the left hand; 23.82% for the right hand and 22.35% for the face.

The individual averaged absolute distortion per participant and body part was then calculated. Results indicated that all patients in PN+ group (100%) were above the cut-off for face and left hand size perception, whilst 80% of them were above for right hand distortion. In contrast, in the PN- group only 25% of participants went over cut-off for the left and right hands, whilst none showed pathological performance in the face task (see Figure 5.15A, B and C for bar graphs of individuals' performance).

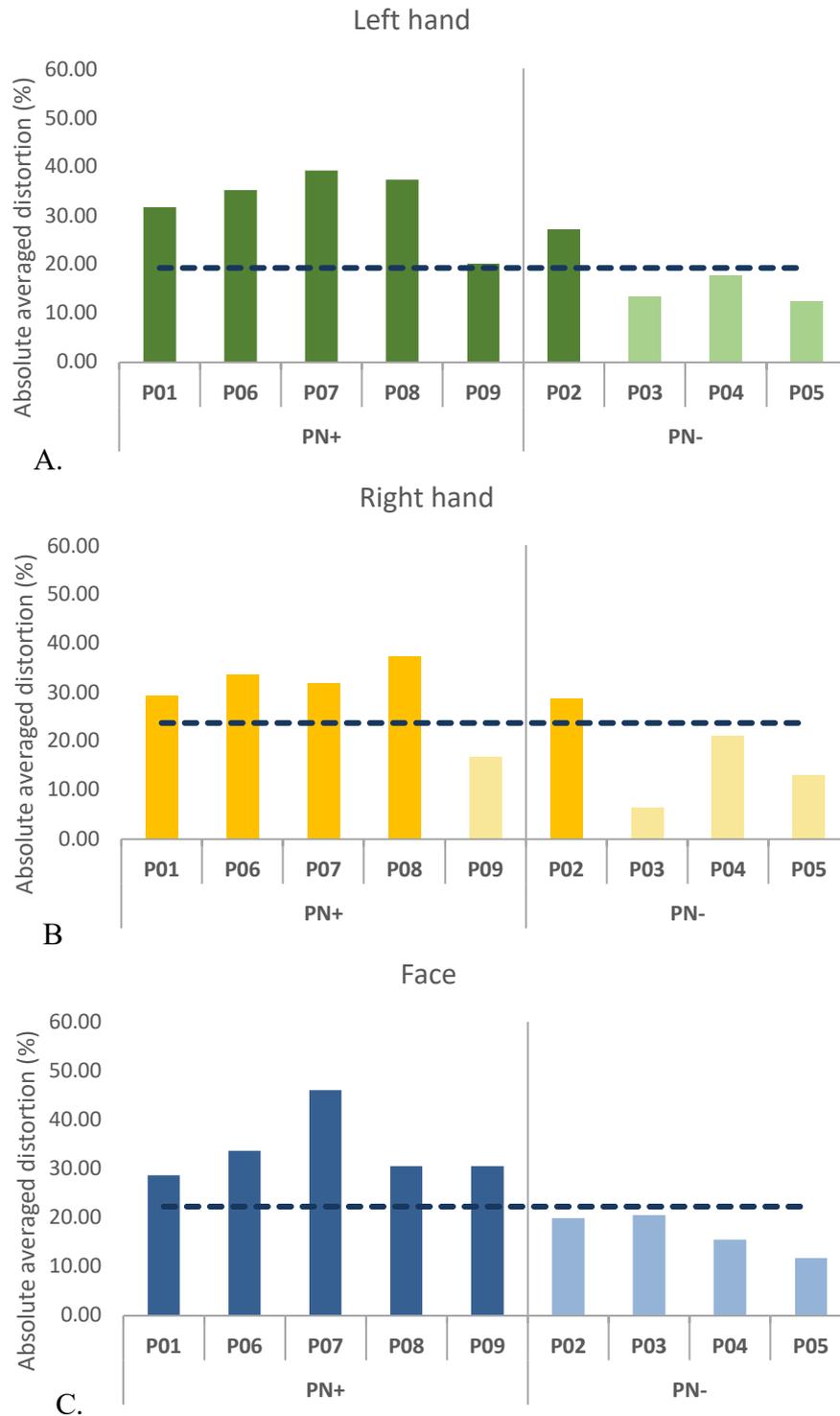


Figure 5.15. Absolute averaged distortion in the body size estimation task per participant.

Representation of the absolute averaged distortion of the left hand (A); right hand (B), and face (C) for all patients. The dashed lines indicate the cut-off for each body part. Abscissa axis indicates the patient's groups (PN+ and PN-) and the numbers for each patient. Pathological performance is indicated by darker-coloured bars (over cut-off).

5.3.4 Discussion

In this study the distortions in the size representation of hands and face were investigated in a group of patients with PN. Their performance was compared with a group of patients without PN (PN-) and a group of healthy controls. Distorted pictures were presented of the participants' right hand, left hand and face in ascending (small to large) and descending (large to small) orders. Participants had to select the picture that matched their real body size. The *Representational Range* was firstly calculated, which was the absolute difference between the averaged percentage of distortion in the ascending and descending trials, a measure of overall uncertainty of body size representation. Straightforward differences were found that showed significantly larger representational range for all body parts for PN+ group ($\approx 65\%$), when compared with PN- ($\approx 35\%$) or Controls ($\approx 20.5\%$), associated with less accuracy and indicative of more ambiguity. It may well be that patients with PN do have a blurrier body image, which consists of a range of sizes. Similarly, patients with eating disorders (ED) present with more labile or tenuous view of their bodies (Holder & Keates, 2006; Touyz, Beumont, Collins, McCabe, & Jupp, 1984), showing more variability in their representation (Espeset, Gulliksen, Nordbø, Skårderud, & Holte, 2012; Mussap, McCabe, & Ricciardelli, 2008), with greater overestimation and underestimation (Gardner & Bokenkamp, 1996). This theory was initially postulated by Slade & Brodie (1994) for ED, and it is possible that PN patients also have a hazier representation of their body, thus accommodating a larger range of sizes. Similarly, the *Allocentric Lock Hypothesis* postulates that patients with ED are 'locked' in an allocentric constructed image of their body, which is distorted (Riva, 2012). In healthy people, the stored body image will be updated by the egocentric online representations, which are short-term, driven by perception, imagery and retrieval, and regulated by

attention (Byrne, Becker, & Burgess, 2007). Due to damage to the parietal lobes and precuneus (Byrne et al., 2007; Cowdrey, Filippini, Park, Smith, & McCabe, 2014), this update does not occur in ED, living with the experience of having a ‘wrong body’ (Osman, Cooper, Hackmann, & Veale, 2004; Riva & Dakanalis, 2018; Riva, Gaudio, & Dakanalis, 2015). Given that parietal damage also underlies PN (Committeri et al., 2007), it is possible that PN patients are also locked to a wrong distorted body image (Di Vita, Palermo, Piccardi, & Guariglia, 2015).

Secondly, the *Body Size Distortion* was computed, which was the percentage of under/overestimation per body part (face, left hand and right hand) and order of presentation (ascending and descending). Controls were quite accurate estimating the size of their body parts in ascending presentation, with minimal distortion for all body parts ($\approx -5\%$). In contrast, they did show larger distortions in descending presentation ($\approx 16\%$). Visual aftereffects have been reported after short exposure to distorted body pictures, explaining this effect. Briefly, exposure to an initially large (thin) picture of the body, habituate participants in such a way that later judgements about real body size will be distorted to a larger (thinner) picture (Gardner & Bokenkamp, 1996). These aftereffects have been found preferentially after enlarged pictures when using size adjustment methods (Gardner & Bokenkamp, 1996), and are more long-lasting (Moseley et al., 2008). Then, within each trial, the initial picture presented could act as an ‘anchor’ for size judgements (Gardner & Boice, 2004). Conditions were counterbalanced to ameliorate this effect, which for Controls was primarily observed in descending trials, with an inclination for bigger sizes.

Preference to larger body parts has been reported in embodiment (Haggard & Jundi, 2009; Pavani & Zampini, 2007), as an adaptive mechanism to accommodate body growth (De Vignemont et al., 2005), suggesting that body size is closely

associated to body ownership (Di Vita et al., 2015). The opposite effect is seen after visual reduction of the size of a body part which causes loss of the sense of ownership of that limb (Ramachandran & Rogers-Ramachandran, 2007). Further, the asymmetric effects in body ownership due to body size magnification or minification are also seen in motor programming (Marino, Stucchi, Nava, Haggard, & Maravita, 2010). More specifically, magnification of the hand modulates grasping responses, with smaller grip apertures for same-sized objects, whilst this is not seen after downsizing the hand. Hence, a shrunken image of the hand would not be associated to one's own body (not 'owned'), wiping out any influences in grasping (Marino et al., 2010). Similarly, owing to reduced ownership over a shrunken limb, chronic pain is reduced, confirming the rehabilitative potential of visual size manipulation (Moseley et al., 2008). To sum up, that a preference for bigger pictures was found in Controls may be part of general preferential processing of the body, where larger body parts are embodied, whereas smaller ones are not.

Instead, the asymmetry in size perception seen in Controls is not seen in patients. Indeed, they showed inaccurate responses in both ends of the size 'spectrum', but more so for the PN+ group. In particular, PN+ underestimated the size of their body parts more in ascending order ($\approx -29\%$) and overestimated more in descending ($\approx 37\%$), whilst less distortion was found in PN- group ($\approx -19\%$ in ascending and $\approx 15\%$ in descending). Following previous hypothesis, it is possible that the mechanisms of preferential ownership of enlarged body parts do not 'work' in PN, due to the uncertainty or disintegration of body representation (Rasmus, 2017). Indeed, body ownership depends of the interaction between multisensory input and internal body models (Tsakiris, 2010). In PN there is a disconnection in multisensory integration of somatosensory/proprioceptive information with representations of the body space

(Coslett, 1998; Galati, Committeri, Sanes, & Pizzamiglio, 2001); hence, patients are more ‘susceptible’ to different influences. In detail, patients with uncertain body representation will be unable to accurately represent their own body to make size judgements (Di Vita et al., 2015). As a result, patients after stroke show more uncertainty in their representation, accommodating a range of distortions. For instance, disrupted multisensory processing has been proposed as the underlying reason to the appearance of macrosomatognosia of the left hemiface in a patient after stroke (Rode et al., 2012).

Moreover, there is also a link between uncertain representation, multisensory disintegration and awareness, seen in studies with bodily illusions. Even though explicit disownership is not characteristic of PN (Ronchi, Heydrich, Serino, & Blanke, 2018), patients are more susceptible to the rubber hand illusion, owing to a pathological reliance on visual information (Llorens et al., 2017), or ‘incomplete’ body representation (Ronchi et al., 2018). Comparatively, an “uncertain, unstable and weak” body image representation has also been proposed for ED patients (Slade & Brodie, 1994, p. 41), who are also more susceptible to illusory incorporation of a rubber hand due to a disruption in multisensory integration (Eshkevari, Rieger, Longo, Haggard, & Treasure, 2012; Mussap & Salton, 2006). Similarly, patients with somatoparaphrenia show pathological awareness linked to a more malleable body representation (van Stralen, van Zandvoort, Kappelle, & Dijkerman, 2013). The association between body representation and body ownership may be linked to insula functioning (Tsakiris, 2010) and damage to this area is associated to neglect (Gandola et al., 2012). Therefore, it is possible that patients with PN are more susceptible to both small and large hands, thus influencing their size judgements.

However, there is a potential influence of the motor capabilities and current condition of the body in the way it is represented. For example, increased malleability in the incorporation of the rubber hand is also seen in hemiplegics (Burin et al., 2015). Sensory and motor information are relevant in memory retrieval, as memory of a particular stimuli or event will be stored in the same underlying ‘machinery’ that processed it (Leemhuis, De Gennaro, & Pazzaglia, 2019). Hence, it is possible that there is an influence of motor performance in the incidence of body representation disorders (Llorens et al., 2017). Indeed, this can explain why PN- patients also showed larger distortion in perceived size of the body, in particular associated to left hand in ascending order. *Learned non-use* has been considered in disorders such as chronic pain, amputees, cerebral palsy and hemiplegic patients (Dohle et al., 2009; Fontes, Moura, & Haase, 2014; Makin et al., 2013; Punt, Cooper, Hey, & Johnson, 2013). In brief, patients that have experienced a traumatic event and become immobile for some time, compensate by using the non-affected limb, declining the trials to move the affected one, with associated shrinkage of cortical representation (Hallett, 2001; Punt et al., 2013). Changes in cortical representation, in turn, distort the representation of the size of the affected body area (Johnson et al., 2002; Lotze & Moseley, 2007; Matamala-Gomez, Nierula, Donegan, Slater, & Sanchez-Vives, 2020). Hence, use-dependent plasticity (Johnson et al., 2002), affects connectivity and structure of the deprived cortex (Leemhuis et al., 2019; Makin et al., 2013). In healthy adults, short-term immobilization causes a reduction of the size of the peripersonal space, whereas the overused limb is perceived as larger (Bassolino et al., 2015). This may explain why PN- patients showed some disruption in the representation of hands in comparison with Controls, as most showed some degree of motor impairment (see Table 5.6). Supporting this, their performance in face size estimation task did not differ from

Controls. Thus, it is possible that some distortion is introduced due to influences in perceived body size, whilst maximum distortion is instead found in PN+, due to a combination of factors, such as distorted stored body representation, attentional influences and hemiplegia (Committeri et al., 2018).

Asymmetries in the size representation of hands in PN+ were not found, which were also equivalent to the face, confirming the premise of an overall pathological body representation (Di Vita et al., 2017; Guariglia & Antonucci, 1992; Palermo et al., 2014). Hence, PN appears to be due to an underlying deficit in all body representations, which includes distortions of size as reported here, impaired body schema (Baas et al., 2011) and deficient topological body map (Palermo et al., 2014).

To conclude, PN has a clear impact in body representation, creating ambiguity in the representation of body size. Others have used this knowledge for specific rehabilitation strategies for disorders such as anorexia nervosa or motor disorders (Iosa et al., 2016). For example, hand size manipulation (magnification) helps rehabilitating motor disorders after stroke (Ambron et al., 2019), whilst improving body representation through virtual reality helps in chronic pain patients (Moseley et al., 2008; Senkowski & Heinz, 2016). Similarly, the mirror box therapy has shown positive effects in improving the distorted representation of the arms in patients post-stroke (Tosi, Romano, & Maravita, 2018). Moreover, body ownership affects representation, and it would be useful to measure its plasticity in further studies.

5.4 General discussion

These two studies have shown a disrupted metric body representation due to damage of cortical structures: left precentral tumour and an attentional disorder (i.e., PN). In both cases altered metric representation has been found, specific for hands in

the case study presented in Experiment 1, whilst it was generalised to all body areas in PN.

Overall, results have shown how damage to different cortical areas, with different functions, can affect the representation of the size of the body. Previous studies have found that modulation of size perception in sensorimotor areas was achieved through repetitive Transcranial Magnetic Stimulation (rTMS), whereas this was not achieved when targeting the inferior parietal lobe (Giurgola et al., 2019). Similarly, the observation that PN patients have a less certain metric representation of the body supports the idea that parietal areas are involved in this body model (Committeri et al., 2018, 2007). Supporting this, a recent study targeted the angular gyrus (parietal) with anodal tDCS to investigate its effect in the size perception of the arm, through a tactile discrimination task. In this study, modulation was achieved, in such a way that size perception was more accurate after the stimulation (Spitoni et al., 2013). Taken together, these studies support the idea that a distributed network of areas processes different aspects of the body, and then constructs an integrated model (Azañón, Tamè, Maravita, Linkenauger, Ferrè, Tajadura-Jiménez, Linkenauger, et al., 2016). Interestingly, somatosensory areas appear to be more specific in their modulation, as seen in Experiment 1, whereas parietal areas (attentional disorder) affect body representation in a more widespread and unspecific manner (i.e., all body areas are distorted). Due to this, impairment in daily functioning is more evident in the latter case.

These results pinpoint to the necessity of understanding how body representation is modulated in health, in order to improve representation in sickness. Indeed, the correct information regarding shape and size of the body is needed for perception and action (Medina & Coslett, 2016), and to interact with the environment.

Specifically, studies have shown how manipulation of perceived body size leads to changes in the perceived size of objects and space, as one's own body size representation 'leads to a scaling' of the environment (Bassolino et al., 2015; Linkenauger, Leyrer, Bühlhoff, & Mohler, 2013; Perera, Newport, & McKenzie, 2017). Therefore, manipulation of a distorted representation of the body may be useful, in particular for rehabilitation or treatment, such as in neuropsychiatric disorders (e.g. anorexia nervosa) or after brain damage (e.g. PN). In these cases, quick modulation of the representation of the body may produce gains that other rehabilitation protocols may take longer to achieve. For example, magnifying the size of a body part (hand) produces gains in motor performance after stroke due to increased cortical excitability (Ambron et al., 2019). Further, modulation of size perception has also helped mitigating the symptoms in chronic pain by using tactile stimulation, mental imagery training (Lotze & Moseley, 2007), or virtual reality environments (Matamala-Gomez et al., 2020; Senkowski & Heinz, 2016). Not only this, but the metrics of the body influence the way the environment is perceived (Linkenauger et al., 2013; Perera et al., 2017; Taylor-Clarke, Jacobsen, & Haggard, 2004); thus, it is important that any disruption to this representation is corrected.

Earlier chapters in this thesis have shown how the metric representation of hands and faces in healthy adults are not accurate, whilst distorted representation after brain injury (as seen in this chapter) appears to be an 'exaggeration' of these distortions. Hence, exploration of the malleability capacity of this representation in healthy adults will help understand underlying mechanisms and support planning potential rehabilitation treatments. The goal of Chapter 6 in this thesis was to modulate the metric representation of the body in healthy adults. In Experiment 1, the body representation was modulated through top-down processes by using transcranial Direct

Current Stimulation (tDCS); whilst in Experiment 2, the modulation was bottom-up by using passive sensory stimulation.

Chapter 6: Neuroplasticity of hands and face size representation



Josephine Cardin Photography

6.1 Introduction

Body size representation crucially depends on multisensory integration (Azañón, Tamè, Maravita, Linkenauger, Ferrè, Tajadura-Jiménez, & Longo, 2016; De Vignemont, 2014), relying on top-down and bottom-up mechanisms that are constantly in interaction to build a coherent representation (Di Vita et al., 2016; Longo, 2015a; Palermo et al., 2014; Pitron et al., 2018; Serino & Haggard, 2010). For instance, afferent sensory information affects the size of a perceived body part almost instantly after acute decreases (anaesthesia) or increases (electrical cutaneous stimulation) of sensory input (Gandevia & Phegan, 1999). In particular, anaesthesia increases the perceived size of body parts, such as the thumb (Gandevia & Phegan, 1999; Paqueron et al., 2003); the lips and teeth (Türker et al., 2005), and the upper or lower limbs (Paqueron et al., 2003), due to a shrinkage of the primary somatosensory cortex representation (Gandevia & Phegan, 1999). Moreover, behavioural changes have been observed after magnification or minification of the size of body parts, affecting reach and grasp (Ambron et al., 2017; Marino et al., 2010); tactile perception (Taylor-Clarke et al., 2004) or pain perception (Mancini, Longo, Kammers, & Haggard, 2011; Moseley et al., 2008). Further, modulation of the size of the body has also been explored through manipulation of the cortical activity. For example, recent studies have found overestimation of hand size after repetitive Transcranial Magnetic Stimulation (rTMS) of somatosensory areas (Giurgola et al., 2019). Yet, the neural substrates of body representation are still not fully understood, and less is known for the specific areas holding the metric representation of the body (Spitoni et al., 2013).

In light of this, the aim of this chapter was to study the neuroplasticity of the body representation through top-down and bottom-up modulatory approaches. One of these methods was the Transcranial Direct Current Stimulation (tDCS) which has

undoubtedly helped disentangle the understanding of brain substrates and functioning for specific cognitive domains both in healthy and clinical populations (Costa, Lapenta, Boggio, & Ventura, 2015; Lefaucheur, 2009; Nitsche et al., 2008). Therefore, this type of stimulation should help learn more about body size representation when targeting specific brain areas involved in representing the metrics of our body. With this aim, Experiment 1 was designed to explore the body model of the hand and face after tDCS on body related areas.

The second method considered in this chapter was passive sensory stimulation, which allowed the study of bottom-up processes in body representation in Experiment 2. For this, a new bespoke-designed experimental device was used to deliver the stimulation. Passive sensory stimulation protocols have been developed in current years to study modulation of different cognitive functions, mainly to induce perceptual learning and behaviour change without training (Beste & Dinse, 2013; Dinse, Ragert, Pleger, Schwenkreis, & Tegenthoff, 2003). This approach has proven useful to improve sensorimotor functions in health (Ladda et al., 2014), or mobility in old age (Kalisch, Tegenthoff, & Dinse, 2008, 2010). In here, bottom-up influences were explored in the size representation of hands and faces by using this type of stimulation. Collectively, the main goal of this chapter was to provide further understanding of the neuroplasticity of body representation that may help guide potential methods for rehabilitation.

6.2 Experiment 1: neuromodulation of hands and face size representation through tDCS

6.2.1 Introduction

tDCS is a type of non-invasive stimulation that modulates cortical activity to elicit specific neural changes that can last up to hours (Batsikadze, Moliadze, Paulus,

Kuo, & Nitsche, 2013; Pirulli, Fertonani, & Miniussi, 2014). tDCS is safe, inexpensive, portable and accessible, and provides reliable results without interrupting brain functioning (Costa et al., 2015). tDCS acts in neural networks that would be involved in learning by practice, potentiating these circuits and facilitating gains that would typically happen due to experience based plasticity (Yau, Celnik, Hsiao, & Desmond, 2014). In detail, tDCS hyperpolarise or depolarise resting state of neuronal membranes, modulating spontaneous activity (Brunoni et al., 2012) and firing likelihood (Lefaucheur, 2009; Mylius, Borckardt, & Lefaucheur, 2012) (see Figure 6.1). Further, polarity of the stimulation determines the shifts of the cortical excitability (Batsikadze et al., 2013). Anodal tDCS works by enhancing cortical activity and excitability, whereas cathodal stimulation will reduce it (Brunoni et al., 2012; Nitsche et al., 2008). However, in reality these effects will vary depending on the parameters used (i.e., intensity and duration of stimulation), as the association between physiological and behavioural effects of stimulation is not clear-cut. For instance, anodal stimulation longer than 26 minutes of duration will cause inhibition of cortical activity (Monte-Silva et al., 2013; Thair, Holloway, Newport, & Smith, 2017), whereas cathodal stimulation may cause an improvement instead (Pirulli et al., 2014) and not inhibition (Jacobson, Koslowsky, & Lavidor, 2012). In particular, long-term potentiation (LTP) occurs for higher intensities and longer duration of cathodal tDCS (Batsikadze et al., 2013; Pirulli et al., 2014). In fact, several studies have shown an improvement in performance if certain parameters are met for intensity and duration, becoming qualitatively equivalent to anodal stimulation (Batsikadze et al., 2013; Pirulli et al., 2014).

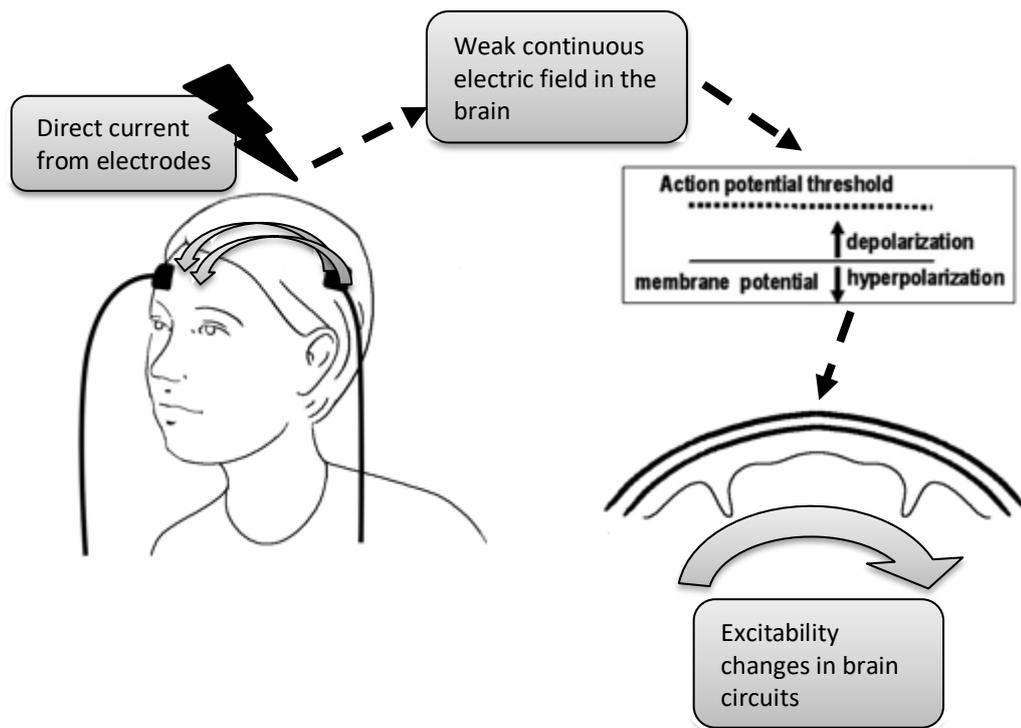


Figure 6.1. Mechanism of action of tDCS.

Electrodes of different sizes are positioned on the scalp over a selected cortical target. A weak current is delivered, that goes from one electrode to the other. This current will cause a reduction or increase of the action potential thresholds of cortical circuits. Modified from Mylius et al. (2012).

The potential of tDCS for rehabilitation has been suggested, having instigated a number of studies in clinical populations (Costa et al., 2015). For example, a recent study investigated the effect of tDCS stimulation in phantom limb pain (Bolognini, Olgiati, Maravita, Ferraro, & Fregni, 2013). In addition, tDCS has been shown to have analgesic effects or induce experimental pain, helping understand the mechanisms for pain processing (Mylius et al., 2012). In healthy participants, modulation of the metrics of the arms was achieved also by targeting the right parietal lobe with tDCS (Spitoni et al., 2013).

Crucially, this and previous research support the idea that right parietal areas are extremely important in body representation (Magnani & Sedda, 2016), in particular PPC (Berlucchi & Aglioti, 2010). In fact, multisensory integration of different signals to construct the body representation occurs in the parietal areas (Corradi-Dell'Acqua et al., 2009; Peviani, Melloni, & Bottini, 2019). Specifically, non-action oriented body representations, which include the metric representation of the body, have been found to be mediated by the supramarginal gyrus (SMG) and somatosensory cortex (Di Vita et al., 2016; Tamè et al., 2017). The right SMG underpins visuo-spatial judgement of body parts (Corradi-Dell'Acqua et al., 2008), whereas the right parietal contains an internal model of visual, anatomical and structural characteristics of the body (Tsakiris et al., 2008). Left parietal areas instead appear more involved in conceptual aspects of body knowledge (Sirigu et al., 1991). Damage to parietal areas is associated with body illusions, denial of motor deficits, delirious beliefs or metric disturbances (Nico et al., 2010), and Personal Neglect (PN) (Committeri et al., 2018, 2007). For all these reasons, it was considered of relevance to explore the potential effect of cathodal tDCS in the metric representation of the body. Modulation of activity in the right angular gyrus through tDCS improves the size perception of the contralateral arm, whereas left-sided stimulation does not (Spitoni et al., 2013). Hence, the role of the right SMG in the size representation of the left hand and face was investigated in Experiment 1A by implementing the localisation task presented in previous chapters.

6.2.2 Experiment 1A: the role of the supramarginal gyrus on the size of the hands and face

6.2.2.1 Method

6.2.2.1.1 Participants

An a priori power analysis was run to determine the required sample size by using G* Power 3.1 (Faul et al., 2009). The effect size (Cohen's d) from the studies in Chapter 4 were considered for this calculation. In this case, the effect size for the independent t-tests for lengths and widths was, on average, 1.15 across experiments. A power analysis for the difference between two dependent means with an effect size of 1.15, alpha of 0.05, and power of 0.8 indicated the adequate sample size would be of 9 participants.

A total of 18 healthy volunteers from Goldsmiths University were recruited (19 – 39 years of age) to take part in the study. Two were later removed as were outliers at baseline. Thus, a total of 16 participants (9 females and 7 males) were considered for final analyses. The mean age was 24.06 years ($SD = 5.26$), with 16.06 years of education ($SD = 1.88$).

Handedness was assessed with the Oldfield Questionnaire (Oldfield, 1971). Values range from -1 to 1, with scores below -0.5 indicating left-handedness; scores between -0.5 to +0.5 indicating ambidexterity; and scores over +0.5 indicating right-handedness. One participant was ambidextrous (score = .36), whilst all other participants were right-handed.

Following safety procedures for transcranial stimulation (Nitsche et al., 2008), all participants were screened to ensure it was safe to administer brain stimulation. All participants had no history of neurologic or psychiatric disorders; did not have a heart pacemaker, cochlear implant, aneurysm clip or any other electronic device or metallic

object within their body; did not have a personal or family history of epileptic fits or seizures; were not pregnant and had not taken part in any other stimulation study within the previous 48 hours (Nitsche et al., 2008). This research was approved by Goldsmiths Ethics Committee and followed the principles of the Declaration of Helsinki.

6.2.2.1.2 Hand apparatus and procedure

In this study, the hand task presented in Chapter 3 was used. Participants were sat on a chair in front of a table. A transparent Perspex sheet (30 x 30 centimetres) was positioned horizontally on top of four metal posts of 8 centimetres each. A small 20 x 20 cm white canvas frame was positioned underneath, onto which the participants rested their hands (one at a time). A remote-controlled camera (Nikon D3200) was positioned at 90 centimetres suspended above the Perspex board and aligned with its central point (see Figure 6.2A). The camera was used to take pictures of each single location response to the different hand landmarks requested. The participant's left hand was positioned under the sheet, on top of the canvas, with fingers spread out comfortably. Participants were required to locate different landmarks on the hand under the sheet by pointing on top of it with their right index finger, whilst blindfolded. Participants did not get any feedback at any point. A total of nine landmarks were requested, in random order, three times per landmark (see Figure 6.2B). Thus, a total of 27 pictures were collected for a single presentation of the hand localisation task.

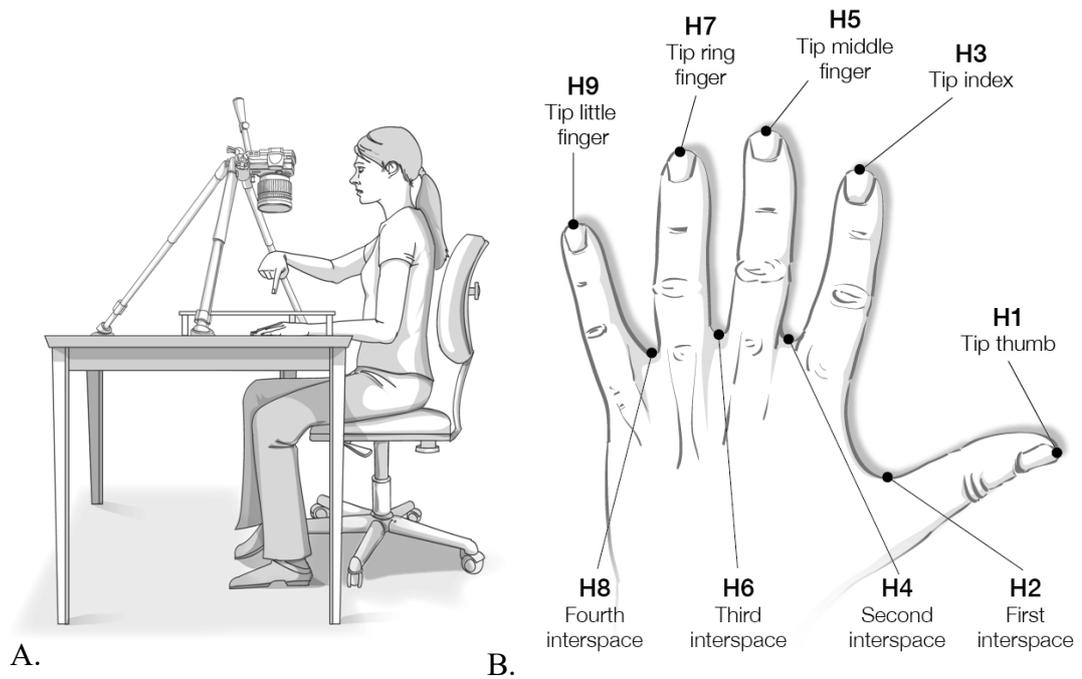


Figure 6.2 Hand task.

Representation of hand apparatus (A) and hand landmarks (B).

6.2.2.1.3 Face apparatus and procedure

The face localisation task reproduces the one included in Chapter 3. Briefly, participants were sat in front of a vertical Perspex board sustained by two metal post of 20 centimetres each. A chin rest was positioned before the board, onto which participants rested their head (see Figure 6.3A). Whilst keeping their eyes closed, they were required to point to 11 landmarks, read aloud in random order, by using their right index finger (see Figure 6.3B). A remote-controlled camera (Nikon D3200) was positioned at a 1 metre distance from the board, with its focus centred in the middle of the board. The camera was used to take pictures of each single pointing response. Each landmark was requested three times; hence, there was a total of 33 pictures for each face task performed.

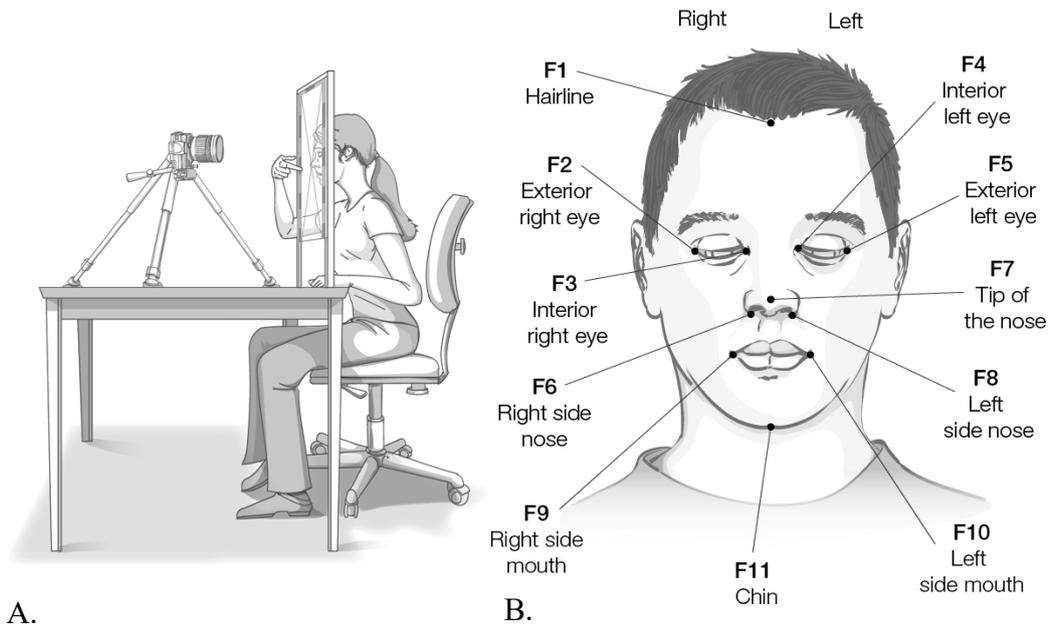


Figure 6.3 Face task.

Face apparatus (A) and face landmarks requested (B). Figure from Mora et al. 2018.

6.2.2.1.4 tDCS protocol

A battery-driven current stimulator (NeuroConn GmbH, Germany) was used to administer the cathodal tDCS. Two saline-soaked sponge electrodes were used (cathodal stimulation electrode was 5 by 5 cm; reference electrode was 7 by 5 cm) to provide cathodal stimulation of 2 mA for 20 minutes. The smaller electrode was chosen to be the active one to provide more focalised stimulation (Costa et al., 2015). The fade in and fade out was set at 15 seconds each, and the stimulation was delivered offline. Previous studies have shown that 20 minutes of 2mA cathodal stimulation result in increased cortical excitability, effect that lasts for at least 120 minutes after stimulation (Batsikadze et al., 2013). LTP has being postulated for higher intensities and longer duration of cathodal tDCS (Batsikadze et al., 2013; Pirulli et al., 2014). This was explored in this study.

The location of the electrodes was arranged following the international 10-20 EEG system (Herwig, Satrapi, & Schönfeldt-Lecuona, 2003) and varied between two stimulation conditions. There were two experimental conditions: cathodal right SMG stimulation (experimental condition) and visual cortex (VC) stimulation (control condition). In SMG stimulation, the cathodal electrode was placed over area CP4, and the reference electrode was positioned in the left supraorbital area, typical location for somatosensory studies (Costa et al., 2015). This set up has already been used in previous studies successfully (e.g., Schaal, Pollok, & Banissy, 2017). For the VC stimulation, the cathodal electrode was placed on OZ, whilst the reference electrode remained in the same position as in SMG condition. This stimulation site was considered to be appropriate to avoid activation of somatosensory or parietal cortices. Participants were naïve to stimulation conditions. In order to illustrate this montage, simulation modelling of the current densities were performed by using SimNIBS 3.1 software (Saturnino, Siebner, Thielscher, & Madsen, 2019) (see Figure 6.4 for electrodes placement and stimulation modelling).

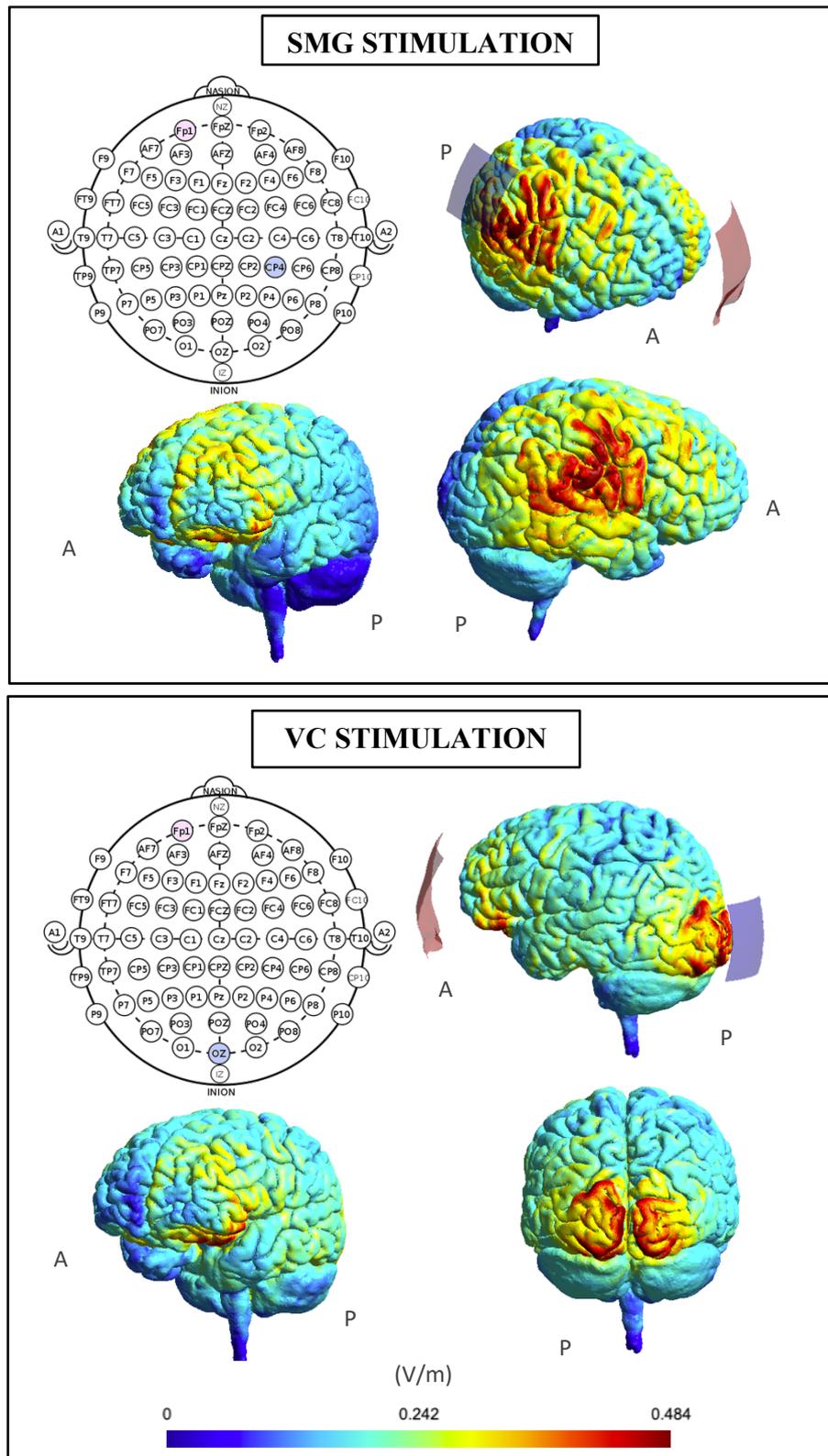


Figure 6.4. tDCS electrodes placement and simulation of tDCS electric field.

Electrode placement representing the location of the cathodal (blue) and reference (pink) electrodes for SMG and VC stimulations. Display of the electric field strength as electric field/current density (V/m) for the electrode setup used in Experiment 1. (P = posterior; A = anterior).

6.2.2.1.5 Experimental protocol

All participants received both experimental and control stimulations in two different sessions. They were randomly assigned to one of the conditions for the first session (Day 1), and to the other condition for the second session (Day 2), to avoid any potential order or practice effects. There was a gap of more than 48 hours between testing sessions as per safety conventions (Nitsche et al., 2008). The total current density for both sessions under active electrode was of 0.08 mA cm^{-2} ($2 \text{ mA}/25 \text{ cm}^2$) and 0.057 mA cm^{-2} ($2 \text{ mA}/35 \text{ cm}^2$) under the reference electrode, as per agreed safety parameters and previous studies (Batsikadze et al., 2013; Nitsche et al., 2008).

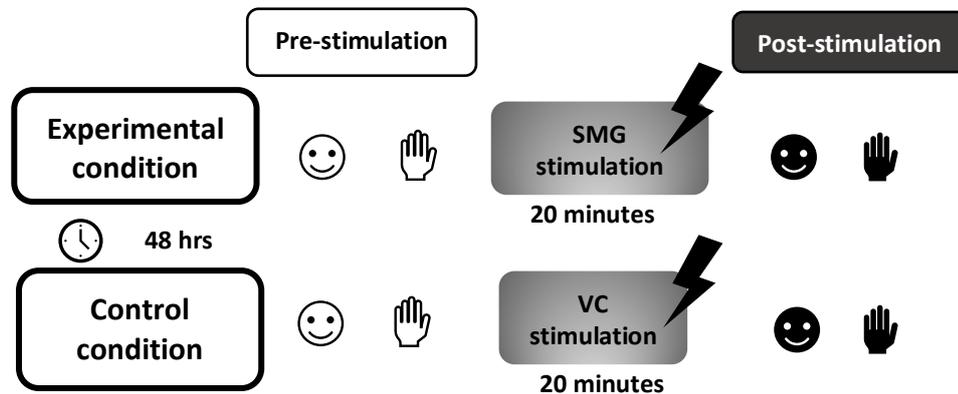


Figure 6.5 Schematic representation of experimental procedure in Experiment 1A.

There were two conditions (experimental and control). There was a gap of at least 48 hours between sessions. The smiley face represents the face task, whilst the hand represents the hand task. Unfilled body parts represent the body task before stimulation, whereas filled ones represent the tasks after stimulation. A filled lightning means active stimulation.

Each participant performed the face and hand localisation task twice: once before stimulation, and once after, in two separate days. Thus, they performed the localisation tasks four times in total for each body part (a total of 132 trials for the face, and a total of 108 for the hand).

6.2.2.1.6 Visuo-spatial task

The right SMG has been linked to attentional processes (e.g., see Danckert & Ferber (2006) for a revision). Hence, a measure of attentional bias was introduced to consider the effects of stimulation and disentangle any influences in the body representation tasks. For this, participants performed a horizontal line bisection task, before and after stimulation. The general population overestimate the left hemispaces, with a tendency to present a leftward error in line bisection (Porac, Searleman, & Karagiannakis, 2006), an effect named pseudoneglect (Bowers & Heilman, 1980). Explanations of this effect attribute a central role on attentional control to the right hemisphere, and in particular to connectivity and activation asymmetries (De Schotten et al., 2011).

Seventeen horizontal lines were presented, varying in length between 7.4 – 15.9 cm long, in the centre of an A4 paper. Each sheet was placed on the table in front the participant who was then asked to indicate the mid-point of each line. This task was performed before and after stimulation, for both conditions.

6.2.2.1.7 General analyses

Borland C++ Builder (2007) was used to create a bespoke programme to process the images (as per previous chapters). Pixel units were converted into centimetres, and the x and y coordinates of each landmark's location and each pointing response were computed. With this data, distances between pairs of landmarks were calculated, to obtain the real size of body features (e.g., eyes) and the perceived size for each. Lastly, the percentage of under/overestimation was calculated for each, as in previous studies (e.g., Longo & Haggard, 2012).

For the hand, the distance between the index and little fingers' interspaces was calculated as a measure of hand width, whilst the length of fingers was calculated as

the distance between each fingertip and its adjacent finger interspace (see Figure 6.6). For the face, as in Chapter 3, the width of five different facial features were considered: right eye, left eye, between eyes, nose and mouth. Further, the overall face length was calculated by taking the distance between the middle of the hairline and the chin (see Figure 6.6).

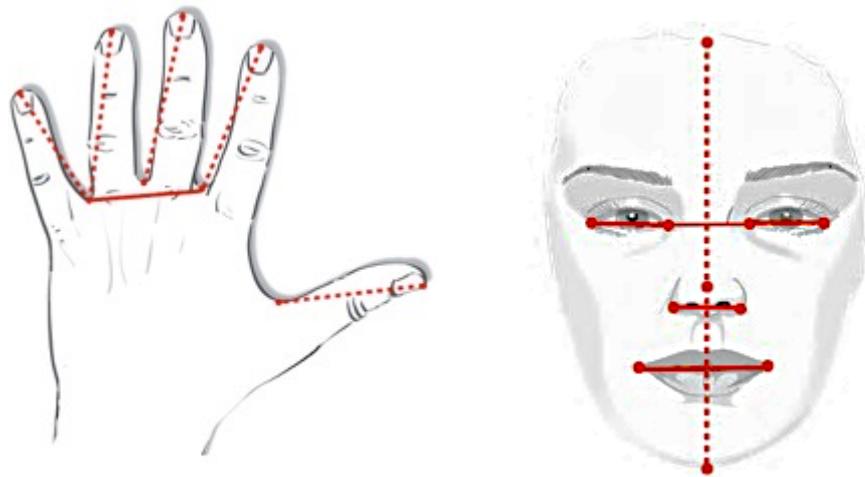


Figure 6.6. Distances between pairs of landmarks for the hand and face.

Widths considered for face features (right eye, between eyes, left eye, nose, mouth) and hand in continuous line; and lengths considered for the face and hand in dotted lines.

6.2.2.1.8 Statistical analyses

The representation of the left hand was considered first, followed by the face. The distortion of size (length or width) was initially tested for significance against zero via one-sample t-tests. Mixed-model ANOVAs were then used to investigate the differences in size representation of length and width in each experiment, comparing the before and after stimulation representation for each condition. Follow-up analyses were carried out for significant interactions by means of Bonferroni corrected t-tests. Lastly, in order to assess the potential effect of stimulation on visuo-spatial processing,

the biases in the line bisection task before and after stimulation conditions were compared via Bonferroni corrected pairwise comparisons.

6.2.2.2 Results

6.2.2.2.1 Hand representation

Finger lengths

The length of fingers was, overall, underestimated in both pre-stimulation conditions (see Figure 6.7). Participants showed an underestimation of -11.77% (SD = 14.46) pre-SMG stimulation, distortion that was significant [$t(15) = -3.26, p = .005, d = .81$]. Similarly, participants underestimated the length of their fingers before VC stimulation (M = -6.76%, SD = 20.27), but this distortion was not significant at baseline [$t(15) = -1.33, p = .2, d = .33$]. Differences between pre-stimulation conditions were not significant [$t(15) = -1.25, p = .23, d = .31$].

A 2 x 5 x 2 mixed-model ANOVA (Time, Fingers and Stimulation) was run to investigate differences between conditions. The ANOVA did not reveal significant differences for the main effect Time [$F(1,15) = 2.51, p = .13, \eta^2 = .14$] or Stimulation [$F(1,15) = .62, p = .45, \eta^2 = .04$]. The main effect Fingers was significant [$F(4,60) = 6.58, p < .001, \eta^2 = .31$], indicating differences in the degree of distortion per finger. Pairwise Bonferroni-corrected comparisons revealed differences between the thumb and little finger ($p = .03, \text{mean difference} = 20.89$), confirming the little finger was the most distorted. There was also a trend between the thumb and the ring finger ($p = .06, \text{mean difference} = 16.4$), being the thumb perceived more accurately. No interactions were significant (all $ps. > .05$).

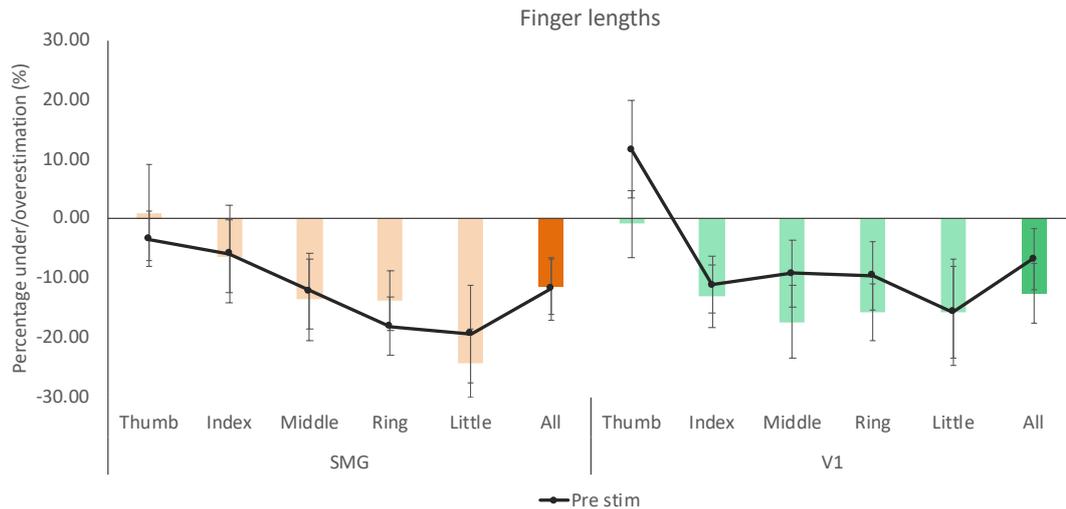


Figure 6.7. Finger lengths Experiment 1A.

Graph representing the percentage of finger length under/overestimation (%) in SMG and VC stimulation conditions. The black lines represent the size distortion before stimulation, whilst bars represent performance after, for each type of stimulation. Error bars represent the Standard Error of the Mean.

Hand width

Pre-stimulation, there was a 38.44% (SD = 31.65) overestimation in the SMG condition, distortion that was significant [$t(15) = 4.86, p < .001, d = 1.22$]. In the pre-VC condition, there was also significant overestimation of hand width (M = 46.19%, SD = 19.71; [$t(15) = 5.48, p < .001, d = 1.37$]). Differences between conditions were not significant at baseline [$t(15) = -1.12, p = .28, d = .28$].

A repeated measures ANOVA (Time by Stimulation) did not show any significant effects of Time [$F(1,15) = .89, p = .36, \eta^2 = .06$]; Stimulation [$F(1,15) = 1.45, p = .25, \eta^2 = .09$], or of Time by Stimulation interaction [$F(1,15) = .17, p = .69, \eta^2 = .01$].

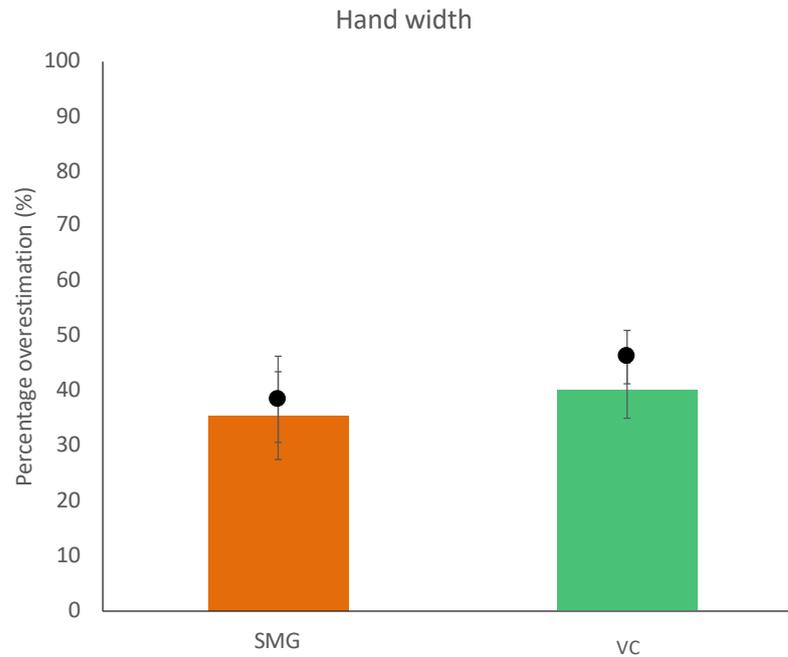


Figure 6.8. Hand width Experiment 1A.

Graph representing the percentage of hand width overestimation (%) in SMG and VC stimulation conditions. The black dots represent the size distortion before stimulation, whilst bars represent performance after, for each type of stimulation. Error bars represent the Standard Error of the Mean.

6.2.2.2.2 Face representation

Face length

Participants perceived the length of their face quite accurately in both pre-stimulation conditions, only showing a small non-significant overestimation before SMG stimulation ($M = .32\%$, $SD = 9.43$; [$t(15) = .14$, $p = .89$, $d = .03$]), and before VC stimulation ($M = .2\%$, $SD = 11.71$; [$t(15) = .07$, $p = .95$, $d = .02$]). Differences between pre-stimulation conditions were not significant [$t(15) = .05$, $p = .96$, $d = .03$].

Differences in the effects of stimulation were tested via a 2 (Time) x 2 (Stimulation) repeated measures ANOVA. No significant differences were found for the main effect Time [$F(1,15) = 3.12$, $p = .1$, $\eta^2 = .17$]; Stimulation [$F(1,15) = .001$, $p = .98$, $\eta^2 < .001$], or for the Time by Stimulation interaction [$F(1,15) = .002$, $p = .96$, $\eta^2 < .001$].

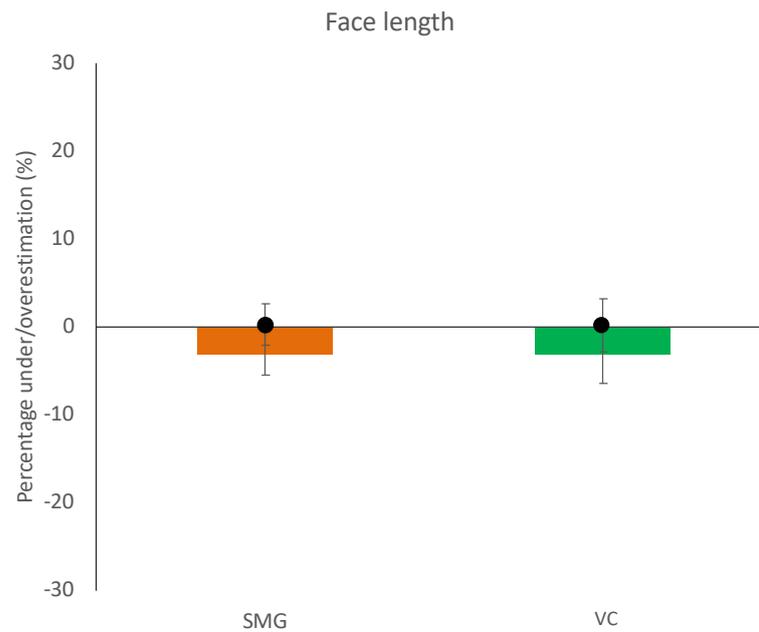


Figure 6.9. Face length Experiment 1A.

Graph representing the percentage of face length under/overestimation (%) in SMG and VC conditions. The black dots represent the size distortion before stimulation, whilst bars represent performance after stimulation. Error bars represent the Standard Error of the Mean.

Face width

On average, participants perceived their face features much wider than their real size, both in pre-SMG condition ($M = 55.07\%$, $SD = 29.92$) and pre-VC stimulation condition ($M = 57.12\%$, $SD = 20.35$). The distortion in pre-SMG stimulation was significant [$t(15) = 7.36$, $p < .001$, $d = 1.84$], as it was pre-VC [$t(15) = 11.23$, $p < .001$, $d = 2.81$]. The distortions were equivalent at baseline between both conditions [$t(15) = -.41$, $p = .69$, $d = .1$].

A Time (2) x Stimulation (2) x Features (5) repeated measures ANOVA was run to identify any differences in performance across conditions. In this case, the main effect Time was significant [$F(1,15) = 12.93$, $p = .003$, $\eta^2 = .46$], whereas the main effect Stimulation was not [$F(1,15) = 1.36$, $p = .26$, $\eta^2 = .08$]. There was also a

significant effect of Features [$F(4,60) = 5.46, p = .001, \eta^2 = .27$], which indicated different magnitude of distortions across facial features. Bonferroni corrected pairwise comparisons showed that the nose was significantly more overestimated than the space between the eyes ($p = .03$, mean difference = 42.28). There was also a trend between the nose and mouth ($p = .06$, mean difference = 18.57). More importantly, the Time by Stimulation interaction was significant [$F(1,15) = 10.52, p = .005, \eta^2 = .41$], indicating differential effects of stimulation. Bonferroni-corrected pairwise comparisons confirmed that this interaction was due to a significant reduction of face width after VC stimulation [$t(15) = 4.86, p < .001, d = 1.21$], and not due to the effects of SMG [$t(15) = .39, p = .7, d = .1$]. Differences in width perception after stimulation conditions (between post-VC and post-SMG) showed a trend [$t(15) = 2.07, p = .056, d = .52$] (see Figure 6.10 for graphs and the face maps). Overall, the distortion of the width of face features was reduced after VC stimulation, relative to the perceived size before stimulation. No other interactions in the ANOVA were significant (all $ps > .05$).

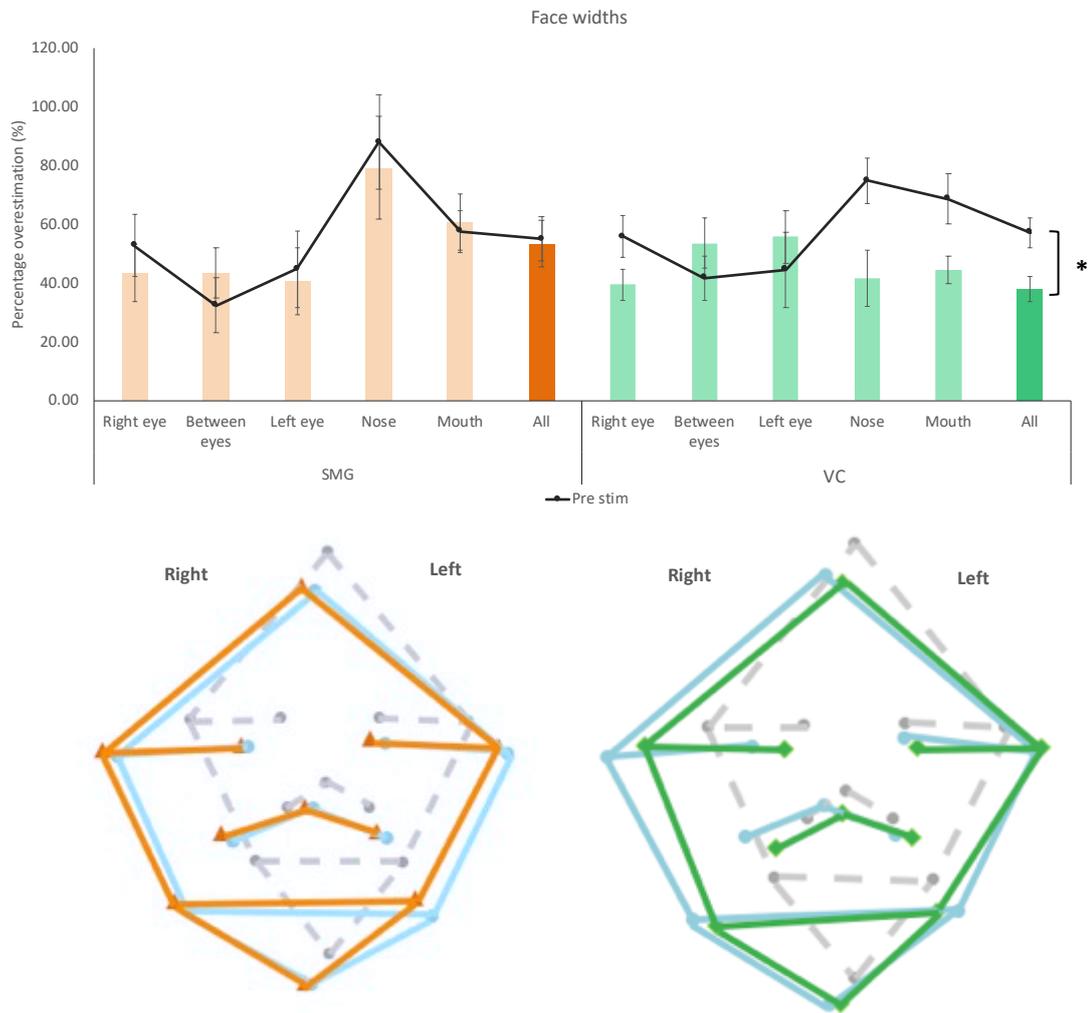


Figure 6.10. Face widths and face maps in Experiment 1A.

The graph represents the percentage of overestimation (%) of the width of facial features before and after SMG and VC stimulations. The maps below depict the face maps averaged across participants for each stimulation condition. Grey dotted lines represent the real size of the face, whilst the blue clear lines depict the face representation before stimulation. Orange lines depict the perceived face representation after SMG stimulation, whereas green lines represent perceived face size after VC stimulation.

6.2.2.2.3 Visuo-spatial task

A small leftwards shift (pseudoneglect) was found pre-stimulation for both conditions, which was significant before SMG stimulation ($M = -.24$ cm, $SD = .27$; [$t(15) = -3.57$, $p = .003$, $d = .89$]) and also before VC stimulation ($M = -.2$ cm, $SD = .24$; [$t(15) = -3.38$, $p = .004$; $d = .84$]). A repeated measures ANOVA (Time (2) x

Stimulation (VC and SMG) was run to identify any differences in the leftwards shift due to stimulation. No significant effect of Time [$F(1,15) = 3.62, p = .08, \eta^2 = .19$], Stimulation [$F(1,15) < .001, p = 1, \eta^2 < .001$], or Time by Stimulation interaction [$F(1, 15) = 3.15, p = .096, \eta^2 = .17$] were found.

6.2.2.3 Preliminary discussion

In this first experiment, the role of the SMG in the metric representation of the left hand and face was investigated. Cathodal stimulation was administered to the same group of participants, in two different stimulation sessions. In one session, the right SMG was stimulated (experimental condition), whereas the VC was targeted in the other session, which was considered the control condition. The localisation task for the left hand and face was performed before and after the stimulation. Unexpectedly, results did not show any modulation on the perceived size of the left hand or face after SMG stimulation. Previous studies had showed the relevance of inferior parietal lobe (IPL) in the metric representation of the body. For example, modulation of the length of the arm was achieved by targeting the angular gyrus (Spitoni et al., 2013). The parietal structures have been presented as areas responsible of the metrics of the body (Longo et al., 2010) but, more specifically, with the integration of different types of multisensory information (Spitoni et al., 2013). Indeed, these areas are critical to integrate inputs from vision and somatosensation in a coherent body representation (Avillac et al., 2005; Lewis & Van Essen, 2000). In light of this, it was expected that activation of SMG through tDCS would modulate the representation of the size of the body, but this was not the case. Similarly, other studies have not been able to find modulation of size representation when targeting parietal areas. For instance, tDCS of PPC in patients with phantom limb does not change its size (Bolognini et al., 2013), whereas hand size modulation is not achieved after rTMS of the IPL (Giurgola et al.,

2019). These results indicated that perceptual size representation of the body may be more involved with primary somatosensory components, rather than higher order representations in the parietal cortex.

Instead, the effect of stimulation was found when targeting VC area, which may be associated to the task used and the different primacy of specific sensory modalities. As presented in Chapter 4, mental imagery appears to be of more relevance in the localisation task, rather than somatosensation (Ganea & Longo, 2017). Tasks recruiting an image of this model will invoke a visual representation in some degree (Darling, Uytman, Allen, Havelka, & Pearson, 2015). Indeed, visual information about the body also influences its size representation (Azañón, Tamè, Maravita, Linkenauger, Ferrè, Tajadura-Jiménez, & Longo, 2016; Peviani et al., 2019). For example, seeing a magnified hand does cause larger motor evoked potentials (MEPs) in the primary motor cortex due to enlargement of the cortical representation (Ambron, White, et al., 2018). Hence, visual information modulates cortical sensorimotor processing (Taylor-Clarke et al., 2002), in the same way that somatosensory information modulates vision (Lunghi, Lo Verde, & Alais, 2017). Further, mental proprioceptive imagery has been postulated as influencing the localisation task (Ganea & Longo, 2017), which shares many characteristics and structures with vision (Ganis, Thompson, & Kosslyn, 2004; Palermo et al., 2013). In other words, there may be a need to invoke a mental image of the body part being considered when performing the location task, as participants are blindfolded (Ganea & Longo, 2017). This process engages the visual cortex (Kosslyn, Thompson, Klm, & Alpert, 1995). Therefore, Experiment 1A emphasized the visual nature of the body model.

However, it is still possible that other factors are involved, such as practice. It would be of interest, then, to compare the performance in the task against a Sham

stimulation condition, in which active stimulation is not present. If practice has an effect, improved performance would be expected post-Sham stimulation. In Experiment 1B, performance in VC condition was compared with performance in a Sham condition that was administered in a second group of participants that were specifically recruited.

6.2.3 Experiment 1B: the role of the primary visual cortex on the size of the hands and face

In this second experiment, a new group was recruited in order to test activate stimulation (VC) against sham stimulation.

6.2.3.1 Method

6.2.3.1.1 Participants

The experimental group included the same participants presented in Experiment 1A. 11 participants were recruited as control group (7 females and 4 males), 20 - 39 years of age. Their demographic details are included in Table 6.1.

Table 6.1. Demographic details for experimental and control groups.

		Experimental group (N = 16)	Control group (N = 11)
Age	Mean	24.06	25.73
	SD	5.26	5.14
	Range	19-39	19-39
Formal education (years)	Mean	16.06	16.73
	SD	1.88	2.65
	Range	14-21	13-21
Edinburgh Handedness Inventory	Mean	.89	.91
	SD	.17	.16
	Range	.36-1	.5-1

In the control group, one participant was ambidextrous (score = .5), whereas all others were right-handed. Groups did not differ on handedness [$t(25) = -.34, p = .74, d = .13$], or education [$t(25) = -.77, p = .45, d = .29$].

Participants included in the control group were also informed about the safety procedures for brain stimulation, and did not have a history of neurologic or psychiatric disorders; did not have a heart pacemaker, cochlear implant, aneurysm clip or any other electronic device or metallic object within their body; did not have a personal or family history of epileptic fits or seizures; were not pregnant and had not taken part in any other stimulation study within the previous 48 hours (Nitsche et al., 2008).

6.2.3.1.2 tDCS protocol and experimental procedure

The control group received sham stimulation only in one session (Day 1). The setup was identical to the experimental conditions. In this condition, the stimulation was stopped after 15 seconds. Previous studies have shown how this short period of stimulation elicits the sensation of being stimulated, but does not cause changes in performance or can be differentiated from real stimulation by participants (Gandiga, Hummel, & Cohen, 2006). As in previous group, participants performed the face and hand tasks before and after stimulation. Thus, they performed the face and hand tasks twice. There were a total of 66 trials for the face, and a total of 54 for the hand) (see Figure 6.11 for the representation of the experiment procedure).

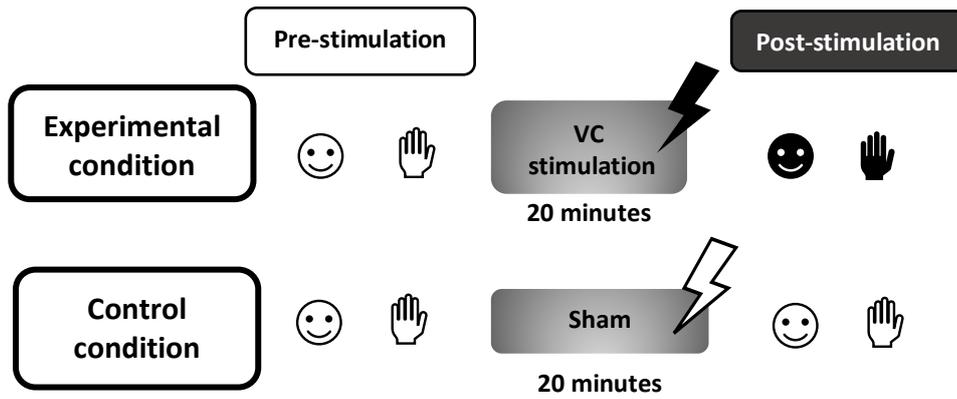


Figure 6.11. Experimental procedure in Experiment 1B.

There were two conditions (experimental and control). The smiley face represents the face task, whilst the hand represents the hand task. Unfilled body parts represent the body task before stimulation, whereas filled ones represent the tasks after stimulation. A filled lightning means active stimulation.

6.2.3.1.3 General analyses

These analyses follow the same pattern than the one described in Experiment 1A.

6.2.3.1.4 Statistical analyses

Statistical analyses follow the same pattern as in Experiment 1A.

6.2.3.2 Results

6.2.3.2.1 Hand representation

Finger lengths

Participants in the Sham group underestimated fingers by -12.01% (SD = 17.65), distortion that was significant [$t(10) = -2.26, p = .048, d = .68$]. There were no differences at baseline between VC stimulation and Sham groups [$t(25) = .7, p = .49, d = .28$] (see Figure 6.12).

A mixed-model ANOVA (Time, Fingers and Stimulation as factors) showed no differences between groups due to Time [$F(1,25) = 1.26, p = .27, \eta^2 = .05$], or Stimulation [$F(1,25) = .12, p = .73, \eta^2 = .005$]. The main factor Fingers was significant [$F(2.98, 74.44) = 9.03, p < .001, \eta^2 = .27$], indicating differences in the distortion of length for fingers. Pairwise Bonferroni-corrected comparisons revealed differences between the thumb and index ($p = .003$, mean difference = 16.79), thumb and middle ($p = .001$, mean difference = 19.09), thumb and ring ($p = .001$, mean difference = 20.29), and thumb and little ($p = .05$, mean difference = 15.99). There were no significant interactions in the main ANOVA (all $ps > .05$). These results indicate there was a lack of stimulation effect on the representation of the left hand, overall.

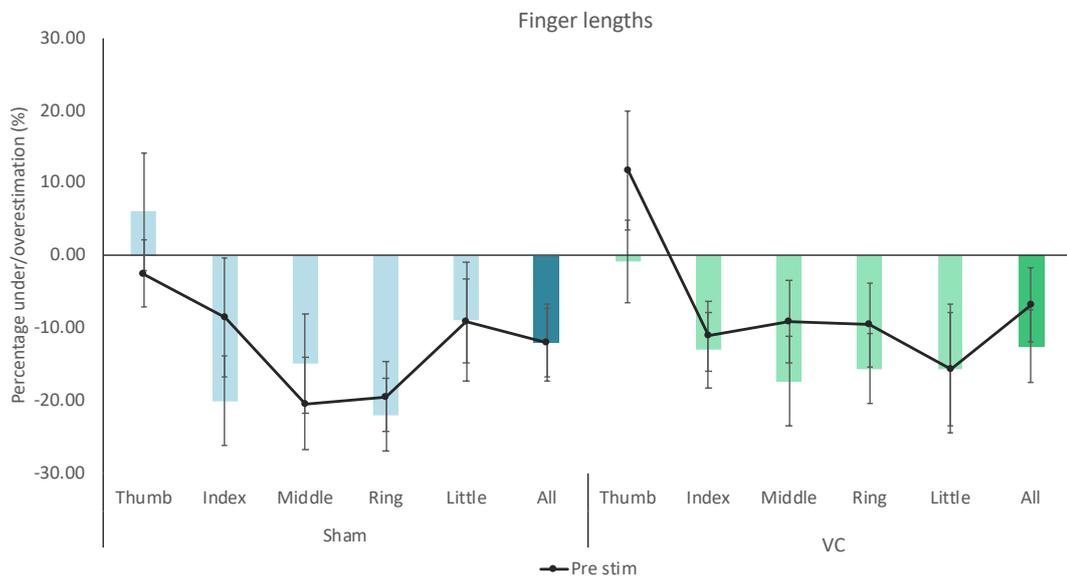


Figure 6.12. Finger lengths in Experiment 1B.

Graph representing the percentage of finger length under/overestimation (%) in VC stimulation and Sham. The black lines represent the size distortion before stimulation, whilst bars represent performance after, for each type of stimulation. Error bars represent the Standard Error of the Mean.

Hand width

On average, participants perceived their left hand overestimated in width at baseline ($M = 50.14\%$, $SD = 21.2$). This distortion was significant [$t(10) = 7.84$, $p < .001$, $d = 2.37$]. Differences between VC stimulation and Sham groups did not reach significance before stimulation [$t(25) = -.5$, $p = .62$, $d = .19$] (see Figure 6.13). The mixed-model ANOVA with Time (pre and post) and Stimulation (VC stimulation and sham) as factors did not identify significant differences due to Time [$F(1,25) = .21$, $p = .65$, $\eta^2 = .01$]; Stimulation [$F(1,25) = 2.96$, $p = .1$, $\eta^2 = .11$]; or Time by Stimulation interaction [$F(1,25) = 2.8$, $p = .11$, $\eta^2 = .1$]. In this case, there were also no effects of stimulation in the perceived width of the left hand.

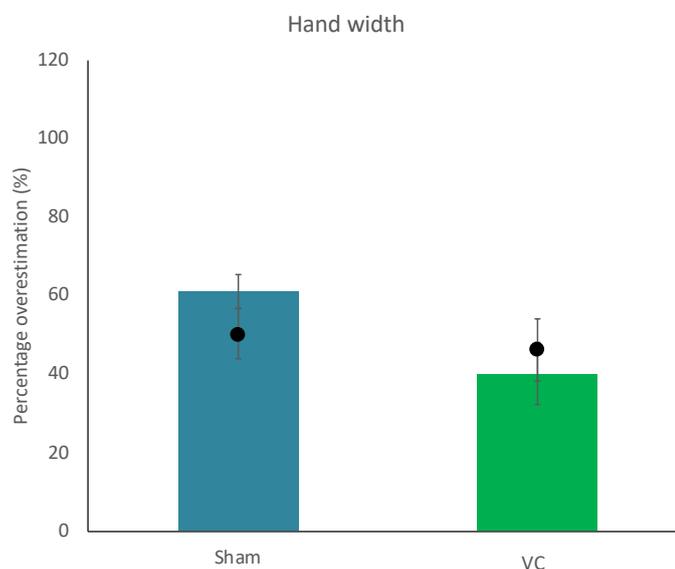


Figure 6.13. Hand width in Experiment 1B.

Graph representing the percentage of hand width overestimation (%) for VC stimulation and Sham. The black dots represent performance before stimulation, whereas the bars represent the performance after. Error bars represent Standard Error of the Mean.

6.2.3.2.2 Face representation

Face length

In this case, participants in the Sham group showed a small overestimation of the length of the face ($M = 2.12\%$, $SD = 26.06$). This distortion was not significant [$t(10) = .27$, $p = .79$, $d = .08$]. Differences in size perception between VC group and Sham group were not significant at baseline [$t(25) = -.26$, $p = .8$, $d = .09$] (see Figure 6.14). The mixed-model ANOVA did not identify any significant effect of Time [$F(1,25) = 2.41$, $p = .13$, $\eta^2 = .09$], Group [$F(1,25) = .07$, $p = .8$, $\eta^2 = .003$], or Time by Group interaction [$F(1,25) = .01$, $p = .94$, $\eta^2 < .001$]. However, considering the extremely small distortion found in length prior stimulation, the lack of significant effect may be due to ‘ceiling effects’ (Pirulli et al., 2014).

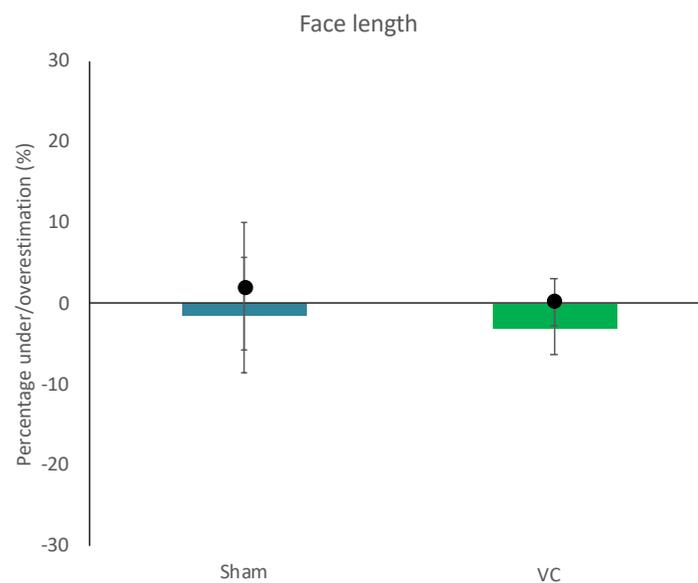


Figure 6.14. Face length in Experiment 1B.

Graph representing the percentage of face length under/overestimation (%) in Sham and VC conditions. The black dots represent the size distortion before stimulation, whilst bars represent performance after stimulation. Error bars represent the Standard Error of the Mean.

Face width

There was an average 44.36% (SD = 27.23) face width overestimation in the Sham group. This distortion was significant [$t(10) = 5.4, p < .001, d = 1.63$]. Differences between VC stimulation and Sham groups were not significant at baseline [$t(25) = 1.39, p = .17, d = .53$] (see Figure 6.15). The Times (2) by Landmarks (5) by Stimulation (2) mixed-model ANOVA revealed a significant main effect of Time [$F(1,25) = 9.54, p = .005, \eta^2 = .28$], as there was a significant reduction of the width distortion after stimulation. The main effect Stimulation was instead not significant [$F(1,25) = .24, p = .63, \eta^2 = .01$], whilst the Landmarks factor was [$F(4,100) = 4.45, p = .002, \eta^2 = .15$], indicating differences in the size perception of face features. Pairwise Bonferroni-corrected comparisons confirmed that the ‘between eyes’ width was less distorted than the nose ($p = .04$, mean difference = 27.28). No other comparisons reached significance (all $ps. > .05$). Further, the Time by Stimulation interaction was significant [$F(1,25) = 6.49, p = .02, \eta^2 = .21$]. This result indicated different effects of the type of stimulation on face width distortion. Subsidiary pairwise Bonferroni-corrected t-tests revealed a significant effect of stimulation in VC group [$t(15) = 4.85, p < .001, d = 1.21$], confirming it was effective in reducing the distortion of width. Instead, there was no significant improvement in the Sham group [$t(15) = .31, p = .76, d = .09$]. Differences between post-stimulation conditions did not reach significance [$t(14.11) = -.45, p = .66, d = .19$] (equality of variances not assumed).

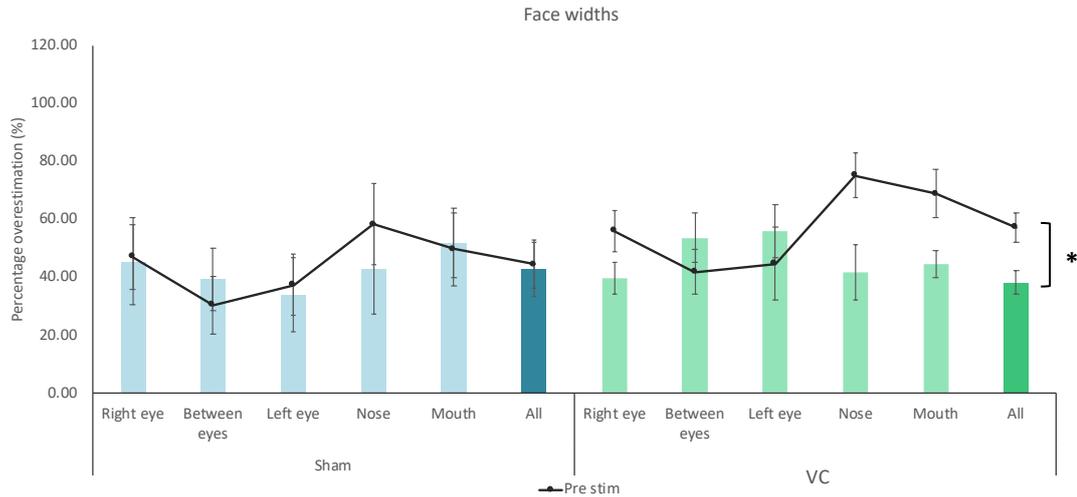


Figure 6.15. Face width in Experiment 1B.

Graph representing the percentage of overestimation (%) for the width of face features for Sham and VC conditions. The black lines represent the size distortion before stimulation, whilst bars represent performance after, for each stimulation condition. Error bars represent Standard Error of the Mean. The * represents significant differences.

6.2.3.2.3 Visuo-spatial task

There was also a leftwards shift in the Sham group pre-stimulation, which was not significant ($M = -.05$, $SD = .29$; [$t(10) = -.55$, $p = .6$, $d = .16$]). Differences in the leftwards shift between the VC stimulation group and Sham group prior stimulation were not significant [$t(25) = -1.52$, $p = .14$, $d = .58$]. After stimulation, there was a small rightwards shift for the Sham group ($M = .04$, $SD = .27$), which was again not significant [$t(10) = .47$, $p = .65$, $d = .14$]. Lastly, differences between pre and post stimulation shift in the Sham group were not significant [$t(10) = -.87$, $p = .4$, $d = 2.62$].

6.2.4 Discussion

This study primarily sought to investigate the involvement of the supramarginal gyrus (SMG) in the body model of the left hand and face. For this, 2mA cathodal tDCS was applied. The cathodal tDCS protocol used in this experiment is

known to produce an increase of neural activity, equivalent to the effects of anodal tDCS, which is effective in inducing cortical facilitation (Batsikadze et al., 2013). In Experiment 1A, this stimulation was targeted on the right SMG, which is involved in the metric representation of the body (Committeri et al., 2018, 2007; Spitoni et al., 2013), whereas the primary visual cortex (VC) was stimulated as active control condition. No differences were found in the representation of the size of the body between pre and post stimulation after SMG stimulation, but there was modulation of the representation after VC stimulation instead. These results directly pointed at the functional properties of the visual cortex (VC) in dealing with the body model. Experiment 1B then confirmed that these results were due to the specific effect of stimulation in the primary visual cortex, when results were compared with a Sham control group. Crucially, the evidence provided indicates that stimulation of VC systematically ameliorates the distortion of the width of face features, but not of the hands. These results seem to partially confirm the key role of the primary visual cortex for some aspects of the body model.

The modulation of face size due to VC stimulation may be due to the reliance on proprioceptive imagery in this task. This has been defined as the “mental imagery for proprioception, that is the ability to imagine one’s limbs in a different posture or location than they are actually in” (Ganea & Longo, 2017, p. 41). Although the locational task may appear to mainly rely on proprioceptive or somatosensory information (Longo, 2014), recent studies have highlighted the relevance of mental imagery instead (Ganea & Longo, 2017; K. D. Stone et al., 2018). In fact, online representations (constructed moment by moment) rely more on sensory information, whilst offline (‘what the body looks like’, such as size representation in this task) do not (Carruthers, 2008). Indeed, the memory of our body is pictorial (Kaplan, Rossell,

Enticott, & Castle, 2013). In other words, a model of the body is stored in the brain and includes the relative metric components of body parts, which are distorted (Ganea & Longo, 2017; Longo et al., 2012; K. D. Stone et al., 2018), in the same way that mental images preserve metric information (Kosslyn, Ball, & Reiser, 1978). The recruitment of the mental image of a body part activates visual areas. For example, visual discrimination of neutral facial expressions engages visual areas, but not somatosensory ones, in contrast to emotional expressions (Sel, Forster, & Calvo-Merino, 2014). This supports the idea of recruitment of visual areas when assessing one's self-face representation, which was requested in neutral expression. Moreover, mental imagery and perception share common representations (Chang, Nemrodov, Lee, & Nestor, 2017). For instance, studies using rTMS over the area 17 have effectively deactivated the visual cortex disrupting not only visual, but also mental image processing (Kosslyn et al., 1999). On the inverse, here the stimulation of VC through tDCS may be influencing mental imagery processing, supporting the hypothesis that the localisation task may rely on a stored mental image of the body. Given that imagery instigate less activation than visual perception (O'Craven & Kanwisher, 2000), tDCS over the visual areas should increase this activation, supporting the recruitment of a more accurate mental image of the face.

Interestingly, this modulation was only seen in the width dimension. As previously postulated, width is more variable throughout adulthood (Hashimoto & Iriki, 2013), and perhaps more susceptible to modulation. Moreover, in the case of the face, length perception is more accurate, with little room for improvement.

However, a question remains. Why would the stimulation of visual areas only have an effect on the face, and not on the hands? Although we rarely see our faces, it may well be that faces are constructed more visually than hands. Indeed, faces have

been defined as “complex visual stimulus” (Sliwinska, Bearpark, Corkhill, McPhillips, & Pitcher, 2019, p. 3), which are learned and stored as pictorial representations (Chang et al., 2017; Keyes, 2012). Also, we see other people’s faces all the time, and this visual experience of faces may help in the construction of our own face representation, as seen for other body parts (K. D. Stone et al., 2018). Even though direct visual exposure to our own face may not be as frequent as seeing others’ faces, we are experts in recognising our own face over others, due to an enhanced perceptual processing of self-face features (Keenan et al., 1999; Sui & Han, 2007). Indeed, self-face representations are highly robust (Keyes & Brady, 2010), and constructed by “extensive visual experience” (Keyes, 2012, p. 11). In comparison with other people’s faces, we see our face at close range, and this has helped fine-tuning featural and configural processing skills for self-face perception, which help constructing the stored representation (Keyes, 2012). Moreover, this mental representation of our face needs to be constructed in such a way that allows certain plasticity to accommodate changes over time (Tajadura-Jiménez et al., 2012), which perhaps explains the distortions found in healthy perception. Being such a visual stimulus, it is possible that it is more susceptible to VC stimulation than the hands.

Following these findings, it may be that hand representation relies less on visual imagery. In other words, recruitment of the face image relies more in visual imagery, whereas for hands, there are other components that are of relevance. For instance, somatosensory tactile stimulation may be found to elicit a modulation of size instead in the case of hands. The link between somatosensation and body image is quite straightforward. For example, complete deafferentation through anaesthesia causes an enlargement of the perceived size of the body (Gandevia & Phegan, 1999; Türker et al., 2005), in the same way that disruption of the cortical activity in somatosensory

areas through rTMS does (Giurgola et al., 2019). Moreover, repetitive cutaneous stimulation has been shown to produce a similar effect, even though less reliably (Gandevia & Phegan, 1999). Indeed, afferent tactile information can and will affect higher precepts of body representation (Serino & Haggard, 2010). It follows that, if reduction of somatosensory information distorts the body, the increase should have the opposite effect. With a similar viewpoint, previous studies had postulated and confirmed that repetitive somatosensory input to a specific body part should have the opposite effect than interruption of tactile feedback in motor performance. That is, reduced tactile input through anaesthesia affects the control of finger movements (Rabin & Gordon, 2004), whereas increases should improve them through enhanced cortical function (Wu, Seo, & Cohen, 2006; Wu, van Gelderen, Hanakawa, Yaseen, & Cohen, 2005). With this ethos, increases of somatosensory information should improve size perception. In Experiment 2 the size modulation of hands and face will be explored instead through passive sensory stimulation. For this, the size estimation task employed in Experiment 2 presented in Chapter 5, will be used.

6.3 Experiment 2: somatosensory modulation of left hand and face size representation through passive sensory stimulation

6.3.1 Introduction

Based on the use-dependent plasticity knowledge and multisensory integration principles (Baumard & Osiurak, 2019), sensory stimulation has been developed as a tool to induce perceptual learning and behaviour change without training (Beste & Dinse, 2013; Dinse et al., 2003). The modulation of perceptual functions is achieved by implementing the so-called coactivation protocol, in which repetitive synchronous stimulation is administered by a solenoid that simultaneously activates a large number of receptive fields (see Figure 6.16). This stimulation increases neural activity boosting

the somatosensory representation and eliciting plastic changes, mimicking what occurs after training or learning (Beste & Dinse, 2013; Pleger et al., 2001). This, in turn, improves sensorimotor functions, such as tactile spatial discrimination (see Figure 6.16) (Dinse, Gatica Tossi, Tegenthoff, & Kalisch, 2011; Dinse et al., 2003; Kalisch et al., 2008; Ladda et al., 2014; Pleger et al., 2001, 2003), or motor function after stroke (Wu et al., 2006). Moreover, the level of amelioration is strongly correlated with the degree of cortical reorganisation in the primary somatosensory cortex; that is, larger reorganisation commensurate to greater behavioural gains (Kalisch, Tegenthoff, & Dinse, 2007; Pleger et al., 2001, 2003). However, no studies have explored the attributes of sensory stimulation in body representation. With this objective in mind, passive sensory stimulation could prove to be a useful tool with this purpose. The aim here was then to study the potential modulatory effect of passive sensory stimulation and, in particular, vibration, in body size perception.

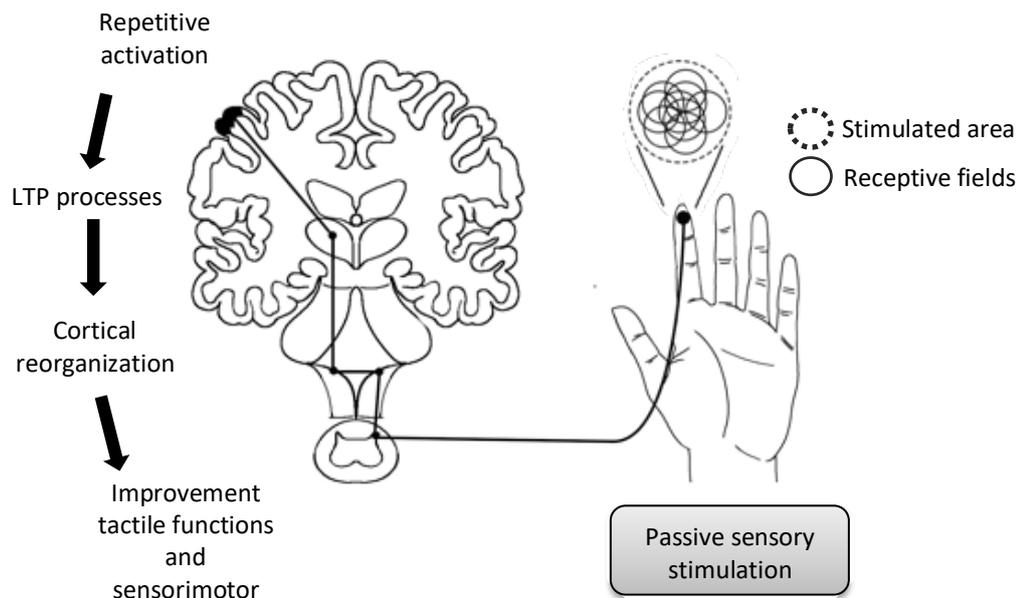


Figure 6.16. Passive sensory stimulation mechanisms.

Drawing representing the positioning of the vibration motor on the index finger and schema of the functional alterations in the somatosensory system that lead to the induction of plastic processes and behavioral/perceptual changes. Modified from Dinse et al. (2011).

6.3.2 Method

6.3.2.1 Participants

An a priori power analysis was run to determine the required sample size by using G* Power 3.1 (Faul et al., 2009). In this case, a power analysis based on an ANCOVA (2 covariates), with an average effect size f of 1.22 (as in Chapter 5, Experiment 2) was run. Alpha was set at 0.05 and power of 0.8. The adequate sample size obtained was 12.

A group of 30 healthy volunteers (20 females and 10 males) was recruited to take part in this study. Half of them ($n = 15$, 10 females and 5 males in each group) were randomly assigned to the face stimulation group, whilst the other half were part of the hand stimulation group (see Demographic information in Table 6.2). Groups did not differ in age [$t(28) = .33$, $p = .74$, $d = .12$] or formal education [$t(28) = -.59$, $p = .56$, $d = -.22$]. There were two left-handed participants in each group, as measured with the Oldfield questionnaire (Oldfield, 1971), and handedness did not differ between groups either [$t(28) = -.17$, $p = .86$, $d = -.06$].

Table 6.2. Demographic table.

Participants' characteristics for face stimulation and hand stimulation

		Face stimulation group	Hand stimulation group
		(N = 15)	(N = 15)
Age (years)	Mean	24.4	24.13
	SD	2.53	1.85
	Range	22 - 31	22 - 28
Education (years)	Mean	16.67	17
	SD	1.63	1.41
	Range	13 - 18	15 - 20
Edinburgh Handedness Inventory	Mean	.61	.65
	SD	.55	.59
	Range	-.89 - 1	-.89 - 1
Body Shape Questionnaire (BSQ)	Mean	64.6	75.13
	SD	23.37	24.32
	Range	36 - 103	49 - 123
Vividness of Visual Images Questionnaire (VVIQ)	Mean	57.6	59.2
	SD	7.46	8.83
	Range	46 - 74	45 - 76

6.3.2.2 Passive sensory stimulation protocol

The experimental portable device was used to deliver the passive sensory stimulation through circular vibration motors (Figure 6.17A) from Precision Microdrives Ltd (type 310-103). These were powered by an adjustable voltage supply built in-house (see picture of equipment in Figure 6.17B). It is crucial that stimulation targets/coactivates a large number of receptors (solenoid of around 8mm), as single-site stimulation (0.8mm² solenoid) has not been found to elicit any activation or perceptual changes (Pleger et al., 2003). Thus, in this study 10 mm sized vibration motors were used. Further, different areas were stimulated as single-finger stimulation has been shown not to extend effects to adjacent or contralateral fingers (Gandevia & Phegan, 1999). Synchronous stimulation was provided, as this is instrumental for multisite stimulation (Kalisch et al., 2007). Hence, a total of 8 motors were used for the face stimulation and 12 for the hand (see location of vibration motors in Figure 6.17C and D) that were attached with medical tape. The hand stimulation was administered in the dominant hand. The current (mA) was adjusted to control the frequency of the stimulation (see graph with motor performance characteristics in Figure 6.17E). High-frequency stimulation (over 10Hz) was delivered as this has been shown to elicit LTP of brain activity, associated with perceptual gains (Beste & Dinse, 2013). Frequencies higher than 50Hz are considered as vibration (Francis et al., 2000). The intensity of vibration was set individually at the highest level the participant could comfortably tolerate for a duration of 20 minutes, given that larger improvements in perceptual abilities seem to follow higher intensity of sensory stimulation (Beste & Dinse, 2013; Ladda et al., 2014; Schlieper & Dinse, 2012).

Participants were told the stimulation could be stopped at any time if they felt any discomfort. All participants were able to tolerate 20 minutes of stimulation. Some

habituation to the stimulation was observed halfway through the procedure as participants reported to feel a reduction of the intensity. After stimulation, participants experienced ‘vibration aftereffects’ for a few minutes, as reported in previous studies (Ladda et al., 2014); only one participant reported some discomfort after stimulation (numbness of the face).

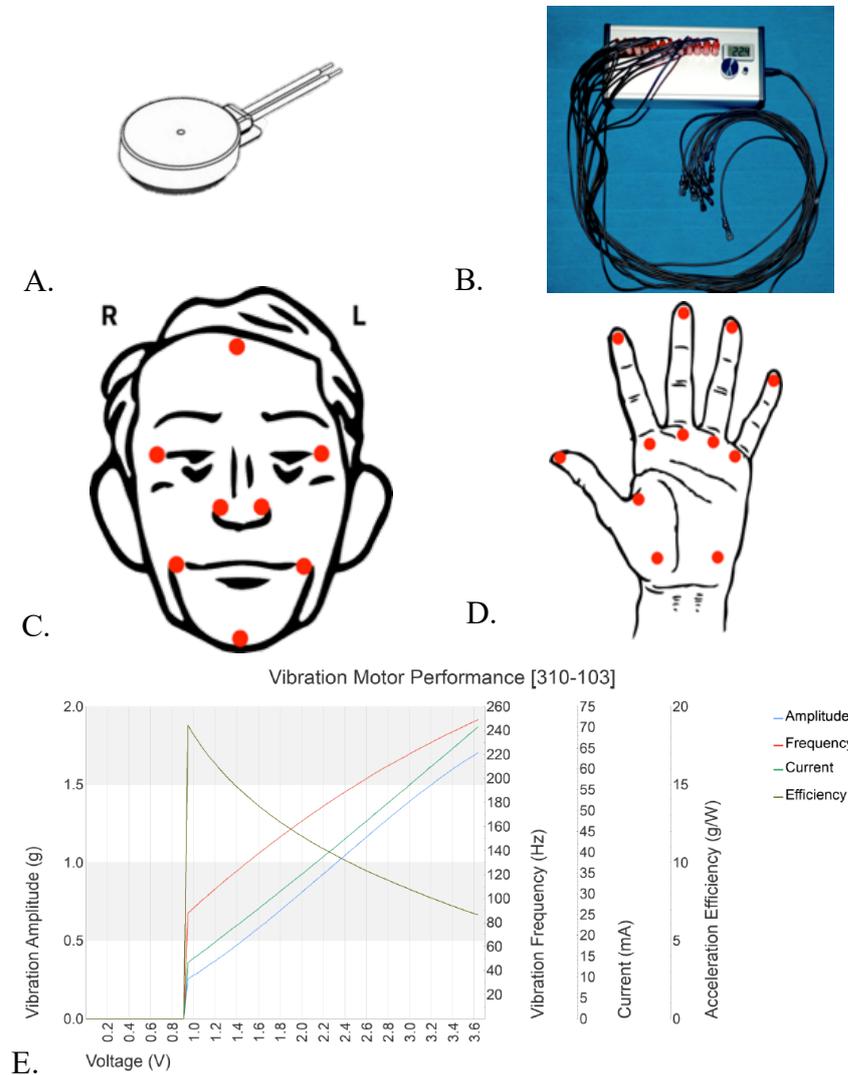


Figure 6.17. Passive sensory stimulation.

Drawing of vibration motor model 310-103 (A); picture of experimental portable vibration device (B); location of 8 vibration motors for the face (C) and 12 vibration motors for the hand (D); and typical performance characteristics of the vibration motors, showing vibration amplitude (g), voltage (V), vibration frequency (Hz), current (mA) and acceleration efficiency (g/W) (E). A and E reproduced from Precision Microdrives product data sheet with permission.

6.3.2.3 Body size estimation task

In this study, the size estimation task presented in Chapter 5 (Experiment 2), was used. This size estimation task has been inspired by the tasks in previous research (Gandevia & Phegan, 1999; Longo & Haggard, 2012; Türker et al., 2005) and consists of presenting distorted pictures of body parts for the participants to assess which one would match their perceived body size (Gardner & Boice, 2004). This task has been reliably used in previous experiments manipulating size perception in health (Gandevia & Phegan, 1999; Paqueron et al., 2003), and in illness, such as in anorexia nervosa (Mohr, Rickmeyer, Hummel, Ernst, & Grabhorn, 2016). Similar tasks have shown that healthy participants show distortions in size perception with wider and shorter faces (D'Amour & Harris, 2017), smaller hands and feet (Giurgola et al., 2019), or even a stouter body in professional swimmers (Urdapilleta, Aspavlo, Masse, & Docteur, 2010). This task was considered most appropriate as administering passive sensory stimulation could interact with the proprioceptive pointing tasks used in other studies.

In this study, single body parts were presented to avoid comparative judgements (Fuentes, Longo, et al., 2013). Moreover, real sized pictures of participants' own bodies were presented as results are susceptible to less distortion due to procedural confounds (Cullari, Vosburgh, Shotwell, Inzodda, & Davenport, 2002; Holder & Keates, 2006).

6.3.2.3.1 Stimuli

One photograph of the face (with neutral expression) was taken and two of the right hand with fingers spread out (one for the dorsum and another for the palm) of each participant at a distance of 1 meter by using a Fujifilm Finepix HS 25EXR camera. The focal point of the camera was centred in the centre of the body part (tip

of the nose for the face, centre of the hand's dorsum for the hand, centre of the palm for palmar view). The background from the pictures was removed and set as standard white by using Paint S programme (version 5.6.9), in order to prevent providing any cues (Gardner & Boice, 2004). Any connection to the body (i.e., the neck or arm) was also removed, leaving a picture of just the head or hand, for the same reason. The face picture was reversed to act as a mirrored image of the participant's face, as this is how they would normally see it (as in D'Amour & Harris, 2017). The image of the right hand was mirrored to produce an image of the left (as per previous studies). The final images were distorted in different dimensions (width and length). For this, a bespoke-designed programme created with Borland C++ builder (2007) was used. Distortions were introduced in 5% intervals, with symmetrical distortion from the midline of each body part. The smallest sized picture was 50% smaller than the real sized picture, whilst the largest picture was 50% larger (thus, from 50% to 150% distortion). There were a total of 21 pictures for the face, and 21 pictures for each hand (a total of 63 pictures for all conditions), with only one being the real sized picture for each body part (100% size). See example for hand presentation in Figure 6.18A.

6.3.2.3.2 Experimental procedure

Participants sat in a chair at about 0.5 metres from a wall. The pictures were projected onto a white screen in real size by using a projector, model NEC NP07LP, connected to a laptop used to present the pictures. The projector was positioned at a distance of approximately 1.8 meters to the wall (behind the participant), on a table at 1 metre of height (see Figure 6.18B). The projected image was adjusted in a way that the real sized picture (100% sized, that is, no distortion) matched the real size of the participant's face or hands. For this, the size of the body parts was measured with a measuring tape and matched it on the projected undistorted image onto the wall. The

images were projected on the right hemisphere. This was implemented in this way to consider possible application of this method in clinical population with hemi-inattention disorders (such as in Chapter 5 with PN patients).

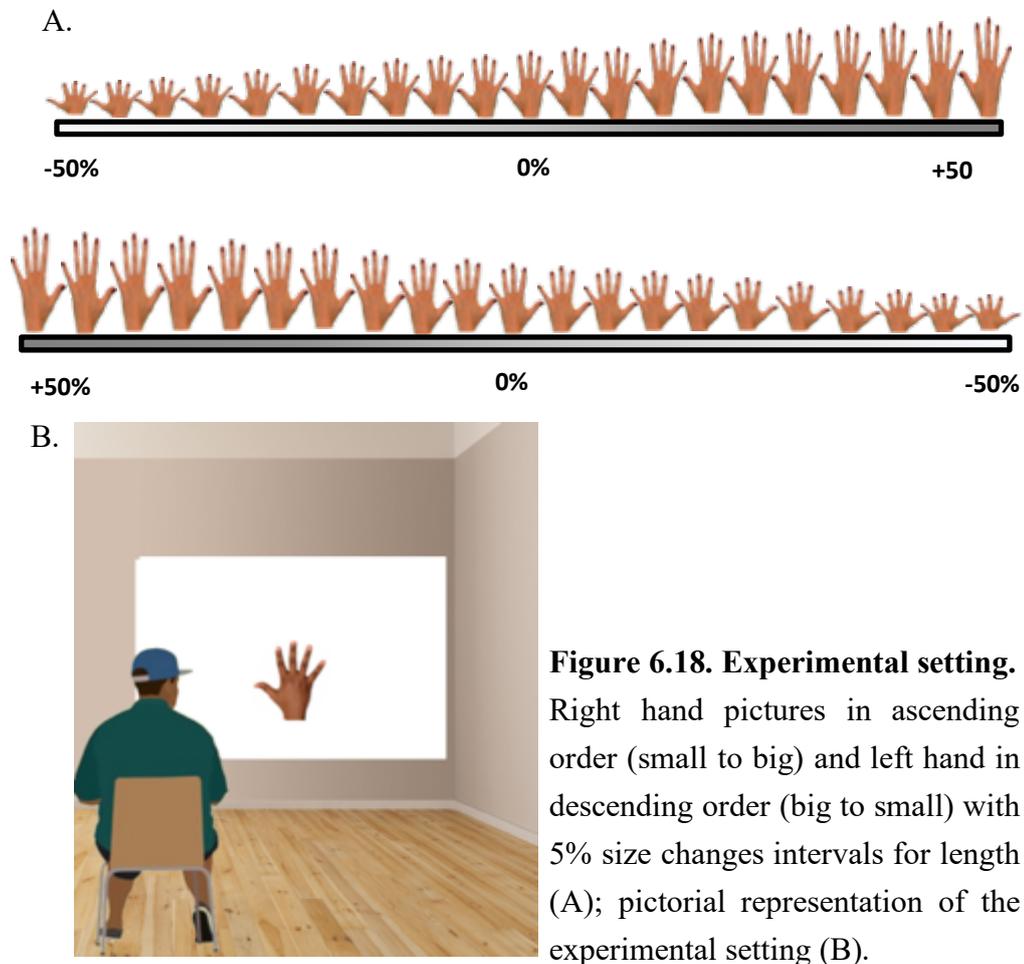


Figure 6.18. Experimental setting. Right hand pictures in ascending order (small to big) and left hand in descending order (big to small) with 5% size changes intervals for length (A); pictorial representation of the experimental setting (B).

One picture was presented at a time. There were two presentation orders: ascending (that is, from smallest to biggest picture), and descending (from biggest to smallest). Half of the participants started with ascending trial, and the other half with descending. The ascending and descending orders were alternated to control for order effects (Auchus, Kose, & Allen, 1993). Pictures were presented twice in each presentation order and for two dimensions (length and width), counterbalanced (a total of 8 trials per body part). Participants were asked to decide if the picture presented on

the wall matched their real sized body part, according to each dimension. If their response was negative, the experimenter presented the next picture in the presentation. The procedure stopped when participants found the picture they considered their veridical size in each trial. Hence, there was a final picture chosen per dimension and presentation order (a total of 8 pictures per body part). Participants performed this task twice in this experiment: before and after passive stimulation.

6.3.2.4 Dexterity assessment

Repetitive sensory stimulation can improve motor performance, in particular when used for longer stimulation periods (Kalisch et al., 2008; Ladda et al., 2014). In order to study the potential effect of the passive stimulation on motor performance, the Nine-hole peg test was administered (Kellor et al., 1971; Mathiowetz et al., 1985). The cardboard version produced by clinicspeak.com was used (Dubuisson et al., 2017). This particular version provides a measure of finger dexterity by counting the time it takes for the participant to put the 9 wooden pegs (6mm x 30mm) into 9 holes, one at a time, and then remove them. The procedure is performed with both the dominant and the non-dominant hand (Mathiowetz et al., 1985). The test was administered before and after passive stimulation.

6.3.2.5 Related measures

Previous research has found differences in body size estimation depending on mental imagery skills (Auchus et al., 1993). Mental imagery is indeed necessary in order to judge the size of one's own body (Auchus et al., 1993; Darling et al., 2015; Smeets et al., 2009), and picture size distortion has been shown to activate the mental representation of the body (Mohr et al., 2010; Spitoni et al., 2013). Also, body dissatisfaction, or 'feeling fat', has been shown to influence body size estimation. Indeed, previous studies have reported differences in size perception of the whole body

due to body concerns (Mohr et al., 2016, 2011; Smeets et al., 2009), or body dissatisfaction (D'Amour & Harris, 2019; Salvato, Romano, De Maio, & Bottini, 2019), whose influence may even be evident in the size estimation of otherwise presumed 'immune' body parts such as the hands (Coelho & Gonzalez, 2018b). Moreover, the appearance of the hands should not be belittled, as insults to their image have acute negative effects associated with social stigma (Sammut, 2002). Hence, in order to control for possible between-groups differences and also to consider their influence in size representation, the participant's body dissatisfaction was measured by means of the Body Shape Questionnaire (BSQ) (Cooper, Taylor, Cooper, & Fairbum, 1987), and visual imagery skills by means of the Vividness of Visual Images Questionnaire (VVIQ) (Marks, 1973).

The BSQ includes 34 items focusing on the experience of 'feeling fat' for the previous four weeks, and each was evaluated with a 6-point Likert scale (from 'never' to 'always'). Thus, scores ranged from 34 points (no concern) to 204 (high concern). Higher scores are indicators of higher body dissatisfaction (see Table 6.2). Differences between groups were not significant [$t(28) = -1.21, p = .24, d = -.44$].

The VVIQ consists of 16 items to visualize, such as the face of a friend or relative. The vividness of the mental image produced is then rated in a Likert-type scale (1 meaning no image at all, and 5 meaning a perfectly clear and vivid as real image), with a maximum score of 80, and a minimum of 16. Low scores will indicate poor imagery, whilst high scores are indicative of stronger visual imagery skills (see mean scores in Table 6.2). The difference in mental imagery between groups was not significant [$t(28) = -.54, p = .59, d = -.2$].

6.3.2.6 General analyses

To investigate the representation of the body the *Representational Range* for each body part was calculated as a measure of uncertainty of representation. This was calculated by obtaining the absolute difference between the averaged percentage of distortion in the ascending and descending trials. As an example, if a participant chose a picture that was 65% the size of the original in ascending trial, and 120% in descending, the total range was 55%. Data were averaged across dimensions (length and width) and views (dorsal and palmar) to obtain an overall representational range for each body part and group.

However, the representational range does not explain the direction of the distortion; that is, if the distortion varies considering the presentation order (ascending and descending) and in which direction. For this, the *Body Size Distortion* was calculated considering the order of presentation by obtaining the percentage of over/underestimation for each body part, as in Chapter 5. Previous studies have identified an asymmetry in the perception of size depending on the presentation order due to cognitive biases (Auchus et al., 1993), and showed that averaged size judgements do not accurately represent the real performance (Gardner & Boice, 2004; Gardner & Bokenkamp, 1996). These studies reported that overall performance is more accurate in ascending presentations (Gardner & Bokenkamp, 1996). Thus, the size estimation results were analysed separating performance in ascending and descending conditions, averaged across body parts, as in Chapter 5.

Further, the relationship between *Body Size Distortion* and two related variables were calculated: VVIQ and BSQ scores. Lastly, the influence of the intensity of the passive stimulation on the final distortion was considered.

6.3.2.7 Statistical analyses

Firstly, differences in the *Representational Range* were analysed by running a mixed-model ANCOVA with three factors: Body part (face, dominant and non-dominant hands); Time (pre and post stimulation) and Group (face stimulation or hand stimulation groups). VVIQ and BSQ scores were introduced as covariates, to control for potential confounding effects. Any significant interactions in the ANCOVA were followed by Bonferroni corrected t-tests.

Similarly, mixed-model ANCOVAs were run for the *Body Size Distortion* results, with the same covariates. Results for each presentation order (ascending and descending) were analysed separately, in order to understand the direction of the distortion (Gardner & Boice, 2004; Gardner & Bokenkamp, 1996). Similarly, each body part was analysed separately, to understand the differential effects of stimulation. Again, significant interactions were followed by Bonferroni corrected t-tests.

Dexterity assessment results were then presented and analysed via a mixed-model ANOVA.

Lastly, Pearson's correlations were run between *Body Size Distortion* results and the related measures (VVIQ and BSQ scores). Correlations were also run with the intensity of the stimulation, to investigate if there was an influence between intensity and effectiveness.

6.3.3 Results

6.3.3.1 Passive sensory stimulation

Not surprisingly, the intensity of vibration that participants were able to tolerate differed between stimulation groups (i.e. stimulated body part). Specifically, the average intensity of stimulation for the face stimulation group that participants were

able to tolerate was of 17.49mA (SD = 3.84), which corresponds to an average frequency of 60Hz. In contrast, the current intensity for the hand group was of 33.02mA (SD = 3.42), an average frequency of 110Hz (see graph in Figure 6.17E). Differences in the intensity of stimulation were significant between groups [$t(28) = -11.71, p < .001, d = -4.28$].

6.3.3.2 Body size estimation task

6.3.3.2.1 Representational range

Significant results were found for the main factor Group [$F(1,26) = 6.09, p = .02, \eta^2 = .19$], with more overall accuracy in the hand stimulation group. There were not significant differences for the main factors of Time [$F(1,26) = .49, p = .49, \eta^2 = .02$], or Body part [$F(1,26) = 2.52, p = .88, \eta^2 = .005$]. Interestingly, and most importantly, the Time by Group interaction was significant [$F(1,26) = 6.18, p = .02, \eta^2 = .19$] due to differential effects of stimulation depending on the site targeted (face or hand). Subsidiary Bonferroni corrected t-tests (corrected p value of .01) showed that differences in size perception before and after stimulation were found only in the hand stimulation group [$t(14) = 3.29, p = .005, d = .85$], with a reduction of the range after stimulation (from 14.64% (SD = 6.63) before stimulation, to 9.39% (SD = 4.78) afterwards). Results did not reach significance in the face stimulation group [$t(14) = .54, p = .59, d = .14$], showing that the stimulation of the face did not affect the accuracy (see Figure 6.19). Differences between pre-stimulation conditions between groups were not significant [$t(25.94) = 1.48, p = .15, d = .54$] (equality of variances not assumed). On the contrary, differences between groups were significant post-stimulation [$t(28) = 3.12, p = .004, d = 1.14$], confirming that size estimation was more accurate after hand stimulation. The other interactions in the ANCOVA did not reach significance (all ps. > .05).

These results confirmed there were distortions on the perceived size of all body parts and that stimulation of the hand reduced the range or variability for all of them, making the body size estimation more accurate.

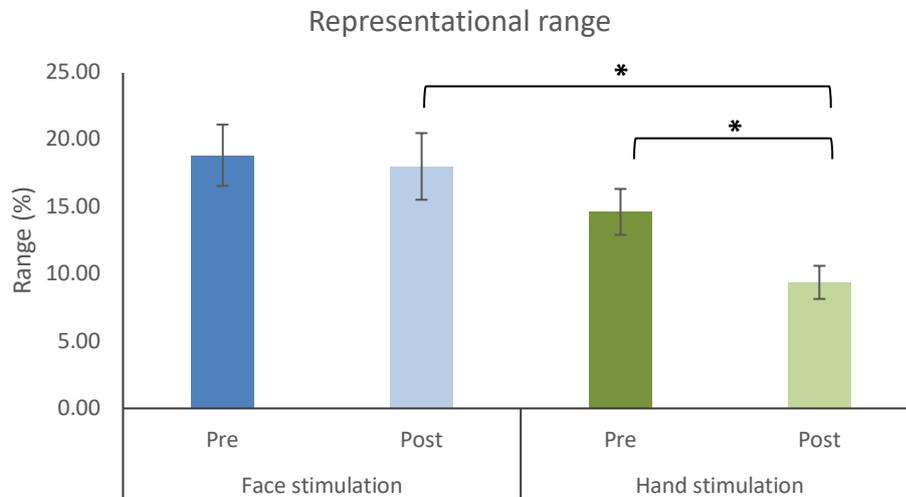


Figure 6.19. Representational range.

Representational range (%) averaged across body areas and stimulation group in both pre and post stimulation conditions. * indicates significant differences.

6.3.3.2.2 Body size distortion

Mean perceived size distortion (percentage of under/overestimation) for all body parts confirmed there was underestimation in the ascending presentations, and overestimation in the descending ones. Hence, this justifies the need to separate the analyses for ascending and descending conditions (Gardner & Boice, 2004; Gardner & Bokenkamp, 1996).

Face

The mixed-model ANCOVA for the ascending presentation detected a non-significant effect of Time [$F(1,26) = .73, p = .4, \eta^2 = .03$], Group [$F(1,26) = .58, p = .45, \eta^2 = .02$], and Time by Group interaction [$F(1,26) = .32, p = .58, \eta^2 = .01$].

In the descending order presentation, the Time factor was not significant [$F(1,26) = 1.06, p = .31, \eta^2 = .04$], whereas the factor Group was [$F(1,26) = 15.33, p = .001, \eta^2 = .37$]. Overall, the face stimulation group showed more distortion ($M = 15.46\%$, $SD = 6.71$) than the hand group ($M = 7.17\%$, $SD = 4.22$). Lastly, the interaction between Time and Group was not significant [$F(1,26) = 2.33, p = .14, \eta^2 = .08$]. Taken together, these results indicated there was no effect of stimulation in the representation of the face (see Figure 6.20).

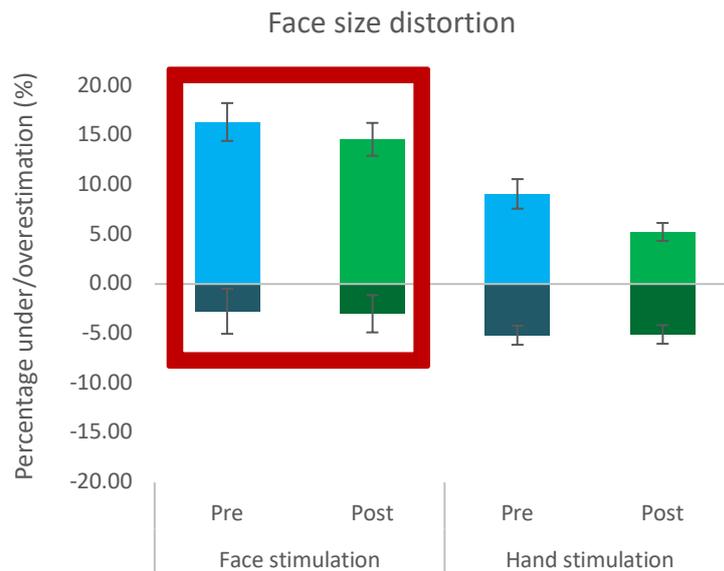


Figure 6.20. Face size distortion before and after stimulation.

Representation of the perceived distortion (percentage of over/underestimation) for the size of the face before and after stimulation, for Face stimulation and Hand stimulation groups. The presentation order is indicated by darker colour bars at the bottom (ascending) and lighter colour bars on top (descending). The red rectangle highlights which group received stimulation on the face. Error bars indicate the Standard Error of the Mean.

Dominant hand

In the ascending condition, Time [$F(1,26) = .24, p = .63, \eta^2 = .01$], Group [$F(1,26) = 84.46, p = .14, \eta^2 = .08$], and Time by Group interaction [$F(1,26) = .98, p = .33, \eta^2 = .04$] were not significant.

For the descending order, the effect of Time was not significant [$F(1,26) = .24$, $p = .63$, $\eta^2 = .01$], whereas Group [$F(1,26) = 8.15$, $p = .01$, $\eta^2 = .24$], and Time by Group interaction [$F(1,26) = 5.37$, $p = .03$, $\eta^2 = .17$] were. The significance of the Group factor confirmed differences in size perception between groups, being the hand stimulation group the most accurate, overall (see Figure 6.21). To explore the interaction between Time and Group, four Bonferroni-corrected t-tests were run (cut-off p value of $< .01$); two between the size perception before and after stimulation within each group (pairwise comparisons), and two between size perception pre and post stimulation between groups (independent group comparisons). Pre and post stimulation differences were minimal and not significant for the face stimulation group [$t(14) = -.13$, $p = .9$, $d = -.03$]. In contrast, differences in the hand group reached significance [$t(14) = 3.6$, $p = .003$, $d = .93$]. Differences between groups pre stimulation were not significant [$t(28) = .99$, $p = .33$, $d = .36$], whereas these were significant post stimulation [$t(16.41) = 3.65$, $p = .002$, $d = 1.33$] (equality of variances not assumed). In this case, these results indicated there was a significant effect of stimulation in the representation of the dominant hand, with a reduction of the baseline distortion.

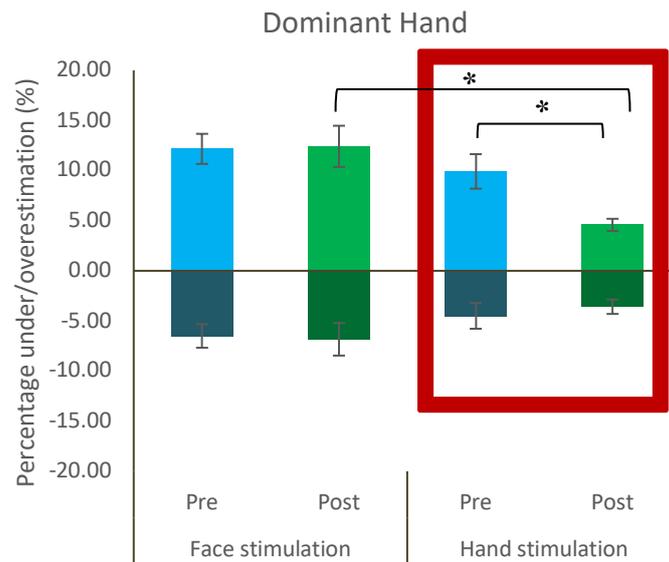


Figure 6.21. Dominant hand size distortion before and after stimulation. Representation of the perceived distortion (percentage of over/underestimation) of the dominant hand before and after stimulation, for Face stimulation and Hand stimulation groups. The presentation order is indicated by darker colour bars at the bottom (ascending) and lighter colour bars on top (descending). The red rectangle highlights which group received stimulation on the dominant hand. Error bars indicate the Standard Error of the Mean. * indicate significant differences.

Non-dominant hand

As seen in previous body parts, in the ascending presentation results did not reach significance for any factor (Time: $[F(1,26) = .003, p = .96, \eta^2 = .00]$; Group: $[F(1,26) = .001, p = .97, \eta^2 = .00]$), indicating no differences between groups or measurements. Equally, the interaction between Time and Group was not significant $[F(1,26) = 3.75, p = .06, \eta^2 = .07]$. Thus, there were no effects of stimulation in the ascending condition.

Results for the descending presentation did not show significant effects for the factor Time $[F(1,26) = 3.56, p = .07, \eta^2 = .12]$ nor for the Time by Group interaction

[F (1,26) = 2.54, p = .12, η^2 = .09], but the Group factor was significant [F (1,26) = 7.35, p = .01, η^2 = .22], confirming that the face stimulation group was less accurate, overall (see Figure 6.22). However, the lack of interaction effect does not support a difference in size distortion due to stimulation effects. To sum up, these results confirmed the lack of effect of the stimulation on the non-dominant hand.

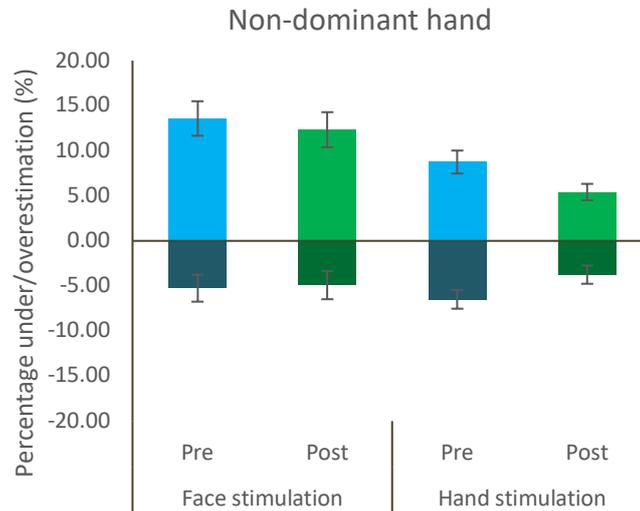


Figure 6.22. Non-dominant hand size distortion before and after stimulation.

Representation of the perceived distortion (percentage of over/underestimation) of the non-dominant hand before and after stimulation, for the Face stimulation and Hand stimulation groups. The presentation order is indicated by darker colour bars at the bottom (ascending) and lighter colour bars on top (descending). Error bars indicate the Standard Error of the Mean.

6.3.3.3 Dexterity

In order to test the effect of passive stimulation on dexterity, the pre and post stimulation results on the Nine-hole peg test were considered for each group. An improvement in performance was predicted after stimulating the dominant hand, following previous studies reporting improved motor performance after hand

stimulation (e.g., Ladda et al., 2014). No effect on dexterity was anticipated after face stimulation. Results are presented in table Table 6.3.

Table 6.3. Nine-hole peg test results.

Performance in the dexterity test (in seconds) with standard deviation (SD), pre and post stimulation for both hands and groups.

	Time	Face stimulation group	Hand stimulation group
		Mean (SD)	Mean (SD)
Dominant hand	Pre	18.06 (2.64)	19.82 (1.74)
	Post	17.49 (2.01)	18.94 (2.04)
Non-dominant hand	Pre	18.57 (2.39)	20.41 (2.45)
	Post	18.08 (2.08)	20.51 (2.49)

A mixed-model ANOVA was run with three factors: Time (pre and post); Hand (dominant and non-dominant), and Group (Face and Hand stimulation groups). There were not significant effects of Time [$F(1,28) = 2.93$, $p = .1$, $\eta^2 = .1$]; whereas the main factor Hand was significant [$F(1,28) = 6.97$, $p = .01$, $\eta^2 = .2$]. There was an overall better performance when using the dominant hand in comparison with the non-dominant (mean difference = .81). Further, there were significant Group differences [$F(1,28) = 8.07$, $p = .008$, $\eta^2 = .22$], with faster execution in the Face stimulation group (mean difference = 1.87). The interactions between Time and Group factors ($p = .8$); Hand and Group ($p = .39$); Time and Hand ($p = .33$); and Time, Hand and Group ($p = .4$), were all not significant. These results did not identify any effect of stimulation in dexterity, measured with the Nine-hole peg test.

6.3.3.4 Related measures effects

In this section, the Pearson's correlations on the pre and post stimulation distortions for each body part with the control measures (VVIQ and BSQ scores) were

considered, to further investigate the effect of these variables in the task. As ascending presentations were considered to be ‘at ceiling’ (as seen in previous chapter), correlations were only run for descending presentation results.

In the pre-stimulation conditions, no significant correlation on the body size distortion was found for any body part with VVIQ or BSQ scores (all $ps. > .05$). Instead, there was a significant positive correlation between VVIQ scores and face distortion after stimulation for the face stimulation group ($r = .66, p = .01$), showing how participants with better imagery score perceived their face as more distorted after stimulation.

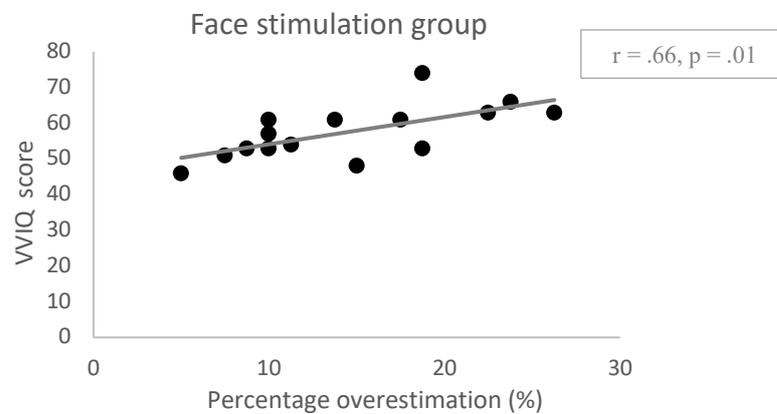


Figure 6.23. Scatterplot for the correlation between VVIQ and face distortion in the face stimulation group.

Scatterplot between VVIQ scores and face size distortion (%) in the descending order after face stimulation.

In the hand stimulation group, there was instead a significant negative correlation after stimulation between BSQ scores and the size distortion of the dominant hand ($r = .59, p = .02$), indicating how higher body concerns were associated with higher distortion. No other correlations came up as significant (all $ps. > .05$) (see Figure 6.24).

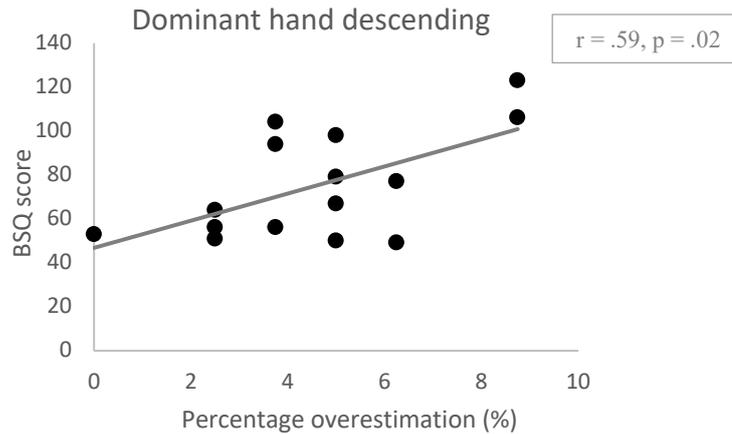


Figure 6.24. Scatterplot for the correlation between BSQ and dominant hand distortion in the hand stimulation group.

Scatterplot between BSQ scores and hand size distortion (%) in the descending order after hand stimulation.

Further, the intensity of stimulation was different from the outset between face and hand stimulation groups, due to participants' tolerance to the stimulation. Previous studies have postulated how higher intensity will be associated with higher gains (Schlieper & Dinse, 2012). Hence, Pearson's correlations were run between the body size distortion for both groups. In this case, correlations were only run with the results after stimulation. No significant correlations were found for the face stimulation group (all $ps. > .05$). Instead, there was a significant negative correlation in the hand stimulation group, between the size distortion of the dominant hand and the stimulation intensity ($r = -.71, p = .003$), confirming that higher intensities were associated with less distortion (see Figure 6.25). No other correlations were significant (all $ps. > .05$).

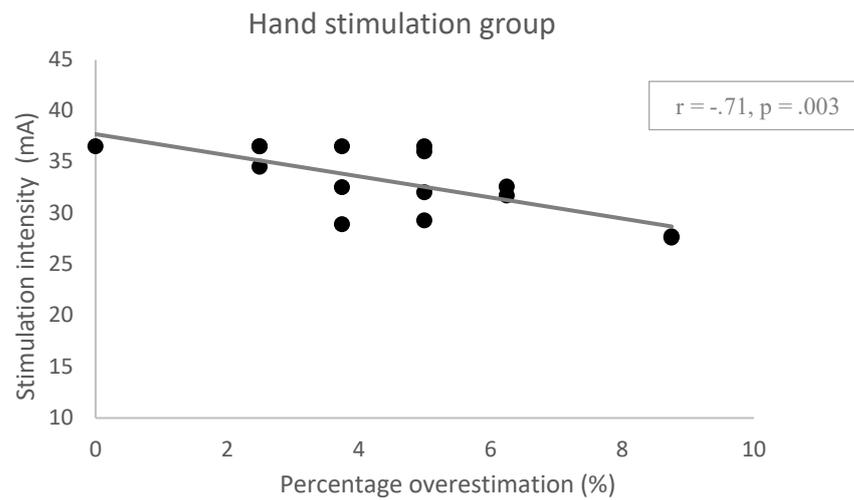


Figure 6.25. Scatterplot for the correlation between stimulation intensity and dominant hand distortion in the hand stimulation group.

Scatterplot between stimulation intensity (mA) and hand size distortion (%) for the descending condition after hand stimulation.

6.3.4 Discussion

This experiment has explored the modulatory effects of passive sensory stimulation in the representation of the size of the hands and face. Passive sensory stimulation was applied to two different body parts in two different groups of participants. For this, a bespoke-made portable device was designed that delivered vibratory stimuli through circular vibration motors. This device administered high frequency stimulation to elicit LTP (Stefan, 2000). One group was stimulated on the face, and the other on their dominant hand. A depictive body size estimation task was administered (as in Chapter 5), both before and after stimulation, in which participants had to judge the perceived size of their face, dominant and non-dominant hands by selecting from an array of distorted pictures. The main aim was, on one hand, to investigate the modulatory capabilities of passive sensory stimulation on size perception whilst, on the other, to explore the specificity of this stimulation. The effects of the passive sensory stimulation were not equal across body parts. That is, the

face stimulation did not modulate its body size, whereas the stimulation of the dominant hand did. In particular, this stimulation was effective in reducing the distortion on the dominant stimulated hand. Passive sensory stimulation appears suitable to modulate size representation, but this modulation is specifically effective for hands.

At the outset, participants were not accurate when estimating the size of hands and face from pictures, with distortions both in ascending and descending presentations. Indeed, as seen in Chapter 5 (Experiment 2), distortions of body image are also found in healthy population, with a tendency to overestimate the body (D'Amour & Harris, 2017; Urdapilleta et al., 2010). As expected, the presentation order (ascending versus descending) had an influence in size judgements, acting as an anchor, in a way that in ascending trials the final judgements were too small, whilst the opposite occurred in descending ones (Caggiano & Cocchini, 2020; Gardner & Boice, 2004; Gardner & Bokenkamp, 1996). Here, the distortion was mainly seen for descending trials, confirming that ascending trials are more accurate (Gardner & Bokenkamp, 1996). This may be due to exposure to extreme body types, which have already been shown for the face (Webster & MacLin, 1999), and bodies (Brooks, Mond, Stevenson, & Stephen, 2016). This finding supports the idea that aftereffects are stronger for larger pictures. As previously explained, this inclination for larger body parts is also seen in embodiment (Haggard & Jundi, 2009; Pavani & Zampini, 2007), perhaps due to long-term body image that allows growth through development (De Vignemont et al., 2005). Considering these findings at baseline, it is not surprising to find that the effects of stimulation are only evident in the descending order. Indeed, the ascending condition could be considered to be 'at ceiling'.

Interestingly, passive sensory stimulation was effective at modulating the size representation of the body, but only for the stimulated hand. Specifically, increased somatosensory input caused a reduction of the distortion, confirming bottom-up modulation of size representation. This type of stimulation activates somatosensory areas (Beste & Dinse, 2013; Pleger et al., 2001; Rode et al., 2012), which appear involved in representing the size of hands. Hence, these results strengthen the link between size representation and somatosensation.

The mechanism of action of passive sensory stimulation is associated with increased cortical excitability after a short period of somatosensory stimulation (Kaelin-Lang et al., 2002; Ridding, Brouwer, Miles, Pitcher, & Thompson, 2000), with intracortical facilitation (Kobayashi, Ng, Théoret, & Pascual-Leone, 2003) and decrease of inhibition (Classen et al., 2000). In particular, excitability changes are associated to GABAergic neurotransmission (Kaelin-Lang et al., 2002) and LTP mechanisms (Stefan, 2000). Inversely, deafferentation causes changes in cortical motor excitability (Ziemann, 2001), associated with a reduction of GABA levels (Levy, Ziemann, Chen, & Cohen, 2002). Moreover, the effects of vibration are not only circumscribed to somatosensory areas. In fact, vibratory stimulus applied to the hand (palm) increase regional cerebral blood flow (rCBF) in contralateral primary and secondary somatosensory areas, parietal cortex and primary and supplementary motor areas (Seitz & Roland, 1992). Hence, it appears to engage a number of areas that are also involved in the representation of the body size (Committeri et al., 2018).

Increased somatosensory information in this case was instrumental for the perceived size of hands, but not for the face. These results confirmed that access to somatosensory and proprioceptive information for hands is prioritized, whereas this may not be the case for the face. For instance, in perceptual competition tasks, visual

awareness of the hands is faster when the participant's hand is held in a congruent position to the presented hand images (Salomon et al., 2013). On the contrary, this effect is not seen for faces, in which proprioceptive information does not appear to be as relevant (Korb et al., 2017). These findings support the idea that the face is more visually constructed (Keyes, 2012), and possibly more resilient to plastic changes due to sensory stimulation. Owing to this visual specialisation, the face may need a different timescale for the integration of proprioceptive signals with visual ones, in comparison to hands (Korb et al., 2017). Instead, multisensory information is normally integrated quickly for the hands, with strong visuo-motor-proprioceptive relationships (Korb et al., 2017). For example, recent studies have explored the recruitment of the somatosensory cortex in working memory tasks with hand images, in contrast to images of objects, which only recruited visual areas (Galvez-Pol, Calvo-Merino, Capilla, & Forster, 2018). Similarly, differences in the integration of multisensory information are also seen between upper and lower limbs, being faster for the hands (van Elk, Forget, & Blanke, 2013). These results indicate that different sensory modalities will have different relevance depending on the body part considered (K. D. Stone et al., 2018).

Competition between sensory modalities helps to understand how different types may prime for different tasks. When performing visually guided actions, in which there is visuo-proprioceptive conflict, the reduction of the involvement of one sensory modality that is not as relevant will, in turn, improve performance. For example, reduction of proprioceptive information through rTMS-induced deafferentation of the hand can improve mirror drawing. In other words, by removing conflicting proprioceptive information, enhanced performance is achieved in the task (Balslev et al., 2004). Following this, it is possible that the opposite is true in the task

in this study. That is, these findings lead to the hypothesis that increasing somatosensory information in a body part that is constructed more visually will, instead, create more conflict. Supporting this, there was a positive and significant correlation between VVIQ imagery scores and face distortion after stimulation of the face. This meant that, participants with better mental imagery skills were worst at estimating the size of their face after sensory stimulation, as if the stimulation would have disrupted their performance. In light of this, ‘high imaginers’ may prioritise visual information over somatosensory. Hence, increasing the later may produce a conflict. However, they were not actually worse in size perception after the stimulation as a group. These results may reinforce the idea that different individuals, depending on their strategy to the task, will rely more on different sensory modalities. To sum up, those who generally rely more on or are more skilled in visual imagery, will worsen their performance when the system is ‘overloaded’ with information from a different sensory modality.

Another possible explanation for the lack of effect of face stimulation may be related to the intensity of the stimulation, which was significantly higher for the hands (average of 33.02mA), when compared with the face (average of 17.49mA). Unfortunately, the intensity of stimulation that participants could tolerate for the face was much lower, and the lack of significant effect in body size representation after face stimulation may be due to this, as in studies testing the forearm (Muret & Dinse, 2018). Indeed, the correlation with the intensity of stimulation was significant and negative for the perceived distortion after stimulation in the hand group, indicating that higher intensities of stimulation were associated with less distortion.

The passive stimulation in this case did not improve motor performance, as seen for the lack of significant results for the peg-test. Previous studies had found

improved motor function after somatosensory stimulation (Kalisch et al., 2008; Wu et al., 2006) due to associated increased of motor cortical excitability (Kaelin-Lang et al., 2002; Ridding et al., 2000). Perhaps, a more challenging version of the peg-test should be implemented that is sensitive enough to the stimulation. Indeed, this has also been reported in previous studies, in which differences in performance were only identified in the most complex version of the task (Ebied, Kemp, & Frostick, 2004; Kalisch et al., 2008).

Lastly, an additional result is the significant correlation between BSQ scores and dominant (stimulated) hand representation after stimulation. These results indicated that those with lower scores in the BSQ (low body concerns) had a more accurate representation, thus being more susceptible to the stimulation. Indeed, healthy body image is associated with better ability to integrate and update it from online multisensory information, whereas disorders are associated with uncertainty and incapacity to update it (Osman et al., 2004; Riva & Dakanalis, 2018; Riva et al., 2015). For instance, this lack of multisensory integration is the source of size distortion (macrosomatognosia) of the left hemiface in a patient after stroke (Rode et al., 2012).

To sum up, passive sensory stimulation administered through this experimental device has proven its capacity to induce subjective change of body size without training. It is an inexpensive device, portable, easy to use, that allows different intensities of vibration. This stimulation may have produced associated cortical activation in somatosensory areas, improving the perceived size of the body. This paradigm may represent an alternative to modulate distorted size representation in patients with body representational deficits.

6.4 General discussion

In the two experiments presented in this chapter modulatory methods have proven effective to ameliorate the distortions in size perception of face and hands. In the first study, tDCS over the primary visual cortex had an effect in reducing the distortion of face width. Instead, passive sensory stimulation was effective at reducing the distortion of the stimulated hand. These differences in the effectiveness of the modulation depended on the relevance of the information considered for each task and for each body part.

Certainly, the body representation is built via multisensory information (Azañón, Tamè, Maravita, Linkenauger, Ferrè, Tajadura-Jiménez, & Longo, 2016), but it is also true that depending on which information primes for each body part, modulation has different effects. Indeed, as postulated previously, each body part will be represented in a given way depending on its functional use. For instance, the influence of the visual experience for lower limbs (i.e., view from top-down), explains the tendency to overestimate the width of the legs (K. D. Stone et al., 2018). Instead, as we experience the hands from multiple viewpoints, this distortion is not found through the size estimation task (Longo, 2015d). On the contrary, when using the localisation task distortions appear for the hands, but not for the legs. This is attributed to the differences in the relevance of somatosensory (tactile) information for hands (Weinstein, 1968), in comparison with the legs (K. D. Stone et al., 2018), which increases distortions (Ganea & Longo, 2017). Hence, in this chapter, visual components may be highly linked with the face, and the task (size estimation task which relies in mental imagery), whereas somatosensory information appeared to be more relevant for the hands. Indeed, the areas of highest tactile acuity are located in fingers and hand palm (Mancini et al., 2014; Weber & Ross, 1978; Weinstein, 1968),

whilst faces are ‘complex visual stimulus’ (Sliwinska et al., 2019, p. 3). These findings are of relevance when planning different interventions and to understand the weighting of the different components and influences that modulate their representation.

Most importantly, this chapter has confirmed that top-down and bottom-up modulation differently affect representations, focusing on neuroplasticity. Interestingly, the underlying neurophysiological mechanisms for both methods are somehow shared. Indeed, GABAergic neurotransmission has been proposed as underlying mechanism in the behavioural gains due to tDCS (Nitsche et al., 2004; Ziemann, 2001) and due to passive sensory stimulation (Kaelin-Lang et al., 2002). GABA is the main inhibitory neurotransmitter in the brain, involved in experience-based reorganization (Feldman, 2000). Hence, this activation and effects in GABA levels are associated with LTP and learning (Batsikadze et al., 2013; Beste & Dinse, 2013; Pirulli et al., 2014; Stefan, 2000). These complementary approaches to training may indeed be of interest for rehabilitation, as these induce lasting changes in behaviour mediating learning (Beste & Dinse, 2013).

Previous studies have used different types of stimulation to rehabilitate motor function after stroke (Wu et al., 2006). The two particular methods presented here could also be used in case of damage. For example, somatosensory stimulation improves function in patients after stroke by stimulating paretic extremities (Golaszewski et al., 2002; Wu et al., 2006). In the same way, non-invasive stimulation through tDCS has improved motor function of the paretic hand after stroke (Hummel & Cohen, 2005). The findings presented here may open up new neuroplastic management strategies for body distortions. It will be the aim of future studies to consider the implementation in groups of patients.

Lastly, it is important to note that in these studies each modulatory technique was applied in isolation. However, it is possible that pairing one of these methods with training could further the gains (Hummel & Cohen, 2005). For instance, a recent study administered cutaneous electrical stimulation and tDCS to patients to successfully treat chronic lower back pain (Schabrun, Jones, Elgueta Cancino, & Hodges, 2014). The potential to combine and use these methods to target distortions of the body representation should be the focus of further studies. In conclusion, the findings presented here corroborate that unattended stimulation protocols alone can satisfactorily drive plastic changes in body size representation.

Chapter 7: **General discussion**



Josephine Cardin Photography

7.1 Overview of studies and main findings

The brain requires information regarding body size to effectively interact with the environment. For example, the changes in the perceived size of the body ‘scale’ the perceived size of objects (Linkenauger et al., 2013). However, there is no specific receptor or afferent signal that determines the size of the body, which has to be indirectly determined and that is stored (Longo et al., 2010; Walsh et al., 2015). This stored information about the size of the body is constructed through experience (Walsh et al., 2015). One of the assumptions is that healthy people perceive their body accurately. However, this is far from the truth. Indeed, several distortions of body size are characteristic of healthy representation and are modulated by different types of information (Longo, 2017b). This representation is not only distorted, but highly malleable, being susceptible to modulation of sensory information, such as the effects of anaesthesia (Gandevia & Phegan, 1999; Türker et al., 2005). Furthermore, it can be highly disrupted after brain damage, as seen in patients with Personal Neglect, who ignore the contralesional side of their body (Baas et al., 2011; Committeri et al., 2007); or in supernumerary phantom limbs disorder, where patients experience ownership of multiple limbs (Hari et al., 1998; McGonigle et al., 2002).

In light of this, it was of interest to further investigate these distortions, how these are measured and constructed, potential influences and modulation. In particular, hands and faces are the most personal parts of the body, they define who we are, and help us interact with others and the environment. Hence, this thesis has included an exploration on how the metrics of the hands and face are represented, and how it can be modulated.

To recap, the main aims of this thesis, presented in Chapter 2, were:

- I. To review the distortions of the metrics of the hands by removing conceptual biases and to provide a clear account of underlying shifts (Experiment 1, Chapter 3).
- II. To investigate the distortions of the metrics of the face by developing a new task based on locational tasks (Experiment 2, Chapter 3).
- III. To understand the effects of long-term expertise (magic and sign language) in the size representation of hands and face (Chapter 4).
- IV. To investigate the effects of damage to the underlying hand cortical area in the representation of the hands and face (Experiment 1, Chapter 5).
- V. To study the representation of the hands and face in patients with Personal Neglect after stroke (Experiment 2, Chapter 5).
- VI. To examine the extent to which modulation of the representation of the size of the body (hands and face) can be achieved by tDCS or passive sensory stimulation, as well as consideration of the differential effect of these methods depending in the body part and sensory modality explored (Chapter 6).

From all these aims, different conclusions have been reached.

7.1.1 The metrics of the hands

Chapter 3 addressed the need for an updated method to understand the distortions of the representation of hands. This study was motivated by the controversy regarding previously reported distortions in hand representation. Mainly, conceptual biases associated with the knuckles had to be overcome. The method developed in the study and presented in this thesis allowed for exploration of the shifts in the location judgements for all landmarks and provided a clear cartographical representation of the

hand. Results showed how the conceptual biases were absent once finger interspaces were targeted rather than knuckles. This was confirmed by the minimal proximo-distal shift of interspaces, which were located quite accurately. However, there was still underestimation of finger lengths. The exploration of the shift of fingertips confirmed that these were misallocated proximally, being located closer to the body than they really were. These results confirmed two points: firstly, that the interspaces are landmarks that are located better and are detached from conceptual biases; secondly, that misallocation responses to fingertips guide the underestimation of the length of fingers. This was explained due to uncertainty associated to the localisation of fingertips, as these show largest range of movement (De Vignemont, 2014). Moreover, fingers are normally seen in a contracted position, and these positions become part of the stored mental image retrieved in order to perform this task (Smeets et al., 2009).

The width of the hand was overestimated due to spatial warping of the skin (perceptual distortion), directly linking metrics with cortical somatosensory representations (Longo et al., 2015). However, the investigation into the shift of locational responses helped shed light on understanding the direction of these distortions was associated to functionality. Overall, there was a tendency to misallocate the less functional fingers (i.e., ring and little fingers); misallocations that, in this case, guided the overestimation of width.

Holistically, these findings were considered under the framework of functionality and manual experience (Fraser & Harris, 2016). That is, increased use of certain segments (i.e., fingers), improve their representation. Moreover, representation is guided by functional use (Caggiano & Cocchini, 2020), which means that shifts follow the direction of movement. Lastly, there was more distortion of width dimension overall, as it accommodates more variability (K. D. Stone et al., 2018).

Indeed, changes in length are slow after adolescence (Visser, Geuze, & Kalverboer, 1998). Hence, the greater variability of width, overall, may be related to the “likelihood of them changing rapidly”, as changes in the muscle mass and fat can vary the width of body segments in a shorter time frame (Walsh et al., 2015, p. 1768).

7.1.2 The body model of the face is distorted

This thesis also presented a new innovative task that allowed for measurement of self-face metric representation, in order to provide a metric configuration of one’s own face. In Experiment 2 in Chapter 3, a description of the face metric representation was provided. This study showed how the facial features were, overall, overestimated in size, whereas length representation was mostly accurate. Interestingly, there was a compartmentalization of the length perception, indicating an effect of functionality on the perceived location of the lower face areas, as seen with the fingertips. The length of the top half of the face, being more stable with less range of movement, was perceived more accurately. Similar compartmentalisation had been found in previous studies (Fuentes, Runa, et al., 2013), supporting the idea of separate representation for these two face portions. Moreover, the direction of shifts may have also been influenced by functionality and usual direction of movement of the body part (Linkenauger et al., 2009; Longo, 2017c). In other words, the overestimation of the lower face may be associated with its broader range of movement.

The width dimension was, once more, the dimension with larger distortion, confirming the tendency to overestimate the body as a whole (Coelho & Gonzalez, 2018b; Longo, 2019; K. D. Stone et al., 2018). The investigation of the shifts of location responses identified a tendency to overrepresent the right side of the face, which follows studies on imbalanced hemispheric activation in right handers in own body representation (Linkenauger et al., 2009). This tendency had already been

reported in a previous study in which participants judged the location of their hips and waist to be further to the right than they were (Hach & Schütz-Bosbach, 2014), asymmetry related with handedness (Linkenauger et al., 2009), or right hemisphere activity (Hu et al., 2016).

The two studies in Chapter 3 indicated how functionality and the type of use of a body part will, in turn, affect its size. This suggested that size representation could be further modulated by practice.

7.1.3 Long-term practice modulates the body size

The studies presented in Chapter 4 investigated the effects of expertise in the representation of the hands and face. For this purpose, two groups of experts in manual dexterity were recruited; a group of expert magicians (Experiment 1), and a group of sign language practitioners (Experiment 2). Long-term practice had been shown to produced changes in performance in different tasks. For example, improved proprioceptive localisation of limbs had been found for dancers (Jola et al., 2011), whilst a recent study has found modulation in the perceived size of the hand in baseball players (Coelho et al., 2019).

Results in these two studies confirmed the malleability of the representation of the size of the hands and face, owing to long-term manual and facial practice. Specifically, magicians were more accurate in the location judgements of fingers, with a reduction of the distortion of length (underestimation) in comparison with controls. Findings from other studies supported the link between frequency of use and representation (Fraser & Harris, 2016). In this case, the different size perception is also linked to improved dexterity of the best represented fingers, with gains in reach-to-grasp tasks (Cavina-Pratesi et al., 2011). Hence, more accurate size representation appeared associated with improved performance in other motor and perceptual tasks.

The accuracy gain was also present for the imagined condition, where participants relied on mental imagery rather than proprioception. This was an interesting finding, as there has been controversy into whether or not this type of task relies on proprioception, and to what degree. It would appear that somatosensory components may not be as relevant for the task, relying instead on mental imagery (Ganea & Longo, 2017). This clearly manifests when this type of information is irrelevant (i.e., the real position of the hand does not match the position of the imagined hand). This study supported the idea that long-term practice and expertise can modulate the metric representation of a body part, even when presented with a task for which participants did not necessarily have any prior expertise.

The width of the hands was not measured in the magicians' study; hence, it was unclear as to whether the gain was specific to the fingers, or whether it could be generalised to the whole hand. This was a pertinent area to explore, as most of the distortions found for hands and faces were seen in the width dimension (as seen in Chapter 3). Moreover, it was of relevance to study the effects of expertise in the metrics of the face. With these goals in mind, Experiment 2 investigated the representation of hands and face in a group of sign language practitioners. This particular group of experts was explicitly recruited to dually investigate the modulation of face representation associated with expertise. In sign language, practitioners use both hands and face as means of communication; thus, the effects of practice may be evident for both. Lastly, previous studies (Chapter 3 and magicians' study in Chapter 4) had identified an effect of practice, functionality and usual manual workspace in the representation of hands. However, the effect of expertise and its link to a specific portion of space had not been explored. Sign language expertise is confined within a specific 3D space around the body (see Figure 4.6 in Chapter 4), which allowed the

exploration of this issue. Hence, the localisation task for the hands was performed twice: in ‘usual’ workspace location (i.e., near-reaching space) and in ‘unusual’ location (i.e., far-reaching space).

Supporting previous study with magicians, the accuracy in the representation of hands was improved in the sign language group. However, this gain was only for the width dimension, with less accuracy when estimating the length of their fingers. Effectively, sign language participants perceived their hands as smaller in comparison with controls. This followed recent findings by Coelho et al. (2019), which showed how professional baseball players perceived their hands to be smaller, and explained the benefit of having a smaller body part for precision movements.

Interestingly, this second study also showed modulation of the face representation due to expertise. Sign language practitioners showed a reduced overestimation of face width when compared to the control group, whilst they tended to underestimate the length of the face to a greater extent than controls. Again, these results showed sign language practitioners represented their face as smaller than controls. It was postulated that this improved representation should not only rely on the better processing of somatosensory information, but also on a more robust and accurate mental image of one’s own body.

Lastly, the gain showed in near-reaching space in hand representation for sign language interpreters was lost when the location judgements were carried out in far-reaching space. Hence, they underestimated their finger lengths to a greater degree in the unusual space. This finding supports the idea of the usual manual workspace influencing location judgements (Fraser & Harris, 2016), as this effect disappears in a new location.

From this pattern of results, it was concluded that modulation of size representation is specific to the type of expertise. Not only that, but contrary to what could be an intuitive conclusion, expertise does not necessarily make one more accurate. In reality, it guides the direction of the distortions in a way that benefits performance on a given task. On some occasions, expertise does improve representation, as seen in the magicians' study and in the width representation in sign language practitioners; whereas at other times, it does not, as seen in finger length perception in sign language experts and in baseball players (Coelho et al., 2019). Similarly, gains in proprioceptive localisation of body segments are only seen for highly trained postures in dancers, but these gains are not generalised to non-trained ones (Jola et al., 2011; Schmitt et al., 2005).

7.1.4 Involvement of sensorimotor cortical areas in the body size

In the same way that expertise modulates size representation of the hands and faces, brain injuries can also modulate it. In the first experiment in Chapter 5, the case study of AM was presented to explore the effect of a glioblastoma located in the left precentral area (hand knob). This pathology offered an opportunity to explore the effects that tumours can have in body size representation, especially considering the location of this tumour in the cortical areas that represent the hand (Sastre-Janer, 1998). Given that previous studies measuring the body model had postulated that the distortions of hand representation were linked to their homuncular representation (Longo & Haggard, 2010; Miller et al., 2016), some type of modulation was expected here.

AM presented with a distorted representation of hands, with particular misperception of the left hand in comparison with the control group. Most importantly, there were changes in the distortions after tumour resection, with overall reduction of

the distortions for both hands, but not face. This study confirmed the effects of a tumour in the cortical representation of the hand, and its involvement in body size representation and potential influence in motor control. This evidence further supported the importance of somatosensory areas to represent the size of the body.

7.1.5 Damage to parietal areas and effects in body size perception

Other relevant areas for body metrics are the parietal areas (Committeri et al., 2018, 2007), which can be targeted to modulate body size (Spitoni et al., 2013). Personal Neglect (PN) is a disorder associated to a disruption of different aspects of body representation, such as the topological map (Palermo et al., 2014) or body schema (Baas et al., 2011). PN is mainly due to damage in parietal areas (Committeri et al., 2007), which cause a generalised body representational disturbance, central to this disorder. However, the unique association between PN and own body size representation had rarely been investigated. With that in mind, in Experiment 2 in Chapter 5, the perceived size of hands and face was assessed in a group of patients with PN by using a size estimation task.

Patients with PN showed a more uncertain body representation, displaying a widely varied perceived range of sizes, compared to controls who tended to be more accurate in size estimations. As all patients had some degree of motor impairment, their performance was also compared with a group of patients after stroke, but without PN. Even though this second group also showed larger distortions than controls, these distortions were more evident for the left affected hand. Hence, this task was able to identify the effects of motor impairment in the perception of body size. These findings supported the idea of uncertain body representation (Rasmus, 2017) showing more susceptibility to different multisensory influences (Llorens et al., 2017). Overall, PN patients showed the maximum distortion due to a combination of motor impairments

together with uncertain stored body representation and attentional deficits (Committeri et al., 2018).

The two studies in Chapter 5 confirmed two points. Firstly, that sensorimotor areas do have an involvement in the size representation of the body. Somatosensory areas hold the point-to-point topological representation of skin surfaces (Penfield & Boldrey, 1937), which are not equally innervated. Hence, larger cortical areas will be dedicated to highly innervated body parts, such as fingers, in comparison with low-innervated ones (the back) (Medina & Coslett, 2016). Secondly, parietal areas (damaged in PN) caused disruption in regard to higher-order aspects of the representation of the metrics of the body. Indeed, parietal lobes are not only engaged in spatial processing, but also in the monitoring of body localisation and positions (Campbell et al., 2007), and storage of the structural and sensorimotor body representation (Corradi-Dell'Acqua et al., 2009; Hashimoto & Iriki, 2013; Tamè et al., 2017). Bilateral activation of the inferior parietal lobes is also associated with own body size perception (Hashimoto & Iriki, 2013). Therefore, a widespread network of cortical areas is involved in the metrics of the body.

7.1.6 Neuroplasticity of body size representation

The neuroplasticity of body representation was explored in the last two experiments in Chapter 6. It was of interest to consider whether the distortions in hand and face size representations could be actively modulated in healthy participants. For this reason, two of the main influences postulated for body representation were explored: somatosensory and visual (mental imagery), with a particular focus on cross-domain modulation.

In the first experiment in Chapter 6, cathodal tDCS over supramarginal gyrus (SMG) was administered to modulate the metric representation of the left contralateral

hand and face in a group of healthy adults. This area has been linked with the metrics of the body (Di Vita et al., 2016; Tamè et al., 2017), specifically the SMG in the right hemisphere (Corradi-Dell'Acqua et al., 2008; Tsakiris et al., 2008). However, there was no effect of this stimulation in size representation. Instead, and unexpectedly, the control active stimulation (administered to primary visual cortex, involved in mental imagery) modulated the size of the face, ameliorating the distortion of width. These results highlighted the relevance of the mental image of the body in the task when measuring the face. Moreover, the specific effect found for the face and not the hands suggested that the face was constructed visually, whereas somatosensory influences may be more relevant for the hands.

In order to explore this modulation for visual versus somatosensory influences further, Experiment 2 in Chapter 6 presented an exploration on the size estimation of the hands and face in a group of healthy adults after administration of passive sensory stimulation. Passive sensory stimulation was applied to either the face or the dominant hand, and participants had to estimate the size of their hands and face by choosing from an array of distorted pictures. Contrary to the previous experiment, modulation of size was only achieved when stimulating the dominant hand with passive stimulation, reducing the perceived distortion of its size. This modulation was not achieved when passive stimulation was administered for the face, indicating that somatosensory representation is more associated with the hands.

These two studies confirmed that the primacy of each type of information will vary depending on how the representation of each body part is constructed, onto which consideration must also be given for their functionality and use. The plasticity shown by the representation of the body is promising for the development of rehabilitation

strategies, which may consider these types of modulation for the specific body part affected.

7.2 Theoretical implications

Following the review of all the chapters, it became clear that certain topics were recurrent throughout the thesis. Here, I will present the main conclusions and theoretical implications of these findings.

7.2.1 Functionality and use

Overall, a growing body of evidence has been presented that supports the relevance of functionality and body part use to body size representation. Specifically, distortions found for the hands and face were linked to functionality and type of use for the body part. This aspect had not been thoroughly considered before, in particular for the representation of hands. Previous explanations of hand size representation mainly followed Longo's and Haggard's (2010) theoretical account, for which distortions of the body model were thought to reflect the inherent characteristics of early somatosensory maps. In this account, the direction of the distortions in hand representation were linked to the somatosensory components, such as the size and shape of receptive fields of the somatosensory neurons (oval-shaped) (Longo et al., 2015), and the differential cortical space dedicated for each finger (Longo, 2019; Longo & Haggard, 2012b; Longo et al., 2015). Hence, following Longo's and Haggard's (2010) original interpretation, the characteristic pattern of distortions of the hand (underestimation of length and overestimation of width) is due to the idiosyncrasy of cortical maps. However, in contrast to this explanation, they later found that the distortion of finger lengths was probably impacted by conceptual biases towards knuckles (Longo et al., 2015; Saulton et al., 2017). Moreover, Medina and

Duckett (2017) recently postulated that hand width overestimation is not due to a perceptual distortion, but to uncertainty. Hence, several influences were affecting the task and perceived hand size, but not much attention had been paid to functional aspects.

The analyses of the shift of locational responses presented in Chapter 3 helped lend further explanation for these distortions. In detail, functionality may be an inherent factor influencing the represented size of the body and its segments (Caggiano & Cocchini, 2020; K. D. Stone et al., 2018). That is, underestimation of fingers appeared associated to functional use of fingertips and their direction of movement, whereas the overestimation of hand width was associated with misallocation of less-functional fingers. The relevance of functionality was further supported in Chapter 4, in which magicians showed a clear advantage on representing the more functional fingers (thumb and index) in the unusual view (palmar view), associated to their expertise. Functional fingers, being extensively used in manual fine motor actions, are better represented (Longo, 2019; Longo & Haggard, 2012b; Longo et al., 2015). Hence, parting from a similar cortical representation, extensive practice modulates how the size of the body is perceived.

Furthermore, the type of use of the body part influences the direction of the distortions. Previous studies had shown how the movement capabilities of the ankle may underly the overestimation of width, which is not seen for the knee as it does not have the same degrees of freedom (K. D. Stone et al., 2018). This is also the case for the wrists, in comparison with the arms and hands (Longo, 2017c). The evidence in this thesis showed that the direction of distortion influenced size perception, in such a way that fingers were underestimated, whereas the lower face was overestimated. In particular, results in this thesis have shown how the effect is specific to the expertise

‘in hand’. In other words, the direction of the body size distortions are influenced by the type of expertise, not being generalised across body parts (K. D. Stone et al., 2018). In accordance with this, magicians’ fingers were represented more accurately (Experiment 1 in Chapter 4), being associated with high levels of dexterity (Cavina-Pratesi et al., 2011); whereas sign language interpreters (Experiment 2 in Chapter 4) benefited from an overall smaller representation of the hand and face for precision movements to sign, similarly to professional baseball players (Coelho et al., 2019). Along these lines, congenitally blind people tend to overestimate the size of their hands and arms, which is associated with their overreliance on these body parts to experience the world (Helders, 1986).

Therefore, one can also assume that impaired use of the body after insult would also affect its representation. Indeed, wheelchair users need to adapt to the chair, and even though they initially fail to recalibrate their new body dimensions (Higuchi, Takada, Matsuura, & Imanaka, 2004), they later adapt to include the assistive device in their representation (Pazzaglia, Galli, Scivoletto, & Molinari, 2013). They show different distortions of body size due to the differential use of their body (Fuentes, Pazzaglia, et al., 2013), and the incorporation of the chair within their body boundaries (Scandola et al., 2019). Similarly, learned non-use reduces the cortical representation of the affected limb (Hallett, 2001; Punt et al., 2013), which also has an impact on its size (Johnson et al., 2002; Lotze & Moseley, 2007; Matamala-Gomez et al., 2020). These findings support the idea of use-dependent plasticity (Johnson et al., 2002), which also influences size perception.

Lastly, the modulatory effects of expertise were specific to the manual workspace (Fraser & Harris, 2016). In other words, these were not present in a subdivision of space not linked to the expertise (far-reaching space), as seen in

Experiment 2 included in Chapter 4. Again, these results further support the idea of body representation being intrinsically linked to functional use of the body.

These results have important implications for further research, as training or rehabilitation packages can be bespoke designed to consider the different types of modulation. Moreover, these results confirm that body size representation is not static and is subject to multisensory influences and practice.

7.2.2 Multimodal conception of the body

Most of the research on the topic of body representation has focused on single sensory modalities, whereas we experience the world by integrating them. It is generally agreed that in order to build a coherent body awareness, information needs to be collected from multiple sources: touch, which is mediated by mechanoreceptors in the skin; proprioception gives us information regarding the position of the body in the space (both static and dynamic); the vestibular system helps with balance and assessment of motion; nociceptors are involved with pain perception; interoception is involved in unconscious regulation of internal homeostasis; vision helps us construct an image of our body (De Vignemont, 2010). Therefore, multisensory integration is necessary to maintain an accurate metric of the body (Perez-Marcos et al., 2018). Afferent (bottom-up) and efferent (top-down) information need to be combined to locate the body in space and to build a coherent representation (Di Vita et al., 2016).

All findings in this thesis suggest the consideration of a multisensory approach, such as the *Multimodality Thesis*, postulated by De Vignemont (2014). In this proposal, cross-modal interaction between sensory modalities is seen in information processing, and is required in order to construct the representation of the body size (De Vignemont, 2014). Following this framework, bodily experience will require the multisensory binding of bodily senses in order to obtain a coherent body

representation. From all the multimodal influences, the ones found to be of greatest relevance, and which have been explored in this thesis, are somatosensation and mental imagery, both being intrinsically linked (De Vignemont, 2014).

On one hand, somatosensation is necessary and influences the construction of the representation of the body size. The relevance of somatosensory information in size perception is evident when there is an interruption on its access. For example, one well-known physiological observation is the quick and temporary change in the size of the body parts with anaesthesia. When body parts are anaesthetised, these are perceived as larger than their real size (Gandevia & Phegan, 1999). This is due to increased anomalous efferent discharge after removal of afferent information, which is associated with a reduced cortical activity in the somatosensory area (Gandevia & Phegan, 1999). Similarly, patients after amputation experience a phantom limb that is perceived as progressively smaller, inside the stump (telescoping phenomena) (Ramachandran, 1993; Ramachandran & Hirstein, 1998), due to maladaptive plasticity of the somatosensory cortex (Flor et al., 2006; Giummarra et al., 2007). Supporting this, the case study of AM in Experiment 1 in Chapter 5 helped show how damage to sensorimotor cortical areas can have an effect in the metric representation of the body. In particular, the modulation was specific to the body area represented in the area of the tumour; the hands. Conversely, increments in somatosensory input can also modulate size, by creating an illusion. One of the typical examples is the *Pinocchio illusion* in which skin vibration on the tendons of the elbow causes the afferent signal to the brain that the elbow is extending (after stimulation of the biceps tendons) or flexing (stimulation of triceps tendons), causing the feeling of the hand moving. If the hand touches another body part (e.g., the nose), a subjective experience of stretching or shrinking will also be elicited, causing the illusion (Lackner, 1988). Similarly,

passive sensory stimulation in Experiment 2 in Chapter 6 was effective in modulating the size of the dominant stimulated hand, due to increased somatosensory afferent information. Hence, somatosensation has a primary role in body representation.

Most of the studies that have explored the body model of hands have postulated that distortions are intrinsically linked to somatosensory representation (Longo & Haggard, 2012a; Longo et al., 2015). However, as presented in this thesis, somatosensory information might not be the only sensory modality required for the construction of the body representation, as it is not accurate by itself. Simply put, the somatosensory cortical maps are highly distorted, and these distortions need to be corrected for an accurate body representation. Vision, or mental imagery, exert a strong influence in how the size of one's own body is represented (Ganea & Longo, 2017), and provide more accuracy to this representation (De Vignemont, 2014). For instance, in Experiment 1 included in Chapter 4, the effect of mental imagery 'improved' the accuracy of the hand representation, in situations in which proprioception was not as relevant. This effect has also been seen when judging the size of rubber hands rather than one's own hand (Saulton et al., 2016). This reliance on mental imagery, rather than just on proprioception, will vary depending on the sensory modality that is more critical for the task (Pazzaglia & Zantedeschi, 2016). Hence, when proprioception is not critical (such as in imagined conditions), mental imagery will be triggered.

Overall, there is a cross-modal interaction between the areas involved in mental imagery and the somatosensory cortex to construct a mental representation of the body size (Azañón, Tamè, Maravita, Linkenauger, Ferrè, Tajadura-Jiménez, Linkenauger, et al., 2016; De Vignemont, 2014; Peviani et al., 2019). This link between vision and somatosensory representation is quite straight forward. For example, vision modulates

the activity in the somatosensory cortex, improving tactile acuity (Taylor-Clarke et al., 2002). Cross-modal interaction is also seen in visual perceptual competition tasks, in which proprioceptive information on hand position influences visual awareness, with an advantage for congruent positions (Salomon et al., 2013). Based on multisensory integration principles (Moseley et al., 2012), incorporation of fake limbs has been achieved with effects in size perception. Virtual reality environments have helped further develop this type of body illusion, showing incorporation of virtual arms (Slater, Perez-Marcos, Ehrsson, & Sanchez-Vives, 2008) or virtual bodies (Petkova & Ehrsson, 2008; Slater, Spanlang, Sanchez-Vives, & Blanke, 2010). Cross-modal interactions of sensory information are also of relevance in rehabilitation. For instance, in the well-known mirror therapy, motor performance is improved by observing a reflection of an unaffected arm performing different movements (Ramachandran & Altschuler, 2009; Toh & Fong, 2012). On the contrary, disruption of this network is instead associated with disorders of body representation, such as Anorexia Nervosa (Favaro et al., 2012). Hence, a multimodal conception of body representation is supported in this thesis.

7.2.3 Specificity

Apart from the relevance of functionality of the body in its representation, this thesis has also demonstrated that cross-modal sensory influences in body representation are associated with specific body parts. In other words, each body part appears to have their own repertoire and fundamental modality. The evidence provided has confirmed this specificity, with the face relying more on visual information, whereas hands appeared more strongly affected by somatosensory information. This was supported by the finding that cathodal tDCS over the visual cortex (VC) did modulate face representation, but not the hands, as seen in Chapter 6 (Experiment 1).

Instead, there was an effect in hand representation when stimulated through passive sensory stimulation, but not for the face (Experiment 2 in Chapter 6). The face is considered more visual and pictorial representations (Chang et al., 2017; Keyes, 2012), which can explain the modulation in size perception due to estimation of primary visual areas. Alternatively, somatosensory information is prioritised for the hands, which integrate cross-modal information faster due to visuo-motor-proprioceptive intrinsic relationships within their use (Korb et al., 2017).

As explained in the recent study by Stone et al. (2018) , “[i]t seems that body representations are, at least in part, a function of the most prominent underlying sensory modality used to perceive the body part” (p. 22), and “each body part elicits their own repertoire of multimodal-based distortions” (p. 32). Hence, the way we construct the representation of a specific body part, will in turn, affect the relevance of the different types of information.

7.3 Concluding remarks

The collective evidence presented in this thesis has contributed to the field of the representation of the size of the body. In particular, it helped to integrate knowledge from previous studies focusing on the hands, expanding these to the face. This thesis has provided an improved method to consider hand representation, at the same time as developing a new one for the face. Further, insights into the effect of expertise and the malleability of these representations have been presented. In particular, due to the overwhelming number of disorders associated with a disrupted representation of the size of the body, modulatory capabilities for body representation ought to be understood as potential rehabilitative techniques (Slade & Brodie, 1994). In this thesis, modulation was achieved with readily accessible, non-invasive and cost-effective

techniques that could be easily implemented in clinical population. Overall, this was a thorough and interesting account of body size representation.

Each chapter has provided an account of the results, implications and theoretical approaches. Studies presented have ranged from healthy population (typical and atypical), to clinical population. As body representation is such a fundamental feature of our daily lives, research aiming to uncover changes across different groups or contexts is necessary to understand further this construct.

To conclude, the evidence presented here prompts for further research. Findings have also highlighted the vast and overwhelming complexity in the study of body representation and have provided encouraging attempts to understand it better. As shown, modulation of size representation can occur in two ways; through long-term training based on functionality and expertise, and through short-term modulation, easily achieved by manipulating afferent and efferent inputs. This thesis approached body size representation from a multimodal and multisensory perspective, and results support the theory that cross-modal mechanisms help contribute to the representation of body size. Limitations have been discussed for each study, which only account for the complexity of the topic. Indeed, some studies had small sample sizes that could be problematic in detecting changes. In others, different questions remained, which require further exploration. Moreover, most of the studies focussed on specific methods or single modulatory techniques in different groups of participants. Instead, a more thorough and complete study on body size representation should incorporate larger samples, a variety of tasks to tackle its multidimensionality, and different modulatory methods to explore their specificity. Still, the evidence provided has further contributed to research in this topic with interesting and compelling findings.

Bibliography

- Allen, J. S., Emmorey, K., Bruss, J., & Damasio, H. (2013). Neuroanatomical differences in visual, motor, and language cortices between congenitally deaf signers, hearing signers, and hearing non-signers. *Frontiers in Neuroanatomy*, 7(JUL), 1–10. <https://doi.org/10.3389/fnana.2013.00026>
- Ambron, E., Jax, S., Schettino, L., & Coslett, H. B. (2019). Increasing perceived hand size improves motor performance in individuals with stroke: a home-based training study. *PeerJ*, 7, e7114. <https://doi.org/10.7717/peerj.7114>
- Ambron, E., Jax, S., Schettino, L. F., & Coslett, H. B. (2018). Magnifying vision improves motor performance in individuals with stroke. *Neuropsychologia*, 119(June), 373–381. <https://doi.org/10.1016/j.neuropsychologia.2018.08.029>
- Ambron, E., Schettino, L. F., Coyle, M., Jax, S., & Coslett, H. B. (2017). When perception trips action! The increase in the perceived size of both hand and target matters in reaching and grasping movements. *Acta Psychologica*, 180(August), 160–168. <https://doi.org/10.1016/j.actpsy.2017.09.011>
- Ambron, E., White, N., Faseyitan, O., Kessler, S. K., Medina, J., & Coslett, H. B. (2018). Magnifying the view of the hand changes its cortical representation. A transcranial magnetic stimulation study. *Journal of Cognitive Neuroscience*. https://doi.org/10.1162/jocn_a_01266
- Ambroziak, K. B., Tamè, L., & Longo, M. R. (2018). Conceptual distortions of hand structure are robust to changes in stimulus information. *Consciousness and Cognition*. <https://doi.org/10.1016/j.concog.2018.01.002>
- Appollonio, I., Leone, M., Isella, V., Piamarta, F., Consoli, T., Villa, M. L., ... Nichelli, P. (2005). The frontal assessment battery (FAB): Normative values in an Italian population sample. *Neurological Sciences*. <https://doi.org/10.1007/s10072-005-0443-4>
- Arcara, G., Bisiacchi, P. S., Mapelli, D., Mondini, S., & Vestri, A. (2011). *Esame neuropsicologico breve 2 (ENB2): Una batteria di test per lo screening neuropsicologico*. Milano: R. Cortina.

- Arnold, P., & Mills, M. (2001). Memory for faces, shoes, and objects by deaf and hearing signers and hearing nonsigners. *Journal of Psycholinguistic Research*, 30(2), 185–195. <https://doi.org/10.1023/A:1010329912848>
- Auchus, M., Kose, G., & Allen, R. (1993). Body-image distortion and mental imagery. *Perceptual and Motor Skills*, 77(3 Pt 1), 719–728. <https://doi.org/10.2466/pms.1993.77.3.719>
- Avillac, M., Denève, S., Olivier, E., Pouget, A., & Duhamel, J. R. (2005). Reference frames for representing visual and tactile locations in parietal cortex. *Nature Neuroscience*. <https://doi.org/10.1038/nn1480>
- Azañón, E., Tamè, L., Maravita, A., Linkenauger, S. A. A., Ferrè, E. R. R., Tajadura-Jiménez, A., ... Linkenauger, S. A. A. (2016). Multimodal Contributions to Body Representation. *Multisensory Research*, 29(April), 635–661. <https://doi.org/10.1163/22134808-00002531>
- Azañón, E., Tamè, L., Maravita, A., Linkenauger, S. A., Ferrè, E. R., Tajadura-Jiménez, A., & Longo, M. R. (2016). Multimodal Contributions to Body Representation. *Multisensory Research*, 29(6–7), 635–661. <https://doi.org/10.1163/22134808-00002531>
- Baas, U., de Haan, B., Grässli, T., Karnath, H. O., Mueri, R., Perrig, W. J., ... Gutbrod, K. (2011). Personal neglect-A disorder of body representation? *Neuropsychologia*, 49(5), 898–905. <https://doi.org/10.1016/j.neuropsychologia.2011.01.043>
- Balslev, D., Christensen, L. O., Lee, J. H., Law, I., Paulson, O. B., & Miall, R. C. (2004). Enhanced Accuracy in Novel Mirror Drawing after Repetitive Transcranial Magnetic Stimulation-Induced Proprioceptive Deafferentation. *Journal of Neuroscience*, 24(43), 9698–9702. <https://doi.org/10.1523/JNEUROSCI.1738-04.2004>
- Barrett, L. F. (2017). The theory of constructed emotion: an active inference account of interoception and categorization. *Social Cognitive and Affective Neuroscience*. <https://doi.org/10.1093/scan/nsw154>
- Barry, D., Bates, M. E., & Labouvie, E. (2008). FAS and CFL Forms of Verbal Fluency Differ in Difficulty: A Meta-analytic Study. *Applied Neuropsychology*,

15(2), 97–106. <https://doi.org/10.1080/09084280802083863>

- Bassolino, M., Finisguerra, A., Canzoneri, E., Serino, A., & Pozzo, T. (2015). Dissociating effect of upper limb non-use and overuse on space and body representations. *Neuropsychologia*, *70*, 385–392. <https://doi.org/10.1016/j.neuropsychologia.2014.11.028>
- Batsikadze, G., Moliadze, V., Paulus, W., Kuo, M. F., & Nitsche, M. A. (2013). Partially non-linear stimulation intensity-dependent effects of direct current stimulation on motor cortex excitability in humans. *Journal of Physiology*, *591*(7), 1987–2000. <https://doi.org/10.1113/jphysiol.2012.249730>
- Baumard, J., & Osiurak, F. (2019). Is Bodily Experience an Epiphenomenon of Multisensory Integration and Cognition? *Frontiers in Human Neuroscience*, *13*(September), 1–6. <https://doi.org/10.3389/fnhum.2019.00316>
- Bellugi, U., & Klima, E. S. (2015). Sign Language. In *International Encyclopedia of the Social & Behavioral Sciences* (Second Ed, Vol. 21, pp. 928–933). Elsevier. <https://doi.org/10.1016/B978-0-08-097086-8.52018-2>
- Benedict, R. H. B., Schretlen, D., Groninger, L., & Brandt, J. (1998). Hopkins verbal learning test - Revised: Normative data and analysis of inter-form and test-retest reliability. *Clinical Neuropsychologist*, *12*(1), 43–55. <https://doi.org/10.1076/clin.12.1.43.1726>
- Benke, T., Luzzatti, C., & Vallar, G. (2004). Hermann Zingerle’s “Impaired Perception of the own Body Due to Organic Brain Disorders”: An Introductory Comment, and an Abridged Translation. *Cortex*, *40*(2), 265–274. [https://doi.org/10.1016/S0010-9452\(08\)70121-7](https://doi.org/10.1016/S0010-9452(08)70121-7)
- Benton, A. L. (1968). Differential behavioral effects in frontal lobe disease. *Neuropsychologia*. [https://doi.org/10.1016/0028-3932\(68\)90038-9](https://doi.org/10.1016/0028-3932(68)90038-9)
- Berlucchi, G., & Aglioti, S. (1997). The body in the brain: Neural bases of corporeal awareness. *Trends in Neurosciences*, *20*(12), 560–564. [https://doi.org/10.1016/S0166-2236\(97\)01136-3](https://doi.org/10.1016/S0166-2236(97)01136-3)
- Berlucchi, G., & Aglioti, S. M. (2010). The body in the brain revisited. *Experimental Brain Research*, *200*(1), 25–35. <https://doi.org/10.1007/s00221-009-1970-7>
- Bermúdez, J. L. E., Marcel, A. J., & Eilan, N. E. (1995). *The body and the self*.

London: The MIT Press.

- Berti, A. (2013). This limb is mine but i do not want it: From anatomy to body ownership. *Brain*. <https://doi.org/10.1093/brain/aws346>
- Bertrand, A. M., Fournier, K., Wick Brasey, M.-G., Kaiser, M.-L., Frischknecht, R., & Diserens, K. (2015). Reliability of maximal grip strength measurements and grip strength recovery following a stroke. *Journal of Hand Therapy*, 28(4), 356–363. <https://doi.org/10.1016/j.jht.2015.04.004>
- Beschin, N., & Robertson, I. H. (1997). Personal versus extrapersonal neglect: a group study of their dissociation using a reliable clinical test. *Cortex*, 33(2), 379–384. [https://doi.org/10.1016/S0010-9452\(08\)70013-3](https://doi.org/10.1016/S0010-9452(08)70013-3)
- Beste, C., & Dinse, H. R. (2013). Learning without training. *Current Biology*, 23(11), R489–R499. <https://doi.org/10.1016/j.cub.2013.04.044>
- Bettger, J. G., Emmorey, K., McCullough, S. H., & Bellugi, U. (1997). Enhanced Facial Discrimination: Effects of Experience With American Sign Language. *Journal of Deaf Studies and Deaf Education*, 2(4), 223–233. <https://doi.org/10.1093/oxfordjournals.deafed.a014328>
- Bianchi, I., Savardi, U., & Bertamini, M. (2008). Estimation and representation of head size (people overestimate the size of their head - Evidence starting from the 15th century). *British Journal of Psychology*, 99(4), 513–531. <https://doi.org/10.1348/000712608X304469>
- Bisiach, E., & Luzzatti, C. (1978). Unilateral Neglect of Representational Space. *Cortex*, 14(1), 129–133. [https://doi.org/10.1016/S0010-9452\(78\)80016-1](https://doi.org/10.1016/S0010-9452(78)80016-1)
- Bisiach, E., Perani, D., Vallar, G., & Berti, A. (1986). Unilateral neglect: Personal and extra-personal. *Neuropsychologia*, 24(6), 759–767. [https://doi.org/10.1016/0028-3932\(86\)90075-8](https://doi.org/10.1016/0028-3932(86)90075-8)
- Bisiach, E., & Vallar, G. (2000). Unilateral neglect in humans. In F. Boller & J. Grafman (Eds.), *Handbook of Neuropsychology* (pp. 459–502). Elsevier.
- Blangero, A., Rossetti, Y., Honoré, J., & Pisella, L. (2009). Influence of gaze direction on pointing to unseen proprioceptive targets. *Advances in Cognitive Psychology*. <https://doi.org/10.2478/v10053-008-0039-7>

- Bolognini, N., Olgiati, E., Maravita, A., Ferraro, F., & Fregni, F. (2013). Motor and parietal cortex stimulation for phantom limb pain and sensations. *Pain, 154*(8), 1274–1280. <https://doi.org/10.1016/j.pain.2013.03.040>
- Borchers, S., Hauser, T. K., & Himmelbach, M. (2011). Bilateral hand representations in human primary proprioceptive areas. *Neuropsychologia, 49*(12), 3383–3391. <https://doi.org/10.1016/j.neuropsychologia.2011.08.013>
- Bowden, S. C., Fowler, K. S., Bell, R. C., Whelan, G., Clifford, C. C., Ritter, A. J., & Long, C. M. (1998). The reliability and internal validity of the Wisconsin Card Sorting Test. *Neuropsychological Rehabilitation*. <https://doi.org/10.1080/713755573>
- Bowers, D., & Heilman, K. M. (1980). Pseudoneglect: Effects of hemispace on a tactile line bisection task. *Neuropsychologia, 18*(4–5), 491–498. [https://doi.org/10.1016/0028-3932\(80\)90151-7](https://doi.org/10.1016/0028-3932(80)90151-7)
- Brasil-Neto, J. P., & de Lima, A. C. (2008). Sensory deficits in the unaffected hand of hemiparetic stroke patients. *Cognitive and Behavioral Neurology, 21*(4), 202–205. <https://doi.org/10.1097/wnn.0b013e3181864a24>
- Bremner, A. J., Holmes, N. P., & Spence, C. (2008). Infants lost in (peripersonal) space? *Trends in Cognitive Sciences, 12*(8), 298–305. <https://doi.org/10.1016/j.tics.2008.05.003>
- Brooks, K. R., Mond, J. M., Stevenson, R. J., & Stephen, I. D. (2016). Body Image Distortion and Exposure to Extreme Body Types: Contingent Adaptation and Cross Adaptation for Self and Other. *Frontiers in Neuroscience, 10*(JUL). <https://doi.org/10.3389/fnins.2016.00334>
- Brunoni, A. R., Nitsche, M. A., Bolognini, N., Bikson, M., Wagner, T., Merabet, L., ... Fregni, F. (2012). Clinical research with transcranial direct current stimulation (tDCS): Challenges and future directions. *Brain Stimulation, 5*(3), 175–195. <https://doi.org/10.1016/j.brs.2011.03.002>
- Burin, D., Livelli, A., Garbarini, F., Fossataro, C., Folegatti, A., Gindri, P., & Pia, L. (2015). Are movements necessary for the sense of body ownership? evidence from the rubber hand illusion in pure hemiplegic patients. *PLoS ONE, 10*(3), 1–12. <https://doi.org/10.1371/journal.pone.0117155>

- Burzynska, A., Finc, K., Taylor, B., Kramer, A., & Knecht, A. (2017). The Dancing Brain: Structural and Functional Signatures of Expert Dance Training. *Frontiers in Human Neuroscience*, *11*(November).
<https://doi.org/10.3389/fnhum.2017.00566>
- Buxbaum, L. J., & Coslett, H. B. (2001). Specialised structural descriptions for human body parts: Evidence from autotopagnosia. *Cognitive Neuropsychology*, *18*(4), 289–306. <https://doi.org/10.1080/02643290126172>
- Buxbaum, L. J., Ferraro, M. K., Veramonti, T., Farne, A., Whyte, J., Ladavas, E., ... Coslett, H. B. (2004). Hemispatial neglect: Subtypes, neuroanatomy, and disability. *Neurology*, *62*(5), 749–756.
<https://doi.org/10.1212/01.WNL.0000113730.73031.F4>
- Buxbaum, L. J., Giovannetti, T., & Libon, D. (2000). The role of the dynamic body schema in praxis: Evidence from primary progressive apraxia. *Brain and Cognition*. <https://doi.org/10.1006/brcg.2000.1227>
- Byrne, P., Becker, S., & Burgess, N. (2007). Remembering the past and imagining the future: A neural model of spatial memory and imagery. *Psychological Review*, *114*(2), 340–375. <https://doi.org/10.1037/0033-295X.114.2.340>
- Caggiano, P., Beschin, N., & Cocchini, G. (2014). Personal neglect following unilateral right and left brain damage. *Procedia - Social and Behavioral Sciences*, *140*, 164–167. <https://doi.org/10.1016/j.sbspro.2014.04.403>
- Caggiano, P., & Cocchini, G. (2020). The functional body: does body representation reflect functional properties? *Experimental Brain Research*, *238*(1), 153–169.
<https://doi.org/10.1007/s00221-019-05705-w>
- Caggiano, P., & Jehkonen, M. (2018). The ‘Neglected’ Personal Neglect. *Neuropsychology Review*, *28*(4), 417–435. <https://doi.org/10.1007/s11065-018-9394-4>
- Callahan, C. (2005). Facial Disfigurement and Sense of Self in Head and Neck Cancer. *Social Work in Health Care*, *40*(2), 73–87.
https://doi.org/10.1300/J010v40n02_05
- Campbell, R., MacSweeney, M., & Waters, D. (2007). Sign Language and the Brain: A Review. *Journal of Deaf Studies and Deaf Education*, *13*(1), 3–20.

<https://doi.org/10.1093/deafed/enm035>

Canzoneri, E., Ferrè, E. R., & Haggard, P. (2014). Combining proprioception and touch to compute spatial information. *Experimental Brain Research*.

<https://doi.org/10.1007/s00221-014-3842-z>

Capek, C. M., McGuire, P. K., Campbell, R., David, A. S., Woll, B., Brammer, M. J., ... Waters, D. (2008). Hand and Mouth: Cortical Correlates of Lexical Processing in British Sign Language and Speechreading English. *Journal of Cognitive Neuroscience*, 20(7), 1220–1234.

<https://doi.org/10.1162/jocn.2008.20084>

Cardinali, L. (2011). *Body schema plasticity after tool-use. Human health and pathology. Université Claude Bernard-Lyon I*. Retrieved from

<http://medcontent.metapress.com/index/A65RM03P4874243N.pdf>

Cardinali, L., Frassinetti, F., Brozzoli, C., Urquizar, C., Roy, A. C., & Farnè, A. (2009). Tool-use induces morphological updating of the body schema. *Current Biology*. <https://doi.org/10.1016/j.cub.2009.05.009>

Carey, M., Knight, R., & Preston, C. (2019). Distinct neural response to visual perspective and body size in the extrastriate body area. *Behavioural Brain Research*, 372(February). <https://doi.org/10.1016/j.bbr.2019.112063>

Carruthers, G. (2008). Types of body representation and the sense of embodiment. *Consciousness and Cognition*, 17(4), 1302–1316.

<https://doi.org/10.1016/j.concog.2008.02.001>

Casey, S. J., & Newell, F. N. (2005). The role of long-term and short-term familiarity in visual and haptic face recognition. *Experimental Brain Research*, 166(3–4), 583–591. <https://doi.org/10.1007/s00221-005-2398-3>

Caulo, M., Briganti, C., Mattei, P. A., Perfetti, B., Ferretti, A., Romani, G. L., ... Colosimo, C. (2007). New morphologic variants of the hand motor cortex as seen with MR imaging in a large study population. *American Journal of Neuroradiology*. <https://doi.org/10.3174/ajnr.A0597>

Cavina-Pratesi, C., Kuhn, G., Ietswaart, M., & da Milner, A. D. (2011). The magic grasp: Motor expertise in deception. *PLoS ONE*, 6(2).

<https://doi.org/10.1371/journal.pone.0016568>

- Chang, C.-H., Nemrodov, D., Lee, A. C. H., & Nestor, A. (2017). Memory and Perception-based Facial Image Reconstruction. *Scientific Reports*, 7(1), 6499. <https://doi.org/10.1038/s41598-017-06585-2>
- Chen-Sea, M. J. (2000). Validating the draw-a-man test as a personal neglect test. *American Journal of Occupational Therapy*, 54(4), 391–397. <https://doi.org/10.5014/ajot.54.4.391>
- Cherner, M., Suarez, P., Lazzaretto, D., Fortuny, L. A. i., Mindt, M. R., Dawes, S., ... Heaton, R. (2007). Demographically corrected norms for the Brief Visuospatial Memory Test-revised and Hopkins Verbal Learning Test-revised in monolingual Spanish speakers from the U.S.-Mexico border region. *Archives of Clinical Neuropsychology*, 22(3), 343–353. <https://doi.org/10.1016/j.acn.2007.01.009>
- Cioffi, M. C., Cocchini, G., Banissy, M. J., & Moore, J. W. (2017). Ageing and agency: Age-related changes in susceptibility to illusory experiences of control. *Royal Society Open Science*, 4(5), 0–8. <https://doi.org/10.1098/rsos.161065>
- Clarke, S., Ragli, L., Janzer, R. C., Assal, G., & de Tribolet, N. (1996). Phantom face. *NeuroReport*, 7(18), 2853–2858. <https://doi.org/10.1097/00001756-199611250-00009>
- Classen, J., Steinfelder, B., Liepert, J., Stefan, K., Celnik, P., Cohen, L. G., ... Hallett, M. (2000). Cutaneomotor integration in humans is somatotopically organized at various levels of the nervous system and is task dependent. *Experimental Brain Research*. <https://doi.org/10.1007/s002210050005>
- Cocchini, G., Beschin, N., & Della Sala, S. (2018). Unawareness for Motor Impairment and Distorted Perception of Task Difficulty. *Journal of the International Neuropsychological Society*, 24(1), 45–56. <https://doi.org/10.1017/S1355617717000662>
- Cocchini, G., Beschin, N., & Jehkonen, M. (2001). The Fluff Test: A simple task to assess body representation neglect. *Neuropsychological Rehabilitation*, 11(1), 17–31. <https://doi.org/10.1080/09602010042000132>
- Cocchini, G., Galligan, T., Mora, L., & Kuhn, G. (2018). The magic hand: Plasticity of mental hand representation. *Quarterly Journal of Experimental Psychology*,

174702181774160. <https://doi.org/10.1177/1747021817741606>

- Coelho, L. A., & Gonzalez, C. L. (2018a). The visual and haptic contributions to hand perception. *Psychological Research*, *82*(5), 866–875.
<https://doi.org/10.1007/s00426-017-0870-x>
- Coelho, L. A., & Gonzalez, C. L. R. (2018b). Chubby hands or little fingers: sex differences in hand representation. *Psychological Research*.
<https://doi.org/10.1007/s00426-018-1003-x>
- Coelho, L. A., Schacher, J. P., Scammel, C., Doan, J. B., & Gonzalez, C. L. R. (2019). Long- but not short-term tool-use changes hand representation. *Experimental Brain Research*, *237*(1), 137–146. <https://doi.org/10.1007/s00221-018-5408-y>
- Coelho, L. A., Zaninelli, G., & Gonzalez, C. L. R. (2017). A kinematic examination of hand perception. *Psychological Research*, *81*(6), 1224–1231.
<https://doi.org/10.1007/s00426-016-0815-9>
- Collin, C., & Wade, D. (1990). Assessing motor impairment after stroke: A pilot reliability study. *Journal of Neurology Neurosurgery and Psychiatry*, *53*(7), 576–579. <https://doi.org/10.1136/jnnp.53.7.576>
- Committeri, G., Piervincenzi, C., & Pizzamiglio, L. (2018). Personal neglect: A comprehensive theoretical and anatomo-clinical review. *Neuropsychology*, *32*(3), 269–279. <https://doi.org/10.1037/neu0000409>
- Committeri, G., Pitzalis, S., Galati, G., Patria, F., Pelle, G., Sabatini, U., ... Pizzamiglio, L. (2007). Neural bases of personal and extrapersonal neglect in humans. *Brain*, *130*(2), 431–441. <https://doi.org/10.1093/brain/awl265>
- Cooper, P. J., Taylor, M. J., Cooper, Z., & Fairbum, C. G. (1987). The development and validation of the body shape questionnaire. *International Journal of Eating Disorders*. [https://doi.org/10.1002/1098-108X\(198707\)6:4<485::AID-EAT2260060405>3.0.CO;2-O](https://doi.org/10.1002/1098-108X(198707)6:4<485::AID-EAT2260060405>3.0.CO;2-O)
- Cormier, K., Fenlon, J., & Schembri, A. (2015). Indicating verbs in British Sign Language favour motivated use of space. *Open Linguistics*, *1*(1), 684–707.
<https://doi.org/10.1515/opli-2015-0025>
- Corradi-Dell'Acqua, C., Hesse, M. D., Rumiati, R. I., & Fink, G. R. (2008). Where is

a nose with respect to a foot? The left posterior parietal cortex processes spatial relationships among body parts. *Cerebral Cortex*, 18(12), 2879–2890.
<https://doi.org/10.1093/cercor/bhn046>

Corradi-Dell'Acqua, C., Tomasino, B., & Fink, G. R. (2009). What Is the Position of an Arm Relative to the Body? Neural Correlates of Body Schema and Body Structural Description. *Journal of Neuroscience*, 29(13), 4162–4171.
<https://doi.org/10.1523/jneurosci.4861-08.2009>

Corti, C., Poggi, G., Massimino, M., Bardoni, A., Borgatti, R., & Urgesi, C. (2018). Visual perception and spatial transformation of the body in children and adolescents with brain tumor. *Neuropsychologia*, 120(February), 124–136.
<https://doi.org/10.1016/j.neuropsychologia.2018.10.012>

Coslett, H. B. (1998). Evidence for a disturbance of the body schema in neglect. *Brain and Cognition*, 37(37), 527–544. <https://doi.org/10.1006/brcg.1998.1011>

Costa, T. L., Lapenta, O. M., Boggio, P. S., & Ventura, D. F. (2015). Transcranial direct current stimulation as a tool in the study of sensory-perceptual processing. *Attention, Perception, & Psychophysics*, 77(6), 1813–1840.
<https://doi.org/10.3758/s13414-015-0932-3>

Cowdrey, F. A., Filippini, N., Park, R. J., Smith, S. M., & McCabe, C. (2014). Increased resting state functional connectivity in the default mode network in recovered anorexia nervosa. *Human Brain Mapping*.
<https://doi.org/10.1002/hbm.22202>

Crawford, J. R., & Garthwaite, P. H. (2002). Investigation of the single case in neuropsychology: Confidence limits on the abnormality of test scores and test score differences. *Neuropsychologia*. [https://doi.org/10.1016/S0028-3932\(01\)00224-X](https://doi.org/10.1016/S0028-3932(01)00224-X)

Crawford, J. R., Garthwaite, P. H., & Porter, S. (2010). Point and interval estimates of effect sizes for the case-controls design in neuropsychology: Rationale, methods, implementations, and proposed reporting standards. *Cognitive Neuropsychology*. <https://doi.org/10.1080/02643294.2010.513967>

Crawford, J. R., & Howell, D. C. (1998). Comparing an individual's test score against norms derived from small samples. *Clinical Neuropsychologist*.

<https://doi.org/10.1076/clin.12.4.482.7241>

- Critchley, M. (1979). Corporeal awareness: body image; body scheme. In *The divine banquet of the brain and other essays* (pp. 99–105). New York: Raven Press.
- Cullari, S., Vosburgh, M., Shotwell, A., Inzodda, J., & Davenport, W. (2002). Body-image Assessment: A Review and Evaluation of a New Computer-aided Measurement Technique. *North American Journal of Psychology*.
- D'Amour, S., & Harris, L. R. (2017). Perceived face size in healthy adults. *PLOS ONE*, *12*(5), e0177349. <https://doi.org/10.1371/journal.pone.0177349>
- D'Amour, S., & Harris, L. R. (2019). The Representation of Body Size: Variations With Viewpoint and Sex. *Frontiers in Psychology*. <https://doi.org/10.3389/fpsyg.2019.02805>
- D'Angelo, M., di Pellegrino, G., Seriani, S., Gallina, P., & Frassinetti, F. (2018). The sense of agency shapes body schema and peripersonal space. *Scientific Reports*, *8*(1), 1–11. <https://doi.org/10.1038/s41598-018-32238-z>
- Dagsdóttir, L. K., Skyt, I., Vase, L., Baad-Hansen, L., Castrillon, E., & Svensson, P. (2016). Reports of perceptual distortion of the face are common in patients with different types of chronic oro-facial pain. *Journal of Oral Rehabilitation*. <https://doi.org/10.1111/joor.12383>
- Danckert, J., & Ferber, S. (2006). Revisiting unilateral neglect. *Neuropsychologia*. <https://doi.org/10.1016/j.neuropsychologia.2005.09.004>
- Dandu, B., Kuling, I. A., & Visell, Y. (2018). Where are my fingers? Assessing multi-digit proprioceptive localization. In *2018 IEEE Haptics Symposium (HAPTICS)* (Vol. 2018-March, pp. 133–138). IEEE. <https://doi.org/10.1109/HAPTICS.2018.8357165>
- Darling, S., Uytman, C., Allen, R. J., Havelka, J., & Pearson, D. G. (2015). Body image, visual working memory and visual mental imagery. *PeerJ*, *2015*(2), 1–22. <https://doi.org/10.7717/peerj.775>
- De Schotten, M. T., Dell'Acqua, F., Forkel, S. J., Simmons, A., Vergani, F., Murphy, D. G. M., & Catani, M. (2011). A lateralized brain network for visuospatial attention. *Nature Neuroscience*. <https://doi.org/10.1038/nn.2905>

- De Vignemont, F. (2010). Body schema and body image—Pros and cons. *Neuropsychologia*, *48*(3), 669–680.
<https://doi.org/10.1016/j.neuropsychologia.2009.09.022>
- De Vignemont, F. (2014). A multimodal conception of bodily awareness. *Mind*, *123*(492), 989–1020. <https://doi.org/10.1093/mind/fzu089>
- De Vignemont, F., Ehrsson, H. H., & Haggard, P. (2005). Bodily illusions modulate tactile perception. *Current Biology*, *15*(14), 1286–1290.
<https://doi.org/10.1016/j.cub.2005.06.067>
- De Vignemont, F., Majid, A., Jola, C., & Haggard, P. (2009). Segmenting the body into parts: Evidence from biases in tactile perception. *Quarterly Journal of Experimental Psychology*. <https://doi.org/10.1080/17470210802000802>
- Debowska, W., Wolak, T., Nowicka, A., Kozak, A., Szwed, M., & Kossut, M. (2016). Functional and structural neuroplasticity induced by short-term tactile training based on braille reading. *Frontiers in Neuroscience*, *10*(OCT), 1–13.
<https://doi.org/10.3389/fnins.2016.00460>
- Demeurisse, G., Demol, O., & Robaye, E. (1980). Motor Evaluation in Vascular Hemiplegia. *European Neurology*, *19*(6), 382–389.
<https://doi.org/10.1159/000115178>
- Di Vita, A., Boccia, M., Palermo, L., & Guariglia, C. (2016). To move or not to move, that is the question! Body schema and non-action oriented body representations: An fMRI meta-analytic study. *Neuroscience and Biobehavioral Reviews*, *68*, 37–46. <https://doi.org/10.1016/j.neubiorev.2016.05.005>
- Di Vita, A., Palermo, L., Boccia, M., & Guariglia, C. (2019). Topological map of the body in post-stroke patients: Lesional and hodological aspects. *Neuropsychology*, *33*(4), 499–507. <https://doi.org/10.1037/neu0000536>
- Di Vita, A., Palermo, L., Piccardi, L., Di Tella, J., Propato, F., & Guariglia, C. (2017). Body representation alterations in personal but not in extrapersonal neglect patients. *Applied Neuropsychology: Adult*, *24*(4), 308–317.
<https://doi.org/10.1080/23279095.2016.1174866>
- Di Vita, A., Palermo, L., Piccardi, L., & Guariglia, C. (2015). Peculiar body representation alterations in hemineglect: a case report. *Neurocase*, *21*(6), 697–

706. <https://doi.org/10.1080/13554794.2014.974620>

Diamond, R., & Carey, S. (1986). Why Faces Are and Are Not Special. An Effect of Expertise. *Journal of Experimental Psychology: General*.

<https://doi.org/10.1037/0096-3445.115.2.107>

Dijkerman, H. C., & de Haan, E. H. F. (2007). Somatosensory processes subserving perception and action. *Behavioral and Brain Sciences*, 30(2), 189–239.

<https://doi.org/10.1017/S0140525X07001392>

Dinse, H. R., Gatica Tossi, M., Tegenthoff, M., & Kalisch, T. (2011). Sensory stimulation for augmenting perception, sensorimotor behaviour and cognition. In I. Segev & H. Markram (Eds.), *Augmenting cognition* (pp. 11–39). EPFL Press.

Dinse, H. R., Ragert, P., Pleger, B., Schwenkreis, P., & Tegenthoff, M. (2003). Pharmacological modulation of perceptual learning and associated cortical reorganization. *Science*, 301(5629), 91–94.

<https://doi.org/10.1126/science.1085423>

Dohle, C., Püllen, J., Nakaten, A., Küst, J., Rietz, C., & Karbe, H. (2009). Mirror Therapy Promotes Recovery From Severe Hemiparesis: A Randomized Controlled Trial. *Neurorehabilitation and Neural Repair*, 23(3), 209–217.

<https://doi.org/10.1177/1545968308324786>

Downing, P. E. (2001). A Cortical Area Selective for Visual Processing of the Human Body. *Science*, 293(5539), 2470–2473.

<https://doi.org/10.1126/science.1063414>

Downing, P. E., & Peelen, M. V. (2016). Body selectivity in occipitotemporal cortex: Causal evidence. *Neuropsychologia*, 83, 138–148.

<https://doi.org/10.1016/j.neuropsychologia.2015.05.033>

Dreyer, D. A., Loe, P. R., Metz, C. B., & Whitsel, B. L. (1975). Representation of head and face in postcentral gyrus of the macaque. *Journal of Neurophysiology*, 38, 714–733. <https://doi.org/10.1152/jn.1975.38.3.714>

Dubois, B., Slachevsky, A., Litvan, I., & Pillon, B. (2000). The FAB: A frontal assessment battery at bedside. *Neurology*, 55(11), 1621–1626.

<https://doi.org/10.1212/WNL.55.11.1621>

- Dubuisson, N., Bauer, A., Buckley, M., Gilbert, R., Paterson, A., Marta, M., ... Thomson, A. (2017). Validation of an environmentally-friendly and affordable cardboard 9-hole peg test. *Multiple Sclerosis and Related Disorders*, 17(April), 172–176. <https://doi.org/10.1016/j.msard.2017.08.002>
- Duncan, R. O., & Boynton, G. M. (2007). Tactile hyperacuity thresholds correlate with finger maps in primary somatosensory cortex (S1). *Cerebral Cortex*, 17(12), 2878–2891. <https://doi.org/10.1093/cercor/bhm015>
- Ebeling, U., Schmid, U. D., Ying, H., & Reulen, H. J. (1992). Safe surgery of lesions near the motor cortex using intra-operative mapping techniques: a report on 50 patients. *Acta Neurochirurgica*, 119(1–4), 23–28. <https://doi.org/10.1007/BF01541777>
- Ebied, A. M., Kemp, G. J., & Frostick, S. P. (2004). The role of cutaneous sensation in the motor function of the hand. *Journal of Orthopaedic Research*, 22(4), 862–866. <https://doi.org/10.1016/j.orthres.2003.12.005>
- Ehrsson, H. H., Wiech, K., Weiskopf, N., Dolan, R. J., & Passingham, R. E. (2007). Threatening a rubber hand that you feel is yours elicits a cortical anxiety response. *Proceedings of the National Academy of Sciences*, 104(23), 9828–9833. <https://doi.org/10.1073/pnas.0610011104>
- Ekroll, V., Sayim, B., Van Der Hallen, R., & Wagemans, J. (2016). Illusory Visual Completion of an Object's Invisible Backside Can Make Your Finger Feel Shorter. *Current Biology*, 26(8), 1029–1033. <https://doi.org/10.1016/j.cub.2016.02.001>
- El-Sais, W. M., & Mohammad, W. S. (2014). Influence of Different Testing Postures on Hand Grip Strength. *European Scientific Journal*, 10(36), 290–301.
- Emmorey, K. (2001). Space on hand: The exploitation of signing space to illustrate abstract thought. In M. Gattis (Ed.), *Spatial schemas and abstract thought* (pp. 147–174). The MIT Press.
- Emmorey, K. (2006). The signer as an embodied mirror neuron system: Neural mechanisms underlying sign language and action. *Action to Language Via the Mirror Neuron System*, 110–135. <https://doi.org/10.1017/CBO9780511541599.005>

- Emmorey, K., Allen, J. S., Bruss, J., Schenker, N., & Damasio, H. (2003). A morphometric analysis of auditory brain regions in congenitally deaf adults. *Proceedings of the National Academy of Sciences of the United States of America*. <https://doi.org/10.1073/pnas.1730169100>
- Emmorey, K., Bosworth, R., & Kraljic, T. (2009). Visual feedback and self-monitoring of sign language. *Journal of Memory and Language*, *61*(3), 398–411. <https://doi.org/10.1016/j.jml.2009.06.001>
- Emmorey, K., Kosslyn, S. M., & Bellugi, U. (1993). Visual imagery and visual-spatial language: Enhanced imagery abilities in deaf and hearing ASL signers. *Cognition*, *46*(2), 139–181. [https://doi.org/10.1016/0010-0277\(93\)90017-P](https://doi.org/10.1016/0010-0277(93)90017-P)
- Emmorey, K., & McCullough, S. (2009). The bimodal bilingual brain: Effects of sign language experience. *Brain and Language*, *109*(2–3), 124–132. <https://doi.org/10.1016/J.BANDL.2008.03.005>
- Emmorey, K., Mehta, S., & Grabowski, T. J. (2007). The neural correlates of sign versus word production. *NeuroImage*, *36*(1), 202–208. <https://doi.org/10.1016/j.neuroimage.2007.02.040>
- Emmorey, K., Thompson, R., & Colvin, R. (2009). Eye gaze during comprehension of American sign language by native and beginning signers. *Journal of Deaf Studies and Deaf Education*, *14*(2), 237–243. <https://doi.org/10.1093/deafed/enn037>
- Eshkevari, E., Rieger, E., Longo, M. R., Haggard, P., & Treasure, J. (2012). Increased plasticity of the bodily self in eating disorders. *Psychological Medicine*, *42*(4), 819–828. <https://doi.org/10.1017/S0033291711002091>
- Espeset, E. M. S., Gulliksen, K. S., Nordbø, R. H. S., Skårderud, F., & Holte, A. (2012). Fluctuations of Body Images in Anorexia Nervosa: Patients' Perception of Contextual Triggers. *Clinical Psychology and Psychotherapy*, *19*(6), 518–530. <https://doi.org/10.1002/cpp.760>
- Farnè, A., Serino, A., & Làdavas, E. (2007). Dynamic Size-Change of Peri-Hand Space Following Tool-Use: Determinants and Spatial Characteristics Revealed Through Cross-Modal Extinction. *Cortex*, *43*(3), 436–443. [https://doi.org/10.1016/S0010-9452\(08\)70468-4](https://doi.org/10.1016/S0010-9452(08)70468-4)

- Faul, F., Erdfelder, E., Buchner, A., & Lang, A.-G. (2009). Statistical power analyses using G*Power 3.1: tests for correlation and regression analyses. *Behavior Research Methods*, *41*(4), 1149–1160. <https://doi.org/10.3758/BRM.41.4.1149>
- Favaro, A., Santonastaso, P., Manara, R., Bosello, R., Bommarito, G., Tenconi, E., & Di Salle, F. (2012). Disruption of visuospatial and somatosensory functional connectivity in anorexia nervosa. *Biological Psychiatry*, *72*(10), 864–870. <https://doi.org/10.1016/j.biopsych.2012.04.025>
- Feldman, D. E. (2000). Inhibition and plasticity. *Nature Neuroscience*, *3*(4), 303–304. <https://doi.org/10.1038/73849>
- Felisberti, F. M., & Musholt, K. (2014). Self-face perception: Individual differences and discrepancies associated with mental self-face representation, attractiveness and self-esteem. *Psychology & Neuroscience*, *7*(2), 65–72. <https://doi.org/10.3922/j.psns.2014.013>
- Ferretti, G. (2016). Through the forest of motor representations. *Consciousness and Cognition*, *43*, 177–196. <https://doi.org/10.1016/j.concog.2016.05.013>
- Fess, E., & Moran, C. (1981). *Clinical assessment recommendations: American Society of Hand Therapists. Garner: the Society.*
- First, M. B., & Fisher, C. E. (2012). Body Integrity Identity Disorder: The Persistent Desire to Acquire a Physical Disability. *Psychopathology*, *45*(1), 3–14. <https://doi.org/10.1159/000330503>
- Flor, H., Mühlnickel, W., Karl, A., Denke, C., Grüsser, S., Kurth, R., & Taub, E. (2000). A neural substrate for nonpainful phantom limb phenomena. *NeuroReport*, *11*(7), 1407–1411. <https://doi.org/10.1097/00001756-200005150-00011>
- Flor, H., Nikolajsen, L., & Staehelin Jensen, T. (2006). Phantom limb pain: a case of maladaptive CNS plasticity? *Nature Reviews Neuroscience*, *7*(11), 873–881. <https://doi.org/10.1038/nrn1991>
- Folstein, M. F., Folstein, S. E., & McHugh, P. R. (1975). “Mini-mental state.” *Journal of Psychiatric Research*, *12*(3), 189–198. [https://doi.org/10.1016/0022-3956\(75\)90026-6](https://doi.org/10.1016/0022-3956(75)90026-6)
- Fontes, P. L. B., Moura, R., & Haase, V. G. (2014). Evaluation of body

- representation in children with hemiplegic cerebral palsy: Toward the development of a neuropsychological test battery. *Psychology & Neuroscience*, 7(2), 139–149. <https://doi.org/10.3922/j.psns.2014.019>
- Fourkas, A. D., Bonavolonta, V., Avenanti, A., & Aglioti, S. M. (2008). Kinesthetic Imagery and Tool-Specific Modulation of Corticospinal Representations in Expert Tennis Players. *Cerebral Cortex*, 18(10), 2382–2390. <https://doi.org/10.1093/cercor/bhn005>
- Francis, S. T., Kelly, E. F., Bowtell, R., Dunseath, W. J. R., Folger, S. E., & McGlone, F. (2000). fMRI of the Responses to Vibratory Stimulation of Digit Tips. *NeuroImage*, 11(3), 188–202. <https://doi.org/10.1006/nimg.2000.0541>
- Fraser, L. E., & Harris, L. R. (2016). Perceived finger orientation is biased towards functional task spaces. *Experimental Brain Research*, 234(12), 3565–3574. <https://doi.org/10.1007/s00221-016-4752-z>
- Fraser, L. E., & Harris, L. R. (2017). The effect of hand position on perceived finger orientation in left- and right-handers. *Experimental Brain Research*, 235(12), 3683–3693. <https://doi.org/10.1007/s00221-017-5090-5>
- Frisoni, G. B., Rozzini, R., Bianchetti, A., & Trabucchi, M. (1993). Principal Lifetime Occupation and MMSE Score in Elderly Persons. *Journal of Gerontology*, 48(6), S310–S314. <https://doi.org/10.1093/geronj/48.6.S310>
- Fuentes, C. T., Longo, M. R., & Haggard, P. (2013). Body image distortions in healthy adults. *Acta Psychologica*, 144(2), 344–351. <https://doi.org/10.1016/j.actpsy.2013.06.012>
- Fuentes, C. T., Pazzaglia, M., Longo, M. R., Scivoletto, G., & Haggard, P. (2013). Body image distortions following spinal cord injury. *Journal of Neurology, Neurosurgery and Psychiatry*, 84(2), 201–207. <https://doi.org/10.1136/jnnp-2012-304001>
- Fuentes, C. T., Runa, C., Blanco, X. A., Orvalho, V., & Haggard, P. (2013). Does My Face FIT?: A Face Image Task Reveals Structure and Distortions of Facial Feature Representation. *PLoS ONE*, 8(10), e76805. <https://doi.org/10.1371/journal.pone.0076805>
- Gadsby, S. (2017). Distorted body representations in anorexia nervosa.

Consciousness and Cognition, 51, 17–33.

<https://doi.org/10.1016/j.concog.2017.02.015>

Galati, G., Committeri, G., Sanes, J. N., & Pizzamiglio, L. (2001). Spatial coding of visual and somatic sensory information in body-centred coordinates. *European Journal of Neuroscience*, 14(4), 737–746. <https://doi.org/10.1046/j.0953-816x.2001.01674.x>

Gallagher, S. (1986). Body image and body schema: A conceptual clarification. *Journal of Mind and Behaviour*, 7(4), 541–544.

Gallagher, S. (2005). *How the Body Shapes the Mind*. Clarendon Press.
<https://doi.org/10.1093/0199271941.001.0001>

Galvez-Pol, A., Calvo-Merino, B., Capilla, A., & Forster, B. (2018). Persistent recruitment of somatosensory cortex during active maintenance of hand images in working memory. *NeuroImage*, 174(March), 153–163.
<https://doi.org/10.1016/j.neuroimage.2018.03.024>

Gandevia, S. C., & Phegan, C. M. L. (1999). Perceptual distortions of the human body image produced by local anaesthesia, pain and cutaneous stimulation. *Journal of Physiology*, 514(2), 609–616. <https://doi.org/10.1111/j.1469-7793.1999.609ae.x>

Gandiga, P. C., Hummel, F. C., & Cohen, L. G. (2006). Transcranial DC stimulation (tDCS): A tool for double-blind sham-controlled clinical studies in brain stimulation. *Clinical Neurophysiology*, 117(4), 845–850.
<https://doi.org/10.1016/j.clinph.2005.12.003>

Gandola, M., Invernizzi, P., Sedda, A., Ferrè, E. R., Sterzi, R., Sberna, M., ... Bottini, G. (2012). An anatomical account of somatoparaphrenia. *Cortex*, 48(9), 1165–1178. <https://doi.org/10.1016/j.cortex.2011.06.012>

Ganea, N., & Longo, M. R. (2017). Projecting the self outside the body: Body representations underlying proprioceptive imagery. *Cognition*, 162, 41–47.
<https://doi.org/10.1016/j.cognition.2017.01.021>

Ganis, G., Thompson, W. L., & Kosslyn, S. M. (2004). Brain areas underlying visual mental imagery and visual perception: an fMRI study. *Cognitive Brain Research*, 20(2), 226–241. <https://doi.org/10.1016/j.cogbrainres.2004.02.012>

- Garbarini, F., Forna, L., Fossataro, C., Pia, L., Gindri, P., & Berti, A. (2014). Embodiment of others' hands elicits arousal responses similar to one's own hands. *Current Biology*, *24*(16), R738–R739. <https://doi.org/10.1016/j.cub.2014.07.023>
- Garbarini, F., Fossataro, C., Berti, A., Gindri, P., Romano, D., Pia, L., ... Neppi-Modona, M. (2015). When your arm becomes mine: Pathological embodiment of alien limbs using tools modulates own body representation. *Neuropsychologia*, *70*, 402–413. <https://doi.org/10.1016/j.neuropsychologia.2014.11.008>
- Gardner, R. M., & Boice, R. (2004). A computer program for measuring body size distortion and body dissatisfaction. *Behavior Research Methods, Instruments, and Computers*, *36*(1), 89–95. <https://doi.org/10.3758/BF03195553>
- Gardner, R. M., & Bokenkamp, E. D. (1996). The role of sensory and nonsensory factors in body size estimations of eating disorder subjects. *Journal of Clinical Psychology*, *52*(1), 3–15. [https://doi.org/10.1002/\(SICI\)1097-4679\(199601\)52:1<3::AID-JCLP1>3.0.CO;2-X](https://doi.org/10.1002/(SICI)1097-4679(199601)52:1<3::AID-JCLP1>3.0.CO;2-X)
- Ghilardi, M. F., Gordon, J., & Ghez, C. (1995). Learning a visuomotor transformation in a local area of work space produces directional biases in other areas. *Journal of Neurophysiology*, *73*(6), 2535–2539. <https://doi.org/10.1152/jn.1995.73.6.2535>
- Giummarra, M. J., Gibson, S. J., Georgiou-Karistianis, N., & Bradshaw, J. L. (2007). Central mechanisms in phantom limb perception: The past, present and future. *Brain Research Reviews*, *54*(1), 219–232. <https://doi.org/10.1016/j.brainresrev.2007.01.009>
- Giurgola, S., Pisoni, A., Maravita, A., Vallar, G., & Bolognini, N. (2019). Somatosensory cortical representation of the body size. *Human Brain Mapping*, *40*(12), 3534–3547. <https://doi.org/10.1002/hbm.24614>
- Golaszewski, S. M., Zschiegner, F., Siedentopf, C. M., Unterrainer, J., Sweeney, R. A., Eisner, W., ... Felber, S. (2002). A new pneumatic vibrator for functional magnetic resonance imaging of the human sensorimotor cortex. *Neuroscience Letters*, *324*(2), 125–128. [https://doi.org/10.1016/S0304-3940\(02\)00229-X](https://doi.org/10.1016/S0304-3940(02)00229-X)

- González-Palau, F., Franco, M., Jiménez, F., Parra, E., Bernate, M., & Solis, A. (2013). Clinical utility of the hopkins verbal test-revised for detecting alzheimer's disease and mild cognitive impairment in spanish population. *Archives of Clinical Neuropsychology*, *28*(3), 245–253. <https://doi.org/10.1093/arclin/act004>
- Graziano, M. S. A., & Botvinick, M. M. (2002). How the brain represents the body: insights from neurophysiology and psychology. In W. Prinz & B. Hommel (Eds.), *Common mechanisms in perception and action: Attention and Performance XIX* (pp. 136–157). Oxford University Press.
- Graziano, M. S. A., & Cooke, D. F. (2006). Parieto-frontal interactions, personal space, and defensive behavior. *Neuropsychologia*, *44*(6), 845–859. <https://doi.org/10.1016/j.neuropsychologia.2005.09.009>
- Gritsenko, V., Krouchev, N. I., & Kalaska, J. F. (2007). Afferent input, efference copy, signal noise, and biases in perception of joint angle during active versus passive elbow movements. *Journal of Neurophysiology*, *98*(3), 1140–1154. <https://doi.org/10.1152/jn.00162.2007>
- Grob, M. (2006). *Quality of Life Assessment after Severe Hand Injury*. Technischen Universität München.
- Guariglia, C., & Antonucci, G. (1992). Personal and extrapersonal space: A case of neglect dissociation. *Neuropsychologia*, *30*(11), 1001–1009. [https://doi.org/10.1016/0028-3932\(92\)90051-M](https://doi.org/10.1016/0028-3932(92)90051-M)
- Guariglia, C., Padovani, A., Pantano, P., & Pizzamiglio, L. (1993). Unilateral neglect restricted to visual imagery. *Nature*, *364*, 235–237.
- Hach, S., & Schütz-Bosbach, S. (2010). Sinistrals' upper hand: Evidence for handedness differences in the representation of body space. *Brain and Cognition*, *72*(3), 408–418. <https://doi.org/10.1016/j.bandc.2009.12.001>
- Hach, S., & Schütz-Bosbach, S. (2014). In (or outside of) your neck of the woods: laterality in spatial body representation. *Frontiers in Psychology*, *5*(February). <https://doi.org/10.3389/fpsyg.2014.00123>
- Haggard, P., Cheng, T., Beck, B., & Fardo, F. (2017). Spatial perception and the sense of touch. In *The Subject's Matter: Self-consciousness and the Body* (pp.

97–114). MIT Press Cambridge, MA.

Haggard, P., & Jundi, S. (2009). Rubber hand illusions and size-weight illusions: Self-representation modulates representation of external objects. *Perception*, 38(12), 1796–1803. <https://doi.org/10.1068/p6399>

Haggard, P., Newman, C., Blundell, J., & Andrew, H. (2000). The perceived position of the hand in space. *Perception & Psychophysics*, 62(2), 363–377. <https://doi.org/10.3758/BF03205556>

Haggard, P., Taylor-Clarke, M., & Kennett, S. (2003). Tactile perception, cortical representation and the bodily self. *Current Biology*, 13(5), R170–R173. [https://doi.org/10.1016/S0960-9822\(03\)00115-5](https://doi.org/10.1016/S0960-9822(03)00115-5)

Hallett, M. (2001). Plasticity of the human motor cortex and recovery from stroke. *Brain Research Reviews*, 36(2–3), 169–174. [https://doi.org/10.1016/S0165-0173\(01\)00092-3](https://doi.org/10.1016/S0165-0173(01)00092-3)

Hari, R., Hänninen, R., Mäkinen, T., Jousmäki, V., Forss, N., Seppä, M., & Salonen, O. (1998). Three hands: Fragmentation of human bodily awareness. *Neuroscience Letters*, 240(3), 131–134. [https://doi.org/10.1016/S0304-3940\(97\)00945-2](https://doi.org/10.1016/S0304-3940(97)00945-2)

Hashimoto, T., & Iriki, A. (2013). Dissociations between the horizontal and dorsoventral axes in body-size perception. *European Journal of Neuroscience*, 37(11), 1747–1753. <https://doi.org/10.1111/ejn.12187>

Head, H., & Holmes, G. (1911). Sensory disturbances from cerebral lesions. *Brain*, 34(2–3), 102–254. <https://doi.org/10.1093/brain/34.2-3.102>

Heilman, K. M., Valenstein, E., & Watson, R. T. (2000). Neglect and related disorders. *Seminars in Neurology*, 20(4), 463–470. <https://doi.org/10.1055/s-2000-13179>

Helders, P. J. M. (1986). Early motor signs of blindness or very low vision in very young children. *Early Intervention*, 359–365.

Hervais-Adelman, A., Moser-Mercer, B., Murray, M. M., & Golestani, N. (2017). Cortical thickness increases after simultaneous interpretation training. *Neuropsychologia*, 98(February 2016), 212–219. <https://doi.org/10.1016/j.neuropsychologia.2017.01.008>

- Herwig, U., Satrapi, P., & Schönfeldt-Lecuona, C. (2003). Using the International 10-20 EEG System for Positioning of Transcranial Magnetic Stimulation. *Brain Topography*, *16*(2), 95–99.
<https://doi.org/10.1023/B:BRAT.0000006333.93597.9d>
- Higuchi, T., Takada, H., Matsuura, Y., & Imanaka, K. (2004). Visual Estimation of Spatial Requirements for Locomotion in Novice Wheelchair Users. *Journal of Experimental Psychology: Applied*, *10*(1), 55–66. <https://doi.org/10.1037/1076-898X.10.1.55>
- Holder, M. D., & Keates, J. (2006). Size of drawings influences body size estimates by women with and without eating concerns. *Body Image*, *3*(1), 77–86.
<https://doi.org/10.1016/j.bodyim.2005.10.002>
- Hu, C., Di, X., Eickhoff, S. B., Zhang, M., Peng, K., Guo, H., & Sui, J. (2016). Distinct and common aspects of physical and psychological self-representation in the brain: A meta-analysis of self-bias in facial and self-referential judgements. *Neuroscience & Biobehavioral Reviews*, *61*, 197–207.
<https://doi.org/10.1016/j.neubiorev.2015.12.003>
- Hummel, F., & Cohen, L. G. (2005). Improvement of Motor Function with Noninvasive Cortical Stimulation in a Patient with Chronic Stroke. *Neurorehabilitation and Neural Repair*, *19*(1), 14–19.
<https://doi.org/10.1177/1545968304272698>
- Huttenlocher, J., Hedges, L. V., & Duncan, S. (1991). Categories and particulars: Prototype effects in estimating spatial location. *Psychological Review*, *98*(3), 352–376. <https://doi.org/10.1037/0033-295X.98.3.352>
- Indefrey, P., & Levelt, W. J. . (2004). The spatial and temporal signatures of word production components. *Cognition*, *92*(1–2), 101–144.
<https://doi.org/10.1016/j.cognition.2002.06.001>
- Ingram, L. A., Butler, A. A., Gandevia, S. C., & Walsh, L. D. (2019). Proprioceptive measurements of perceived hand position using pointing and verbal localisation tasks. *PLOS ONE*, *14*(1), e0210911.
<https://doi.org/10.1371/journal.pone.0210911>
- Ionta, S., & Blanke, O. (2009). Differential influence of hands posture on mental

- rotation of hands and feet in left and right handers. *Experimental Brain Research*, 195(2), 207–217. <https://doi.org/10.1007/s00221-009-1770-0>
- Iosa, M., Guariglia, C., Matano, A., Paolucci, S., & Pizzamiglio, L. (2016). Recovery of personal neglect. *European Journal of Physical and Rehabilitation Medicine*, 52(6), 791–798.
- Jacobson, L., Koslowsky, M., & Lavidor, M. (2012). TDCS polarity effects in motor and cognitive domains: A meta-analytical review. *Experimental Brain Research*, 216(1), 1–10. <https://doi.org/10.1007/s00221-011-2891-9>
- Jain, N., Qi, H., Catania, K. C., & Kaas, J. H. (2001). Anatomic correlates of the face and oral cavity representations in the somatosensory cortical area 3b of monkeys. *The Journal of Comparative Neurology*, 429(3), 455–468. [https://doi.org/10.1002/1096-9861\(20010115\)429:3<455::AID-CNE7>3.0.CO;2-F](https://doi.org/10.1002/1096-9861(20010115)429:3<455::AID-CNE7>3.0.CO;2-F)
- Jakobson, L. S., & Goodale, M. A. (1991). Factors affecting higher-order movement planning: a kinematic analysis of human prehension. *Experimental Brain Research*, 86(1). <https://doi.org/10.1007/BF00231054>
- Johnson, S. H., Sprehn, G., & Saykin, A. J. (2002). Intact motor imagery in chronic upper limb hemiplegics: Evidence for activity-independent action representations. *Journal of Cognitive Neuroscience*, 14(6), 841–852. <https://doi.org/10.1162/089892902760191072>
- Jola, C., Davis, A., & Haggard, P. (2011). Proprioceptive integration and body representation: Insights into dancers' expertise. *Experimental Brain Research*, 213(2–3), 257–265. <https://doi.org/10.1007/s00221-011-2743-7>
- Kaelin-Lang, A., Luft, A. R., Sawaki, L., Burstein, A. H., Sohn, Y. H., & Cohen, L. G. (2002). Modulation of human corticomotor excitability by somatosensory input. *The Journal of Physiology*, 540(2), 623–633. <https://doi.org/10.1113/jphysiol.2001.012801>
- Kalisch, T., Tegenthoff, M., & Dinse, H. R. (2007). Differential effects of synchronous and asynchronous multifinger coactivation on human tactile performance. *BMC Neuroscience*, 8(1), 58. <https://doi.org/10.1186/1471-2202-8-58>

- Kalisch, T., Tegenthoff, M., & Dinse, H. R. (2008). Improvement of sensorimotor functions in old age by passive sensory stimulation. *Clinical Interventions in Aging*, 3(4), 673–690.
- Kalisch, T., Tegenthoff, M., & Dinse, H. R. (2010). Repetitive Electric Stimulation Elicits Enduring Improvement of Sensorimotor Performance in Seniors. *Neural Plasticity*, 2010, 1–11. <https://doi.org/10.1155/2010/690531>
- Kami, A., Meyer, G., Jezzard, P., Adams, M. M., Turner, R., & Ungerleider, L. G. (1995). Functional MRI evidence for adult motor cortex plasticity during motor skill learning. *Nature*, 377(6545), 155–158. <https://doi.org/10.1038/377155a0>
- Kammers, M. P. M., de Vignemont, F., Verhagen, L., & Dijkerman, H. C. (2009). The rubber hand illusion in action. *Neuropsychologia*, 47(1), 204–211. <https://doi.org/10.1016/j.neuropsychologia.2008.07.028>
- Kammers, M. P. M., Longo, M. R., Tsakiris, M., Chris Dijkerman, H., & Haggard, P. (2009). Specificity and coherence of body representations. *Perception*, 38(12), 1804–1820. <https://doi.org/10.1068/p6389>
- Kaplan, R. A., Rossell, S. L., Enticott, P. G., & Castle, D. J. (2013). Own-body perception in body dysmorphic disorder. *Cognitive Neuropsychiatry*, 18(6), 594–614. <https://doi.org/10.1080/13546805.2012.758878>
- Keehner, M., & Gathercole, S. E. (2007). Cognitive adaptations arising from nonnative experience of sign language in hearing adults. *Memory & Cognition*, 35(4), 752–761. <https://doi.org/10.3758/BF03193312>
- Keenan, J. P., McCutcheon, B., Freund, S., Gallup, G. G., Sanders, G., & Pascual-Leone, A. (1999). Left hand advantage in a self-face recognition task. *Neuropsychologia*, 37(12), 1421–1425. [https://doi.org/10.1016/S0028-3932\(99\)00025-1](https://doi.org/10.1016/S0028-3932(99)00025-1)
- Keith, R. A., Granger, C. V., Hamilton, B. B., & Sherwin, F. S. (1987). The functional independence measure: a new tool for rehabilitation. In M. Eisenberg & R. Grzesiak (Eds.), *Advances in clinical rehabilitation* (pp. 6–18). New York: Springer Verlag.
- Kellor, M., Frost, J., Silberberg, N., Iversen, I., & Cummings, R. (1971). Hand strength and dexterity. *The American Journal of Occupational Therapy*, 25, 77–

- Kerkhoff, G. (2001). Spatial hemineglect in humans. *Progress in Neurobiology*, 63(1), 1–27. [https://doi.org/10.1016/S0301-0082\(00\)00028-9](https://doi.org/10.1016/S0301-0082(00)00028-9)
- Keyes, H. (2012). Categorical perception effects for facial identity in robustly represented familiar and self-faces: The role of configural and featural information. *Quarterly Journal of Experimental Psychology*, 65(4), 760–772. <https://doi.org/10.1080/17470218.2011.636822>
- Keyes, H., & Brady, N. (2010). Self-face recognition is characterized by “bilateral gain” and by faster, more accurate performance which persists when faces are inverted. *Quarterly Journal of Experimental Psychology*, 63(5), 840–847. <https://doi.org/10.1080/17470211003611264>
- Klein, C., Metz, S. I., Elmer, S., & Jäncke, L. (2018). The interpreter’s brain during rest — Hyperconnectivity in the frontal lobe. *PLOS ONE*, 13(8), e0202600. <https://doi.org/10.1371/journal.pone.0202600>
- Kobayashi, M., Ng, J., Théoret, H., & Pascual-Leone, A. (2003). Modulation of intracortical neuronal circuits in human hand motor area by digit stimulation. *Experimental Brain Research*, 149(1), 1–8. <https://doi.org/10.1007/s00221-002-1329-9>
- Korb, S., Osimo, S. A., Suran, T., Goldstein, A., & Rumiati, R. I. (2017). Face proprioception does not modulate access to visual awareness of emotional faces in a continuous flash suppression paradigm. *Consciousness and Cognition*, 51(April), 166–180. <https://doi.org/10.1016/j.concog.2017.03.008>
- Kosslyn, S. M., Ball, T. M., & Reiser, B. J. (1978). Visual images preserve metric spatial information: Evidence from studies of image scanning. *Journal of Experimental Psychology: Human Perception and Performance*, 4(1), 47–60. <https://doi.org/10.1037/0096-1523.4.1.47>
- Kosslyn, S. M., Pascual-Leone, A., Felician, O., Camposano, S., Keenan, J. P., Thompson, W. L., ... Alpert, N. M. (1999). The Role of Area 17 in Visual Imagery: Convergent Evidence from PET and rTMS. *Science*, 284(5411), 167–170. <https://doi.org/10.1126/science.284.5411.167>
- Kosslyn, S. M., Thompson, W. L., Klm, I. J., & Alpert, N. M. (1995). Topographical

- representations of mental images in primary visual cortex. *Nature*, 378(6556), 496–498. <https://doi.org/10.1038/378496a0>
- Kothari, S. F., Dagsdóttir, L. K., Kothari, M., Blicher, J. U., Kumar, A., Buchholtz, P. E., ... Svensson, P. (2020). Effect of repetitive transcranial magnetic stimulation on altered perception of One's own face. *Brain Stimulation*, 13(3), 554–561. <https://doi.org/10.1016/j.brs.2020.01.001>
- Króliczak, G., Heard, P., Goodale, M. A., & Gregory, R. L. (2006). Dissociation of perception and action unmasked by the hollow-face illusion. *Brain Research*, 1080(1), 9–16. <https://doi.org/10.1016/j.brainres.2005.01.107>
- Kuni, B., & Schmitt, H. (2004). Kraft und Propriozeption am Sprunggelenk bei Tänzern in der professionellen Ausbildung. *Sportverletzung · Sportschaden*, 18(01), 15–21. <https://doi.org/10.1055/s-2004-813047>
- Lackner, J. R. (1988). Some proprioceptive influences on the perceptual representation of body shape and orientation. *Brain*, 111(2), 281–297. <https://doi.org/10.1093/brain/111.2.281>
- Ladda, A. M., Pfannmoeller, J. P., Kalisch, T., Roschka, S., Platz, T., Dinse, H. R., & Lotze, M. (2014). Effects of combining 2 weeks of passive sensory stimulation with active hand motor training in healthy adults. *PLoS ONE*, 9(1). <https://doi.org/10.1371/journal.pone.0084402>
- Leemhuis, De Gennaro, & Pazzaglia. (2019). Disconnected Body Representation: Neuroplasticity Following Spinal Cord Injury. *Journal of Clinical Medicine*, 8(12), 2144. <https://doi.org/10.3390/jcm8122144>
- Lefaucheur, J.-P. (2009). Methods of therapeutic cortical stimulation. *Neurophysiologie Clinique/Clinical Neurophysiology*, 39(1), 1–14. <https://doi.org/10.1016/j.neucli.2008.11.001>
- Letourneau, S. M., & Mitchell, T. V. (2011). Gaze Patterns during Identity and Emotion Judgments in Hearing Adults and Deaf Users of American Sign Language. *Perception*, 40(5), 563–575. <https://doi.org/10.1068/p6858>
- Levin, H. S., O'Donnell, V. M., & Grossman, R. G. (1979). The Galveston Orientation and Amnesia Test. *The Journal of Nervous and Mental Disease*, 167(11), 675–684. <https://doi.org/10.1097/00005053-197911000-00004>

- Levy, L. M., Ziemann, U., Chen, R., & Cohen, L. G. (2002). Rapid modulation of GABA in sensorimotor cortex induced by acute deafferentation. *Annals of Neurology*, *52*(6), 755–761. <https://doi.org/10.1002/ana.10372>
- Lewis, J. W., & Van Essen, D. C. (2000). Corticocortical connections of visual, sensorimotor, and multimodal processing areas in the parietal lobe of the macaque monkey. *The Journal of Comparative Neurology*, *428*(1), 112–137. [https://doi.org/10.1002/1096-9861\(20001204\)428:1<112::AID-CNE8>3.0.CO;2-9](https://doi.org/10.1002/1096-9861(20001204)428:1<112::AID-CNE8>3.0.CO;2-9)
- Liepert, J., Tegenthoff, M., & Malin, J. P. (1995). Changes of cortical motor area size during immobilization. *Electroencephalography and Clinical Neurophysiology/ Electromyography*, *97*(6), 382–386. [https://doi.org/10.1016/0924-980X\(95\)00194-P](https://doi.org/10.1016/0924-980X(95)00194-P)
- Linkenauger, S. A., Leyrer, M., Bühlhoff, H. H., & Mohler, B. J. (2013). Welcome to Wonderland: The Influence of the Size and Shape of a Virtual Hand On the Perceived Size and Shape of Virtual Objects. *PLoS ONE*, *8*(7), 1–16. <https://doi.org/10.1371/journal.pone.0068594>
- Linkenauger, S. A., Witt, J. K., Bakdash, J. Z., Stefanucci, J. K., & Proffitt, D. R. (2009). Asymmetrical body perception: A possible role for neural body representations. *Psychological Science*, *20*(11), 1373–1380. <https://doi.org/10.1111/j.1467-9280.2009.02447.x>
- Linkenauger, S. A., Wong, H. Y., Geuss, M., Stefanucci, J. K., McCulloch, K. C., Bühlhoff, H. H., ... Proffitt, D. R. (2015). The perceptual homunculus: The perception of the relative proportions of the human body. *Journal of Experimental Psychology: General*, *144*(1), 103–113. <https://doi.org/10.1037/xge0000028>
- Lissek, S., Wilimzig, C., Stude, P., Pleger, B., Kalisch, T., Maier, C., ... Dinse, H. R. (2009). Immobilization Impairs Tactile Perception and Shrinks Somatosensory Cortical Maps. *Current Biology*, *19*(10), 837–842. <https://doi.org/10.1016/j.cub.2009.03.065>
- Liu, J., Harris, A., & Kanwisher, N. (2010). Perception of Face Parts and Face Configurations: An fMRI Study. *Journal of Cognitive Neuroscience*, *22*(1), 203–211. <https://doi.org/10.1162/jocn.2009.21203>

- Llorens, R., Borrego, A., Palomo, P., Cebolla, A., Noé, E., i Badia, S. B., & Baños, R. (2017). Body schema plasticity after stroke: Subjective and neurophysiological correlates of the rubber hand illusion. *Neuropsychologia*, *96*(January 2019), 61–69.
<https://doi.org/10.1016/j.neuropsychologia.2017.01.007>
- Loetscher, T. (2006). Misoplegia: a review of the literature and a case without hemiplegia. *Journal of Neurology, Neurosurgery & Psychiatry*, *77*(9), 1099–1100. <https://doi.org/10.1136/jnnp.2005.087163>
- Longo, M. R. (2014). The effects of immediate vision on implicit hand maps. *Experimental Brain Research*, *232*(4), 1241–1247.
<https://doi.org/10.1007/s00221-014-3840-1>
- Longo, M. R. (2015a). Implicit and explicit body representations. *European Psychologist*, *20*(1), 6–15. <https://doi.org/10.1027/1016-9040/a000198>
- Longo, M. R. (2015b). Intuitive anatomy: Distortions of conceptual knowledge of hand structure. *Cognition*, *142*(September), 230–235.
<https://doi.org/10.1016/j.cognition.2015.05.024>
- Longo, M. R. (2015c). Posture modulates implicit hand maps. *Consciousness and Cognition*, *36*(June), 96–102. <https://doi.org/10.1016/j.concog.2015.06.009>
- Longo, M. R. (2015d). Three-dimensional coherence of the conscious body image. *Quarterly Journal of Experimental Psychology*, *68*(6), 1116–1123.
<https://doi.org/10.1080/17470218.2014.975731>
- Longo, M. R. (2016). Types of Body Representation. In Y. Coello & H. Fischer (Eds.), *Foundations of Embodied Cognition, Volume 1: Perceptual and Emotional Embodiment* (Vol. 1, pp. 117–134). London: Routledge.
- Longo, M. R. (2017a). Body representations and the sense of self. In *The subject's matter: Self-consciousness and the body* (pp. 75–96). The MIT Press Cambridge (Mass.).
- Longo, M. R. (2017b). Distorted body representations in healthy cognition. *Quarterly Journal of Experimental Psychology*, *70*(3), 378–388.
<https://doi.org/10.1080/17470218.2016.1143956>
- Longo, M. R. (2017c). Expansion of Perceptual Body Maps Near – But Not Across –

- The Wrist. *Frontiers in Human Neuroscience*, 11.
<https://doi.org/10.3389/fnhum.2017.00111>
- Longo, M. R. (2018). The effects of instrumental action on perceptual hand maps. *Experimental Brain Research*, 236(11), 3113–3119.
<https://doi.org/10.1007/s00221-018-5360-x>
- Longo, M. R. (2019). Sex differences in perceptual hand maps: A meta-analysis. *Acta Psychologica*, 196(November 2018), 1–10.
<https://doi.org/10.1016/j.actpsy.2019.03.002>
- Longo, M. R., Azañón, E., & Haggard, P. (2010). More than skin deep: Body representation beyond primary somatosensory cortex. *Neuropsychologia*, 48(3), 655–668. <https://doi.org/10.1016/j.neuropsychologia.2009.08.022>
- Longo, M. R., & Haggard, P. (2010). An implicit body representation underlying human position sense. *Proceedings of the National Academy of Sciences*, 107(26), 11727–11732. <https://doi.org/10.1073/pnas.1003483107>
- Longo, M. R., & Haggard, P. (2012a). A 2.5-D representation of the human hand. *Journal of Experimental Psychology: Human Perception and Performance*, 38(1), 9–13. <https://doi.org/10.1037/a0025428>
- Longo, M. R., & Haggard, P. (2012b). Implicit body representations and the conscious body image. *Acta Psychologica*, 141(2), 164–168.
<https://doi.org/10.1016/j.actpsy.2012.07.015>
- Longo, M. R., Long, C., & Haggard, P. (2012). Mapping the Invisible Hand: A Body Model of a Phantom Limb. *Psychological Science*, 23(7), 740–742.
<https://doi.org/10.1177/0956797612441219>
- Longo, M. R., & Lourenco, S. F. (2007). Space perception and body morphology: Extent of near space scales with arm length. *Experimental Brain Research*, 177(2), 285–290. <https://doi.org/10.1007/s00221-007-0855-x>
- Longo, M. R., Mattioni, S., & Ganea, N. (2015). Perceptual and Conceptual Distortions of Implicit Hand Maps. *Frontiers in Human Neuroscience*, 9(December), 1–12. <https://doi.org/10.3389/fnhum.2015.00656>
- Lotze, M., & Moseley, G. L. (2007). Role of distorted body image in pain. *Current Rheumatology Reports*, 9(6), 488–496. <https://doi.org/10.1007/s11926-007->

- Lourenco, S. F., & Longo, M. R. (2009). The plasticity of near space: Evidence for contraction. *Cognition*, *112*(3), 451–456.
<https://doi.org/10.1016/j.cognition.2009.05.011>
- Lunghi, C., Lo Verde, L., & Alais, D. (2017). Touch Accelerates Visual Awareness. *I-Perception*, *8*(1), 1–14. <https://doi.org/10.1177/2041669516686986>
- MacSweeney, M., Capek, C. M., Campbell, R., & Woll, B. (2008). The signing brain: the neurobiology of sign language. *Trends in Cognitive Sciences*, *12*(11), 432–440. <https://doi.org/10.1016/j.tics.2008.07.010>
- MacSweeney, M., Woll, B., Campbell, R., Calvert, G. A., McGuire, P. K., David, A. S., ... Brammer, M. J. (2002). Neural Correlates of British Sign Language Comprehension: Spatial Processing Demands of Topographic Language. *Journal of Cognitive Neuroscience*, *14*(7), 1064–1075.
<https://doi.org/10.1162/089892902320474517>
- Magnani, F. G., & Sedda, A. (2016). Paying the price for body evolution. *Medical Hypotheses*, *98*, 81–86. <https://doi.org/10.1016/j.mehy.2016.11.013>
- Magni, E., Binetti, G., Bianchetti, A., Rozzini, R., & Trabucchi, M. (1996). Mini-Mental State Examination: a normative study in Italian elderly population, (I 996), 198–202.
- Mahoney, F., & Barthel, D. (1965). Baltimore City Medical Society Functional Evaluation : the Barthel Index. *Maryland State Medical Journal*, *14*, 56–61.
- Makin, T. R., Cramer, A. O., Scholz, J., Hahamy, A., Slater, D. H., Tracey, I., & Johansen-Berg, H. (2013). Deprivation-related and use-dependent plasticity go hand in hand. *ELife*, *2*(November2013), 1–15.
<https://doi.org/10.7554/eLife.01273>
- Mancini, F., Bauleo, A., Cole, J., Lui, F., Porro, C. A., Haggard, P., & Iannetti, G. D. (2014). Whole-body mapping of spatial acuity for pain and touch. *Annals of Neurology*, *75*(6), 917–924. <https://doi.org/10.1002/ana.24179>
- Mancini, F., Longo, M. R., Kammers, M. P. M., & Haggard, P. (2011). Visual distortion of body size modulates pain perception. *Psychological Science*, *22*(3), 325–330. <https://doi.org/10.1177/0956797611398496>

- Maravita, A., & Iriki, A. (2004). Tools for the body (schema). *Trends in Cognitive Sciences*, 8(2), 79–86. <https://doi.org/10.1016/j.tics.2003.12.008>
- Margolis, A. N., & Longo, M. R. (2014). Visual detail about the body modulates tactile localisation biases. *Experimental Brain Research*, 233(2), 351–358. <https://doi.org/10.1007/s00221-014-4118-3>
- Marini, F., Tagliabue, C. F., Sposito, A. V., Hernandez-Arieta, A., Brugger, P., Estévez, N., & Maravita, A. (2014). Crossmodal representation of a functional robotic hand arises after extensive training in healthy participants. *Neuropsychologia*, 53(1), 178–186. <https://doi.org/10.1016/j.neuropsychologia.2013.11.017>
- Marino, B. F. M., Stucchi, N., Nava, E., Haggard, P., & Maravita, A. (2010). Distorting the visual size of the hand affects hand pre-shaping during grasping. *Experimental Brain Research*, 202(2), 499–505. <https://doi.org/10.1007/s00221-009-2143-4>
- Marks, D. F. (1973). Visual Imagery Differences in the Recall of Pictures. *British Journal of Psychology*, 64(1), 17–24. <https://doi.org/10.1111/j.2044-8295.1973.tb01322.x>
- Martuzzi, R., van der Zwaag, W., Farthouat, J., Gruetter, R., & Blanke, O. (2014). Human finger somatotopy in areas 3b, 1, and 2: A 7T fMRI study using a natural stimulus. *Human Brain Mapping*, 35(1), 213–226. <https://doi.org/10.1002/hbm.22172>
- Matamala-Gomez, Nierula, Donegan, Slater, M., & Sanchez-Vives. (2020). Manipulating the Perceived Shape and Color of a Virtual Limb Can Modulate Pain Responses. *Journal of Clinical Medicine*, 9(2), 291. <https://doi.org/10.3390/jcm9020291>
- Mathiowetz, V., Weber, K., Kashman, N., & Volland, G. (1985). Adult Norms for the Nine Hole Peg Test of Finger Dexterity. *The Occupational Therapy Journal of Research*, 5(1), 24–38. <https://doi.org/10.1177/153944928500500102>
- McCormack, G. L. (2014). The Significance of Somatosensory Stimulation to the Hand: Implications for Occupational Therapy Practice. *The Open Journal of Occupational Therapy*, 2(4). <https://doi.org/10.15453/2168-6408.1141>

- McCullough, S., & Emmorey, K. (1997). Face Processing by Deaf ASL Signers: Evidence for Expertise in Distinguishing Local Features. *Journal of Deaf Studies and Deaf Education*, 2(4), 212–222.
<https://doi.org/10.1093/oxfordjournals.deafed.a014327>
- McGonigle, D. J., Hänninen, R., Salenius, S., Hari, R., Frackowiak, R. S. J., & Frith, C. D. (2002). Whose arm is it anyway? An fMRI case study of supernumerary phantom limb. *Brain : A Journal of Neurology*, 125(Pt 6), 1265–1274.
<https://doi.org/10.1093/brain/awf139>
- McIntosh, R. D., Brodie, E. E., Beschin, N., & Robertson, I. H. (2000). Improving the Clinical Diagnosis of Personal Neglect: A Reformulated Comb and Razor Test. *Cortex*, 36(2), 289–292. [https://doi.org/10.1016/S0010-9452\(08\)70530-6](https://doi.org/10.1016/S0010-9452(08)70530-6)
- Medina, J., & Coslett, H. B. (2016). What can errors tell us about body representations? *Cognitive Neuropsychology*, 33(1–2), 5–25.
<https://doi.org/10.1080/02643294.2016.1188065>
- Medina, J., & Duckett, C. (2017). Domain-general biases in spatial localization: Evidence against a distorted body model hypothesis. *Journal of Experimental Psychology: Human Perception and Performance*, 43(7), 1430–1443.
<https://doi.org/10.1037/xhp0000397>
- Medina, J., Jax, S. A., Brown, M. J., & Coslett, H. B. (2010). Contributions of efference copy to limb localization: Evidence from deafferentation. *Brain Research*, 1355, 104–111. <https://doi.org/10.1016/j.brainres.2010.07.063>
- Medina, J., & Rapp, B. (2014). Rapid experience-dependent plasticity following somatosensory damage. *Current Biology*, 24(6), 677–680.
<https://doi.org/10.1016/j.cub.2014.01.070>
- Meier, J., Topka, M. S., & Hänggi, J. (2016). Differences in Cortical Representation and Structural Connectivity of Hands and Feet between Professional Handball Players and Ballet Dancers. *Neural Plasticity*, 2016, 1–17.
<https://doi.org/10.1155/2016/6817397>
- Melzack, R. (1992). Phantom Limbs. *Scientific American*, 266(4), 120–125.
<https://doi.org/10.1038/scientificamerican0492-120>
- Miller, L. E., Longo, M. R., & Saygin, A. P. (2016). Mental body representations

- retain homuncular shape distortions: Evidence from Weber's illusion. *Consciousness and Cognition*, 40, 17–25.
<https://doi.org/10.1016/j.concog.2015.12.008>
- Mitchell, T. V. (2017). Category selectivity of the N170 and the role of expertise in deaf signers. *Hearing Research*, 343, 150–161.
<https://doi.org/10.1016/j.heares.2016.10.010>
- Mitchell, T. V., Letourneau, S. M., & Maslin, M. C. T. (2013). Behavioral and neural evidence of increased attention to the bottom half of the face in deaf signers. *Restorative Neurology and Neuroscience*, 31(2), 125–139.
<https://doi.org/10.3233/RNN-120233>
- Mohr, H. M., Rickmeyer, C., Hummel, D., Ernst, M., & Grabhorn, R. (2016). Altered Visual Adaptation to Body Shape in Eating Disorders: Implications for Body Image Distortion. *Perception*, 45(7), 725–738.
<https://doi.org/10.1177/0301006616633385>
- Mohr, H. M., Röder, C., Zimmermann, J., Hummel, D., Negele, A., & Grabhorn, R. (2011). Body image distortions in bulimia nervosa: Investigating body size overestimation and body size satisfaction by fMRI. *NeuroImage*, 56(3), 1822–1831. <https://doi.org/10.1016/j.neuroimage.2011.02.069>
- Mohr, H. M., Zimmermann, J., Röder, C., Lenz, C., Overbeck, G., & Grabhorn, R. (2010). Separating two components of body image in anorexia nervosa using fMRI. *Psychological Medicine*, 40(9), 1519–1529.
<https://doi.org/10.1017/S0033291709991826>
- Mölbert, S. C., Klein, L., Thaler, A., Mohler, B. J., Brozzo, C., Martus, P., ... Giel, K. E. (2017). Depictive and metric body size estimation in anorexia nervosa and bulimia nervosa: A systematic review and meta-analysis. *Clinical Psychology Review*, 57(December 2016), 21–31. <https://doi.org/10.1016/j.cpr.2017.08.005>
- Monte-Silva, K., Kuo, M.-F., Hessenthaler, S., Fresnoza, S., Liebetanz, D., Paulus, W., & Nitsche, M. A. (2013). Induction of Late LTP-Like Plasticity in the Human Motor Cortex by Repeated Non-Invasive Brain Stimulation. *Brain Stimulation*, 6(3), 424–432. <https://doi.org/10.1016/j.brs.2012.04.011>
- Mora, L., Cowie, D., Banissy, M. J., & Cocchini, G. (2018). My true face:

- Unmasking one's own face representation. *Acta Psychologica*, 191(May), 63–68. <https://doi.org/10.1016/j.actpsy.2018.08.014>
- Moseley, G. L., Gallace, A., & Spence, C. (2012). Bodily illusions in health and disease: Physiological and clinical perspectives and the concept of a cortical “body matrix.” *Neuroscience and Biobehavioral Reviews*, 36(1), 34–46. <https://doi.org/10.1016/j.neubiorev.2011.03.013>
- Moseley, G. L., Parsons, T. J., & Spence, C. (2008). Visual distortion of a limb modulates the pain and swelling evoked by movement. *Current Biology*, 18(22), R1047–R1048. <https://doi.org/10.1016/j.cub.2008.09.031>
- Muir, L. J., & Richardson, I. E. G. (2005). Perception of sign language and its application to visual communications for deaf people. *Journal of Deaf Studies and Deaf Education*, 10(4), 390–401. <https://doi.org/10.1093/deafed/eni037>
- Muret, D., & Dinse, H. R. (2018). Tactile learning transfer from the hand to the face but not to the forearm implies a special hand-face relationship. *Scientific Reports*, 8(1), 11752. <https://doi.org/10.1038/s41598-018-30183-5>
- Mussap, A. J., McCabe, M. P., & Ricciardelli, L. A. (2008). Implications of accuracy, sensitivity, and variability of body size estimations to disordered eating. *Body Image*, 5(1), 80–90. <https://doi.org/10.1016/j.bodyim.2007.07.003>
- Mussap, A. J., & Salton, N. (2006). A ‘Rubber-hand’ Illusion Reveals a Relationship between Perceptual Body Image and Unhealthy Body Change. *Journal of Health Psychology*, 11(4), 627–639. <https://doi.org/10.1177/1359105306065022>
- Mylius, V., Borekardt, J. J., & Lefaucheur, J. P. (2012). Noninvasive cortical modulation of experimental pain. *Pain*, 153(7), 1350–1363. <https://doi.org/10.1016/j.pain.2012.04.009>
- Nelson, H. E. (1976). A Modified Card Sorting Test Sensitive to Frontal Lobe Defects. *Cortex*, 12(4), 313–324. [https://doi.org/10.1016/S0010-9452\(76\)80035-4](https://doi.org/10.1016/S0010-9452(76)80035-4)
- Nguyen, B. T., Inui, K., Hoshiyama, M., Nakata, H., & Kakigi, R. (2005). Face representation in the human secondary somatosensory cortex. *Clinical Neurophysiology*, 116(6), 1247–1253. <https://doi.org/10.1016/j.clinph.2005.01.018>

- Nico, D., Daprati, E., Nighoghossian, N., Carrier, E., Duhamel, J.-R. R., & Sirigu, A. (2010). The role of the right parietal lobe in anorexia nervosa. *Psychological Medicine*, *40*(9), 1531–1539. <https://doi.org/10.1017/S0033291709991851>
- Niki, C., Maruyama, T., Muragaki, Y., & Kumada, T. (2014). Perseveration Found in a Human Drawing Task: Six-Fingered Hands Drawn by Patients with Right Anterior Insula and Operculum Damage. *Behavioural Neurology*, *2014*, 1–7. <https://doi.org/10.1155/2014/405726>
- Nikishina, V. B., Lazarenko, V. A., Petrash, E. A., & Ahmetzyanova, A. I. (2016). Disturbance of body image in patients with meningiomas of parieto-occipital localization. *Zhurnal Nevrologii i Psikhiatrii Im. S.S. Korsakova*, *116*(12), 20. <https://doi.org/10.17116/jnevro201611612120-24>
- Nitsche, M. A., Cohen, L. G., Wassermann, E. M., Priori, A., Lang, N., Antal, A., ... Pascual-Leone, A. (2008). Transcranial direct current stimulation: State of the art 2008. *Brain Stimulation*, *1*(3), 206–223. <https://doi.org/10.1016/j.brs.2008.06.004>
- Nitsche, M. A., Liebetanz, D., Schlitterlau, A., Henschke, U., Fricke, K., Frommann, K., ... Tergau, F. (2004). GABAergic modulation of DC stimulation-induced motor cortex excitability shifts in humans. *European Journal of Neuroscience*, *19*(10), 2720–2726. <https://doi.org/10.1111/j.0953-816X.2004.03398.x>
- O’Craven, K. M., & Kanwisher, N. (2000). Mental Imagery of Faces and Places Activates Corresponding Stimulus-Specific Brain Regions. *Journal of Cognitive Neuroscience*, *12*(6), 1013–1023. <https://doi.org/10.1162/08989290051137549>
- O’Shaughnessy, B. (1980). *The Will: A Dual Aspect Theory*. Cambridge University Press.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*(1), 97–113. [https://doi.org/10.1016/0028-3932\(71\)90067-4](https://doi.org/10.1016/0028-3932(71)90067-4)
- Opie, G. M., Evans, A., Ridding, M. C., & Semmler, J. G. (2016). Short-term immobilization influences use-dependent cortical plasticity and fine motor performance. *Neuroscience*, *330*, 247–256. <https://doi.org/10.1016/j.neuroscience.2016.06.002>

- Osman, S., Cooper, M., Hackmann, A., & Veale, D. (2004). Spontaneously occurring images and early memories in people with body dysmorphic disorder. *Memory*, *12*(4), 428–436. <https://doi.org/10.1080/09658210444000043>
- Oxford Grice, K., Vogel, K. A., Le, V., Mitchell, A., Muniz, S., & Vollmer, M. A. (2003). Adult Norms for a Commercially Available Nine Hole Peg Test for Finger Dexterity. *American Journal of Occupational Therapy*, *57*(5), 570–573. <https://doi.org/10.5014/ajot.57.5.570>
- Paillard, J. (1983). Localization Without Content. *Archives of Neurology*, *40*(9), 548. <https://doi.org/10.1001/archneur.1983.04050080048008>
- Paillard, J. (1999). Body Schema and Body Image - A Double Dissociation in Deafferented Patients. In G. N. Gantchev, S. Mori, & J. Massion (Eds.), *Motor control, today and tomorrow* (pp. 197–214). Academic Publishing House.
- Palermo, L., Di Vita, A., Boccia, M., Nemmi, F., Brunelli, S., Trallesesi, M., ... Guariglia, C. (2018). Action and Non-Action Oriented Body Representations: Insight from Behavioural and Grey Matter Modifications in Individuals with Lower Limb Amputation. *BioMed Research International*, *2018*, 1–11. <https://doi.org/10.1155/2018/1529730>
- Palermo, L., Di Vita, A., Piccardi, L., Trallesesi, M., & Guariglia, C. (2014). Bottom-up and top-down processes in body representation: A study of brain-damaged and amputee patients. *Neuropsychology*, *28*(5), 772–781. <https://doi.org/10.1037/neu0000086>
- Palermo, L., Nori, R., Piccardi, L., Zeri, F., Babino, A., Giusberti, F., & Guariglia, C. (2013). Refractive Errors Affect the Vividness of Visual Mental Images. *PLoS ONE*, *8*(6), 2–9. <https://doi.org/10.1371/journal.pone.0065161>
- Paqueron, X., Leguen, M., Rosenthal, D., Coriat, P., Willer, J. C., & Danziger, N. (2003). The phenomenology of body image distortions induced by regional anaesthesia. *Brain*, *126*(3), 702–712. <https://doi.org/10.1093/brain/awg063>
- Parasnis, I., Samar, V. J., Bettger, J. G., & Sathe, K. (1996). Does Deafness Lead to Enhancement of Visual Spatial Cognition in Children?: Negative Evidence from Deaf Nonsigners. *Journal of Deaf Studies and Deaf Education*, *1*(2), 145–152. <https://doi.org/10.1093/oxfordjournals.deafed.a014288>

- Pavani, F., & Zampini, M. (2007). The role of hand size in the fake-hand illusion paradigm. *Perception*, *36*(10), 1547–1554. <https://doi.org/10.1068/p5853>
- Pazzaglia, M., Galli, G., Scivoletto, G., & Molinari, M. (2013). A Functionally Relevant Tool for the Body following Spinal Cord Injury. *PLoS ONE*, *8*(3), e58312. <https://doi.org/10.1371/journal.pone.0058312>
- Pazzaglia, M., & Zantedeschi, M. (2016). Plasticity and Awareness of Bodily Distortion. *Neural Plasticity*, *2016*, 1–7. <https://doi.org/10.1155/2016/9834340>
- Peltz, E., Seifert, F., Lanz, S., Müller, R., & Maihöfner, C. (2011). Impaired Hand Size Estimation in CRPS. *The Journal of Pain*, *12*(10), 1095–1101. <https://doi.org/10.1016/j.jpain.2011.05.001>
- Penfield, W., & Boldrey, E. (1937). Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. *Brain*, *60*(4), 389–443. <https://doi.org/10.1093/brain/60.4.389>
- Penfield, W., & Rasmussen, T. (1950). *The cerebral cortex of man; a clinical study of localization of function*. New York: Macmillan.
- Penhune, V. B., Cismaru, R., Dorsaint-Pierre, R., Petitto, L.-A., & Zatorre, R. J. (2003). The morphometry of auditory cortex in the congenitally deaf measured using MRI. *NeuroImage*, *20*(2), 1215–1225. [https://doi.org/10.1016/S1053-8119\(03\)00373-2](https://doi.org/10.1016/S1053-8119(03)00373-2)
- Perera, A. T. marie, Newport, R., & McKenzie, K. J. (2017). Changing hands: persistent alterations to body image following brief exposure to multisensory distortions. *Experimental Brain Research*, *235*(6), 1809–1821. <https://doi.org/10.1007/s00221-017-4935-2>
- Perez-Marcos, D., Martini, M., Fuentes, C. T., Bellido Rivas, A. I., Haggard, P., & Sanchez-Vives, M. V. (2018). Selective distortion of body image by asynchronous visuotactile stimulation. *Body Image*, *24*, 55–61. <https://doi.org/10.1016/j.bodyim.2017.11.002>
- Petkova, V. I., & Ehrsson, H. H. (2008). If I Were You: Perceptual Illusion of Body Swapping. *PLoS ONE*, *3*(12), e3832. <https://doi.org/10.1371/journal.pone.0003832>
- Peviani, V., & Bottini, G. (2018). The distorted hand metric representation serves

- both perception and action. *Journal of Cognitive Psychology*, 30(8), 880–893.
<https://doi.org/10.1080/20445911.2018.1538154>
- Peviani, V., Liotta, J., & Bottini, G. (2020). The motor system (partially) deceives body representation biases in absence of visual correcting cues. *Acta Psychologica*, 203(July 2019), 103003.
<https://doi.org/10.1016/j.actpsy.2020.103003>
- Peviani, V., Melloni, L., & Bottini, G. (2019). Visual and somatosensory information contribute to distortions of the body model, (August), 1–9.
<https://doi.org/10.1038/s41598-019-49979-0>
- Phillips, F., Natter, M. B., & Egan, E. J. L. (2015). Magically deceptive biological motion—the French Drop Sleight. *Frontiers in Psychology*, 6.
<https://doi.org/10.3389/fpsyg.2015.00371>
- Pick, A. (1922). Störung der Orientierung am eigenen Körper - Beitrag zur Lehre vom Bewußtsein des eigenen Körpers. *Psychologische Forschung*, 1(1), 303–318. <https://doi.org/10.1007/BF00410392>
- Piepers, D. W., & Robbins, R. A. (2012). A Review and Clarification of the Terms “holistic,” “configural,” and “relational” in the Face Perception Literature. *Frontiers in Psychology*, 3(DEC), 1–11.
<https://doi.org/10.3389/fpsyg.2012.00559>
- Pirulli, C., Fertoni, A., & Miniussi, C. (2014). Is neural hyperpolarization by cathodal stimulation always detrimental at the behavioral level? *Frontiers in Behavioral Neuroscience*, 8(JUNE), 1–10.
<https://doi.org/10.3389/fnbeh.2014.00226>
- Pitcher, D., Walsh, V., Yovel, G., & Duchaine, B. (2007). TMS Evidence for the Involvement of the Right Occipital Face Area in Early Face Processing. *Current Biology*, 17(18), 1568–1573. <https://doi.org/10.1016/j.cub.2007.07.063>
- Pitron, V., Alsmith, A., & de Vignemont, F. (2018). How do the body schema and the body image interact? *Consciousness and Cognition*, 65(September), 352–358. <https://doi.org/10.1016/j.concog.2018.08.007>
- Pitron, V., & de Vignemont, F. (2017). Beyond differences between the body schema and the body image: insights from body hallucinations. *Consciousness and*

- Cognition*, 53(June), 115–121. <https://doi.org/10.1016/j.concog.2017.06.006>
- Pleger, B., Dinse, H. R., Ragert, P., Schwenkreis, P., Malin, J. P., & Tegenthoff, M. (2001). Shifts in cortical representations predict human discrimination improvement. *Proceedings of the National Academy of Sciences of the United States of America*, 98(21), 12255–12260. <https://doi.org/10.1073/pnas.191176298>
- Pleger, B., Foerster, A.-F., Ragert, P., Dinse, H. R., Schwenkreis, P., Malin, J.-P., ... Tegenthoff, M. (2003). Functional Imaging of Perceptual Learning in Human Primary and Secondary Somatosensory Cortex. *Neuron*, 40(3), 643–653. [https://doi.org/10.1016/s0896-6273\(03\)00677-9](https://doi.org/10.1016/s0896-6273(03)00677-9)
- Porac, C., Searleman, A., & Karagiannakis, K. (2006). Pseudoneglect: Evidence for both perceptual and attentional factors. *Brain and Cognition*, 61(3), 305–311. <https://doi.org/10.1016/j.bandc.2006.01.003>
- Punt, D. T., Cooper, L., Hey, M., & Johnson, M. I. (2013). Neglect-like symptoms in complex regional pain syndrome: Learned nonuse by another name? *Pain*, 154(2), 200–203. <https://doi.org/10.1016/j.pain.2012.11.006>
- Rabin, E., & Gordon, A. M. (2004). Tactile feedback contributes to consistency of finger movements during typing. *Experimental Brain Research*, 155(3), 362–369. <https://doi.org/10.1007/s00221-003-1736-6>
- Ramachandran, V. S. (1993). Behavioral and magnetoencephalographic correlates of plasticity in the adult human brain. *Proceedings of the National Academy of Sciences*, 90(22), 10413–10420. <https://doi.org/10.1073/pnas.90.22.10413>
- Ramachandran, V. S., & Altschuler, E. L. (2009). The use of visual feedback, in particular mirror visual feedback, in restoring brain function. *Brain*, 132(7), 1693–1710. <https://doi.org/10.1093/brain/awp135>
- Ramachandran, V. S., & Hirstein, W. (1998). The perception of phantom limbs. *Brain*, 121(9), 1603–1630. <https://doi.org/10.1093/brain/121.9.1603>
- Ramachandran, V. S., & Rogers-Ramachandran, D. (2007). It's All Done with Mirrors. *Scientific American Mind*, 18(4), 16–18. Retrieved from <http://www.jstor.org/stable/24939678>
- Ramsay, J. R., & Riddoch, M. J. (2001). Position-matching in the upper limb:

- Professional ballet dancers perform with outstanding accuracy. *Clinical Rehabilitation*, 15(3), 324–330. Retrieved from <http://www.embase.com/search/results?subaction=viewrecord&from=export&id=L32471892%5Cnhttp://dx.doi.org/10.1191/026921501666288152>
- Rasmus, M. (2017). Body representation in patients after vascular brain injuries. *Cognitive Processing*, 18(4), 359–373. <https://doi.org/10.1007/s10339-017-0831-8>
- Rensink, R. A., & Kuhn, G. (2015). A framework for using magic to study the mind. *Frontiers in Psychology*, 5. <https://doi.org/10.3389/fpsyg.2014.01508>
- Ridding, M. C., Brouwer, B., Miles, T. S., Pitcher, J. B., & Thompson, P. D. (2000). Changes in muscle responses to stimulation of the motor cortex induced by peripheral nerve stimulation in human subjects. *Experimental Brain Research*, 131(1), 135–143. <https://doi.org/10.1007/s002219900269>
- Rissanen, O., Pitkänen, P., Juvonen, A., Kuhn, G., & Hakkarainen, K. (2014). Expertise among professional magicians: an interview study. *Frontiers in Psychology*, 5, 1484. <https://doi.org/10.3389/fpsyg.2014.01484>
- Riva, G. (2012). Neuroscience and eating disorders: The allocentric lock hypothesis. *Medical Hypotheses*, 78(2), 254–257. <https://doi.org/10.1016/j.mehy.2011.10.039>
- Riva, G., & Dakanalis, A. (2018). Altered Processing and Integration of Multisensory Bodily Representations and Signals in Eating Disorders: A Possible Path Toward the Understanding of Their Underlying Causes. *Frontiers in Human Neuroscience*, 12(February), 1–7. <https://doi.org/10.3389/fnhum.2018.00049>
- Riva, G., Gaudio, S., & Dakanalis, A. (2015). The Neuropsychology of Self-Objectification. *European Psychologist*, 20(1), 34–43. <https://doi.org/10.1027/1016-9040/a000190>
- Rode, G., Vallar, G., Revol, P., Tilikete, C., Jacquin-Courtois, S., Rossetti, Y., & Farnè, A. (2012). Facial macrosomatognosia and pain in a case of Wallenberg's syndrome: Selective effects of vestibular and transcutaneous stimulations. *Neuropsychologia*, 50(2), 245–253.

<https://doi.org/10.1016/j.neuropsychologia.2011.11.018>

- Romano, D., Uberti, E., Caggiano, P., Cocchini, G., & Maravita, A. (2019). Different tool training induces specific effects on body metric representation. *Experimental Brain Research*, 237(2), 493–501. <https://doi.org/10.1007/s00221-018-5405-1>
- Ronchi, R., Heydrich, L., Serino, A., & Blanke, O. (2018). Illusory hand ownership in a patient with personal neglect for the upper limb, but no somatoparaphenia. *Journal of Neuropsychology*, 12(3), 442–462. <https://doi.org/10.1111/jnp.12123>
- Rosselli, M., Ardila, A., Salvatierra, J., Marquez, M., Matos, L., & Weekes, V. A. (2002). A cross-linguistic comparison of verbal fluency tests. *International Journal of Neuroscience*, 112(6), 759–776. <https://doi.org/10.1080/00207450290025752>
- Rossetti, Y., Rode, G., & Boisson, D. (1995). Implicit processing of somaesthetic information. *NeuroReport*, 6(3), 506–510. <https://doi.org/10.1097/00001756-199502000-00025>
- Rousseaux, M., Honoré, J., & Saj, A. (2014). Body representations and brain damage. *Neurophysiologie Clinique*, 44(1), 59–67. <https://doi.org/10.1016/j.neucli.2013.10.130>
- Salanova, V., Andermann, F., Rasmussen, T., Olivier, A., & Quesney, L. F. (1995). Parietal lobe epilepsy clinical manifestations and outcome in 82 patients treated surgically between 1929 and 1988. *Brain*, 118(3), 607–627. <https://doi.org/10.1093/brain/118.3.607>
- Salomon, R., Lim, M., Herbelin, B., Hesselmann, G., & Blanke, O. (2013). Posing for awareness: Proprioception modulates access to visual consciousness in a continuous flash suppression task. *Journal of Vision*, 13(7), 2–2. <https://doi.org/10.1167/13.7.2>
- Salvato, G., Romano, D., De Maio, G., & Bottini, G. (2019). Implicit mechanisms of body image alterations: The covert attention exposure effect. *Attention, Perception, & Psychophysics*. <https://doi.org/10.3758/s13414-019-01921-2>
- Sammut, D. (2002). Fingertip injuries: a review of indications and methods of management. *Current Orthopaedics*, 16(4), 271–285.

<https://doi.org/10.1054/cuor.2002.0278>

- Sandler, W. (2018). The body as evidence for the nature of language. *Frontiers in Psychology, 9*(OCT), 1–21. <https://doi.org/10.3389/fpsyg.2018.01782>
- Sastre-Janer, F. (1998). Three-dimensional reconstruction of the human central sulcus reveals a morphological correlate of the hand area. *Cerebral Cortex, 8*(7), 641–647. <https://doi.org/10.1093/cercor/8.7.641>
- Saturnino, G. B., Siebner, H. R., Thielscher, A., & Madsen, K. H. (2019). Accessibility of cortical regions to focal TES: Dependence on spatial position, safety, and practical constraints. *NeuroImage, 203*, 116183. <https://doi.org/10.1016/j.neuroimage.2019.116183>
- Saulton, A., Bühlhoff, H. H., & de la Rosa, S. (2017). Conceptual biases explain distortion differences between hand and objects in localization tasks. *Journal of Experimental Psychology: Human Perception and Performance, 43*(7), 1444–1453. <https://doi.org/10.1037/xhp0000396>
- Saulton, A., Dodds, T. J., Bühlhoff, H. H., & de la Rosa, S. (2015). Objects exhibit body model like shape distortions. *Experimental Brain Research, 233*(5), 1471–1479. <https://doi.org/10.1007/s00221-015-4221-0>
- Saulton, A., Longo, M. R., Wong, H. Y., Bühlhoff, H. H., & de la Rosa, S. (2016). The role of visual similarity and memory in body model distortions. *Acta Psychologica, 164*, 103–111. <https://doi.org/10.1016/j.actpsy.2015.12.013>
- Scandola, M., Togni, R., Tieri, G., Avesani, R., Brambilla, M., Aglioti, S. M., & Moro, V. (2019). Embodying their own wheelchair modifies extrapersonal space perception in people with spinal cord injury. *Experimental Brain Research, 237*(10), 2621–2632. <https://doi.org/10.1007/s00221-019-05618-8>
- Schaal, N. K., Pollok, B., & Banissy, M. J. (2017). Hemispheric differences between left and right supramarginal gyrus for pitch and rhythm memory. *Scientific Reports, 7*, 1–6. <https://doi.org/10.1038/srep42456>
- Schabrun, S. M., Jones, E., Elgueta Cancino, E. L., & Hodges, P. W. (2014). Targeting Chronic Recurrent Low Back Pain From the Top-down and the Bottom-up: A Combined Transcranial Direct Current Stimulation and Peripheral Electrical Stimulation Intervention. *Brain Stimulation, 7*(3), 451–

459. <https://doi.org/10.1016/j.brs.2014.01.058>

Schaefer, S. Y., Haaland, K. Y., & Sainburg, R. L. (2007). Ipsilesional motor deficits following stroke reflect hemispheric specializations for movement control. *Brain*, *130*(8), 2146–2158. <https://doi.org/10.1093/brain/awm145>

Schlieper, S., & Dinse, H. R. (2012). Perceptual improvement following repetitive sensory stimulation depends monotonically on stimulation intensity. *Brain Stimulation*, *5*(4), 647–651. <https://doi.org/10.1016/j.brs.2011.07.002>

Schmalzl, L., & Ehrsson, H. H. (2011). Experimental Induction of a Perceived “Telescoped” Limb Using a Full-Body Illusion. *Frontiers in Human Neuroscience*, *5*(April), 1–13. <https://doi.org/10.3389/fnhum.2011.00034>

Schmitt, H., Kuni, B., & Sabo, D. (2005). Influence of Professional Dance Training on Peak Torque and Proprioception at the Ankle. *Clinical Journal of Sport Medicine*, *15*(5), 331–339. <https://doi.org/10.1097/01.jsm.0000181437.41268.56>

Schwoebel, J., & Coslett, H. B. (2005). Evidence for multiple, distinct representations of the human body. *Journal of Cognitive Neuroscience*, *17*(4), 543–553. <https://doi.org/10.1162/0898929053467587>

Sedda, A., Ambrosini, E., Dirupo, G., Tonin, D., Valsecchi, L., Redaelli, T., ... Bottini, G. (2019). Affordances after spinal cord injury. *Journal of Neuropsychology*, *13*(2), 354–369. <https://doi.org/10.1111/jnp.12151>

Sehyr, Z. S., & Cormier, K. (2016). Perceptual categorization of handling handshapes in British Sign Language. *Language and Cognition*, *8*(4), 501–532. <https://doi.org/10.1017/langcog.2015.4>

Seitz, R. J., Huang, Y., Knorr, U., Tellmann, L., Herzog, H., & Freund, H. J. (1995). Large-scale plasticity of the human motor cortex. *NeuroReport*, *6*(5), 742–744. <https://doi.org/10.1097/00001756-199503270-00009>

Seitz, R. J., & Roland, P. E. (1992). Vibratory stimulation increases and decreases the regional cerebral blood flow and oxidative metabolism: a positron emission tomography (PET) study. *Acta Neurologica Scandinavica*, *86*(1), 60–67. <https://doi.org/10.1111/j.1600-0404.1992.tb08055.x>

Sel, A., Forster, B., & Calvo-Merino, B. (2014). The Emotional Homunculus: ERP

- Evidence for Independent Somatosensory Responses during Facial Emotional Processing. *Journal of Neuroscience*, 34(9), 3263–3267.
<https://doi.org/10.1523/JNEUROSCI.0106-13.2014>
- Senkowski, D., & Heinz, A. (2016). Chronic pain and distorted body image: Implications for multisensory feedback interventions. *Neuroscience and Biobehavioral Reviews*, 69, 252–259.
<https://doi.org/10.1016/j.neubiorev.2016.08.009>
- Serino, A., Bassolino, M., Farnè, A., & Làdavas, E. (2007). Extended multisensory space in blind cane users. *Psychological Science*, 18(7), 642–648.
<https://doi.org/10.1111/j.1467-9280.2007.01952.x>
- Serino, A., & Haggard, P. (2010). Touch and the body. *Neuroscience and Biobehavioral Reviews*, 34(2), 224–236.
<https://doi.org/10.1016/j.neubiorev.2009.04.004>
- Shah, S., Vanclay, F., & Cooper, B. (1989). Improving the sensitivity of the Barthel Index for stroke rehabilitation. *Journal of Clinical Epidemiology*, 42(8), 703–709. [https://doi.org/10.1016/0895-4356\(89\)90065-6](https://doi.org/10.1016/0895-4356(89)90065-6)
- Shield, A., & Meier, R. P. (2018). Learning an Embodied Visual Language: Four Imitation Strategies Available to Sign Learners. *Frontiers in Psychology*, 9(MAY). <https://doi.org/10.3389/fpsyg.2018.00811>
- Siple, P. (1978). Visual Constraints for Sign Language Communication. *Sign Language Studies*, 1019(1), 95–110. <https://doi.org/10.1353/sls.1978.0010>
- Sirigu, A., Grafman, J., Bressler, K., & Sunderland, T. (1991). Multiple representations contribute to body knowledge processing : evidence from a case of autotopagnosia. *Brain*, 114(1), 629–642.
<https://doi.org/10.1093/brain/114.1.629>
- Skrzypek, S., Wehmeier, P. M., & Remschmidt, H. (2001). Body image assessment using body size estimation in recent studies on anorexia nervosa. A brief review. *European Child & Adolescent Psychiatry*, 10(4), 215–221.
<https://doi.org/10.1007/s007870170010>
- Slade, P. D., & Brodie, D. (1994). Body-image distortion and eating disorder: A reconceptualization based on the recent literature. *European Eating Disorders*

Review, 2(1), 32–46. <https://doi.org/10.1002/erv.2400020105>

- Slade, P. D., & Russell, G. F. M. (1973). Awareness of body dimensions in anorexia nervosa: cross-sectional and longitudinal studies. *Psychological Medicine*, 3(2), 188–199. <https://doi.org/10.1017/S0033291700048510>
- Slater, M., Perez-Marcos, D., Ehrsson, H. H., & Sanchez-Vives, M. V. (2008). Towards a digital body: The virtual arm illusion. *Frontiers in Human Neuroscience*, 2, 6. <https://doi.org/10.3389/neuro.09.006.2008>
- Slater, M., Spanlang, B., Sanchez-Vives, M. V., & Blanke, O. (2010). First person experience of body transfer in virtual reality. *PLoS ONE*. <https://doi.org/10.1371/journal.pone.0010564>
- Sliwiska, M., Bearpark, C., Corkhill, J., McPhillips, A., & Pitcher, D. (2019). Dissociable pathways for moving and static face perception begin in early visual cortex: evidence from an acquired prosopagnosic. <https://doi.org/10.31234/osf.io/sdtrv>
- Smeets, M. A. M., Klugkist, I. G., Rooden, S. van, Anema, H. A., & Postma, A. (2009). Mental body distance comparison: A tool for assessing clinical disturbances in visual body image. *Acta Psychologica*, 132(2), 157–165. <https://doi.org/10.1016/j.actpsy.2009.03.011>
- Smit, M., Van Stralen, H. E., Van den Munckhof, B., Snijders, T. J., & Dijkerman, H. C. (2018). The man who lost his body: Suboptimal multisensory integration yields body awareness problems after a right temporoparietal brain tumour. *Journal of Neuropsychology*, 1–10. <https://doi.org/10.1111/jnp.12153>
- Spitoni, G. F., Pireddu, G., Cimmino, R. L., Galati, G., Priori, A., Lavidor, M., ... Pizzamiglio, L. (2013). Right but not left angular gyrus modulates the metric component of the mental body representation: a tDCS study. *Experimental Brain Research*, 228(1), 63–72. <https://doi.org/10.1007/s00221-013-3538-9>
- Sposito, A., Bolognini, N., Vallar, G., & Maravita, A. (2012). Extension of perceived arm length following tool-use: Clues to plasticity of body metrics. *Neuropsychologia*, 50(9), 2187–2194. <https://doi.org/10.1016/j.neuropsychologia.2012.05.022>
- Stefan, K. (2000). Induction of plasticity in the human motor cortex by paired

- associative stimulation. *Brain*, *123*(3), 572–584.
<https://doi.org/10.1093/brain/123.3.572>
- Stefanucci, J. K., & Geuss, M. N. (2010). Duck! Scaling the height of a horizontal barrier to body height. *Attention, Perception & Psychophysics*, *72*(5), 1338–1349. <https://doi.org/10.3758/APP.72.5.1338>
- Stone, K. D., Keizer, A., & Dijkerman, H. C. (2018). The influence of vision, touch, and proprioception on body representation of the lower limbs. *Acta Psychologica*, *185*, 22–32. <https://doi.org/10.1016/j.actpsy.2018.01.007>
- Stone, K. D., Kornblad, C. A. E., Engel, M. M., Dijkerman, H. C., Blom, R. M., & Keizer, A. (2020). An Investigation of Lower Limb Representations Underlying Vision, Touch, and Proprioception in Body Integrity Identity Disorder. *Frontiers in Psychiatry*, *11*(February), 15.
<https://doi.org/10.3389/fpsy.2020.00015>
- Stone, S. P., Wilson, B., Wroot, A., Halligan, P. W., Lange, L. S., Marshall, J. C., & Greenwood, R. J. (1991). The assessment of visuo-spatial neglect after acute stroke. *Journal of Neurology Neurosurgery and Psychiatry*, *54*(4), 345–350.
<https://doi.org/10.1136/jnnp.54.4.345>
- Strauss, E., Sherman, E. M., & Spreen, O. (1998). *A Compendium of Neuropsychological Tests: Administration, Norms, and Commentary. Administration Norms And Commentary*. American Chemical Society.
- Suchan, B., Bauser, D. S., Busch, M., Schulte, D., Grönemeyer, D., Herpertz, S., & Vocks, S. (2013). Reduced connectivity between the left fusiform body area and the extrastriate body area in anorexia nervosa is associated with body image distortion. *Behavioural Brain Research*.
<https://doi.org/10.1016/j.bbr.2012.12.002>
- Suchan, B., Busch, M., Schulte, D., Grönemeyer, D., Herpertz, S., & Vocks, S. (2010). Reduction of gray matter density in the extrastriate body area in women with anorexia nervosa. *Behavioural Brain Research*, *206*(1), 63–67.
<https://doi.org/10.1016/j.bbr.2009.08.035>
- Sui, J., & Han, S. (2007). Self-Construal Priming Modulates Neural Substrates of Self-Awareness. *Psychological Science*, *18*(10), 861–866.

<https://doi.org/10.1111/j.1467-9280.2007.01992.x>

- Sui, J., & Humphreys, G. W. (2015). Super-size me: self biases increase to larger stimuli. *Psychonomic Bulletin and Review*, 22(2), 550–558.
<https://doi.org/10.3758/s13423-014-0690-6>
- Sunderland, A., Tinson, D., Bradley, L., & Hewer, R. L. (1989). Arm function after stroke. An evaluation of grip strength as a measure of recovery and a prognostic indicator. *Journal of Neurology, Neurosurgery & Psychiatry*, 52(11), 1267–1272. <https://doi.org/10.1136/jnnp.52.11.1267>
- Sutton-Spence, R., Woll, B., & Allsop, L. (1990). Variation and recent change in fingerspelling in British Sign Language. *Language Variation and Change*, 2(03), 313. <https://doi.org/10.1017/S0954394500000399>
- Tajadura-Jiménez, A., Longo, M. R., Coleman, R., & Tsakiris, M. (2012). The person in the mirror: Using the enfacement illusion to investigate the experiential structure of self-identification. *Consciousness and Cognition*, 21(4), 1725–1738. <https://doi.org/10.1016/j.concog.2012.10.004>
- Tajadura-Jiménez, A., Vakali, M., Fairhurst, M. T., Mandrigin, A., Bianchi-Berthouze, N., & Deroy, O. (2017). Contingent sounds change the mental representation of one's finger length. *Scientific Reports*, 7(1), 5748.
<https://doi.org/10.1038/s41598-017-05870-4>
- Tamayo, F., Casals-Coll, M., Sánchez-Benavides, G., Quintana, M., Manero, R. M., Rognoni, T., ... Peña-Casanova, J. (2012). Estudios normativos españoles en población adulta joven (Proyecto NEURONORMA jóvenes): normas para las pruebas span verbal, span visuoespacial, Letter-Number Sequencing, Trail Making Test y Symbol Digit Modalities Test. *Neurología*, 27(6), 319–329.
<https://doi.org/10.1016/j.nrl.2011.12.020>
- Tamè, L., Dransfield, E., Quettier, T., & Longo, M. R. (2017). Finger posture modulates structural body representations. *Scientific Reports*, 7(1), 43019.
<https://doi.org/10.1038/srep43019>
- Taylor-Clarke, M., Jacobsen, P., & Haggard, P. (2004). Keeping the world a constant size: Object constancy in human touch. *Nature Neuroscience*, 7(3), 219–220.
<https://doi.org/10.1038/nn1199>

- Taylor-Clarke, M., Kennett, S., & Haggard, P. (2002). Vision Modulates Somatosensory Cortical Processing. *Current Biology*, *12*(3), 233–236. [https://doi.org/10.1016/S0960-9822\(01\)00681-9](https://doi.org/10.1016/S0960-9822(01)00681-9)
- Taylor, J. C., Wiggett, A. J., & Downing, P. E. (2007). Functional MRI Analysis of Body and Body Part Representations in the Extrastriate and Fusiform Body Areas. *Journal of Neurophysiology*, *98*(3), 1626–1633. <https://doi.org/10.1152/jn.00012.2007>
- Thair, H., Holloway, A. L., Newport, R., & Smith, A. D. (2017). Transcranial Direct Current Stimulation (tDCS): A Beginner’s Guide for Design and Implementation. *Frontiers in Neuroscience*, *11*(NOV), 1–13. <https://doi.org/10.3389/fnins.2017.00641>
- Toh, S. F. M., & Fong, K. N. K. (2012). Systematic review on the effectiveness of mirror therapy in training upper limb hemiparesis after stroke. *Hong Kong Journal of Occupational Therapy*, *22*(2), 84–95. <https://doi.org/10.1016/j.hkjot.2012.12.009>
- Tosi, G., Romano, D., & Maravita, A. (2018). Mirror Box Training in Hemiplegic Stroke Patients Affects Body Representation. *Frontiers in Human Neuroscience*, *11*(January), 1–10. <https://doi.org/10.3389/fnhum.2017.00617>
- Touyz, S. W., Beumont, P. J. V., Collins, J. K., McCabe, M., & Jupp, J. (1984). Body Shape Perception and its Disturbance in Anorexia Nervosa. *British Journal of Psychiatry*, *144*(2), 167–171. <https://doi.org/10.1192/bjp.144.2.167>
- Tsakiris, M. (2008). Looking for myself: Current multisensory input alters self-face recognition. *PLoS ONE*, *3*(12). <https://doi.org/10.1371/journal.pone.0004040>
- Tsakiris, M. (2010). My body in the brain: A neurocognitive model of body-ownership. *Neuropsychologia*, *48*(3), 703–712. <https://doi.org/10.1016/j.neuropsychologia.2009.09.034>
- Tsakiris, M., Costantini, M., & Haggard, P. (2008). The role of the right temporo-parietal junction in maintaining a coherent sense of one’s body. *Neuropsychologia*, *46*(12), 3014–3018. <https://doi.org/10.1016/j.neuropsychologia.2008.06.004>
- Tsakiris, M., Tajadura-Jiménez, A., & Costantini, M. (2011). Just a heartbeat away

from one's body: Interoceptive sensitivity predicts malleability of body-representations. *Proceedings of the Royal Society B: Biological Sciences*, 278(1717), 2470–2476. <https://doi.org/10.1098/rspb.2010.2547>

Tsao, D. Y., & Livingstone, M. S. (2008). Mechanisms of Face Perception. *Annual Review of Neuroscience*, 31(1), 411–437.

<https://doi.org/10.1146/annurev.neuro.30.051606.094238>

Türker, K. S., Yeo, P. L. M., & Gandevia, S. C. (2005). Perceptual distortion of face deletion by local anaesthesia of the human lips and teeth. *Experimental Brain Research*, 165(1), 37–43. <https://doi.org/10.1007/s00221-005-2278-x>

Uher, R., Murphy, T., Friederich, H.-C., Dalgleish, T., Brammer, M. J., Giampietro, V., ... Treasure, J. (2005). Functional Neuroanatomy of Body Shape Perception in Healthy and Eating-Disordered Women. *Biological Psychiatry*, 58(12), 990–997. <https://doi.org/10.1016/j.biopsych.2005.06.001>

Ullrich, D. P., & Woolsey, C. N. (1954). Trigeminal nerve representation in the “upper head area” of the postcentral gyrus of *Macaca mulatta*. *Transactions of the American Neurological Association*, 13, 23–28.

Urdapilleta, I., Aspavlo, D., Masse, L., & Docteur, A. (2010). Use of a picture distortion technique to examine perceptive and ideal body image in male and female competitive swimmers. *Psychology of Sport and Exercise*, 11(6), 568–573. <https://doi.org/10.1016/j.psychsport.2010.06.006>

Urgesi, C., Berlucchi, G., & Aglioti, S. M. (2004). Magnetic Stimulation of Extrastriate Body Area Impairs Visual Processing of Nonfacial Body Parts. *Current Biology*, 14(23), 2130–2134. <https://doi.org/10.1016/j.cub.2004.11.031>

Urgesi, C., Calvo-Merino, B., Haggard, P., & Aglioti, S. M. (2007). Transcranial Magnetic Stimulation Reveals Two Cortical Pathways for Visual Body Processing. *Journal of Neuroscience*, 27(30), 8023–8030. <https://doi.org/10.1523/JNEUROSCI.0789-07.2007>

Urgesi, C., Fornasari, L., Perini, L., Canalaz, F., Cremaschi, S., Faleschini, L., ... Brambilla, P. (2012). Visual body perception in anorexia nervosa. *International Journal of Eating Disorders*, 45(4), 501–511. <https://doi.org/10.1002/eat.20982>

Vallar, G. (1998). Spatial hemineglect in humans. *Progress in Neurobiology*, 2(3),

87–98. [https://doi.org/10.1016/S1364-6613\(98\)01145-0](https://doi.org/10.1016/S1364-6613(98)01145-0)

- van Elk, M., Forget, J., & Blanke, O. (2013). The effect of limb crossing and limb congruency on multisensory integration in peripersonal space for the upper and lower extremities. *Consciousness and Cognition*, 22(2), 545–555. <https://doi.org/10.1016/j.concog.2013.02.006>
- van Stralen, H. E., van Zandvoort, M. J. E., Kappelle, L. J., & Dijkerman, H. C. (2013). The Rubber Hand Illusion in a Patient with Hand Disownership. *Perception*, 42(9), 991–993. <https://doi.org/10.1068/p7583>
- Villalobos, D., Bilbao, Á., Espejo, A., & García-Pacios, J. (2018). Efficacy of an intervention programme for rehabilitation of awareness of deficit after acquired brain injury: A pilot study. *Brain Injury*, 32(2), 158–166. <https://doi.org/10.1080/02699052.2017.1387931>
- Visser, J., Geuze, R. H., & Kalverboer, A. F. (1998). The relationship between physical growth, the level of activity and the development of motor skills in adolescence: Differences between children with DCD and controls. *Human Movement Science*, 17(4–5), 573–608. [https://doi.org/10.1016/S0167-9457\(98\)00014-1](https://doi.org/10.1016/S0167-9457(98)00014-1)
- Vuilleumier, P., Reverdin, A., & Landis, T. (1997). Four Legs: Illusory Reduplication of the Lower Limbs After Bilateral Parietal Lobe Damage. *Archives of Neurology*, 54, 1543–1547. Retrieved from <http://archneur.jamanetwork.com/>
- Walsh, L. D., Hoad, D., Rothwell, J. C., Gandevia, S. C., & Haggard, P. (2015). Anaesthesia changes perceived finger width but not finger length. *Experimental Brain Research*, 233(6), 1761–1771. <https://doi.org/10.1007/s00221-015-4249-1>
- Walton, B. R. P., & Hills, P. J. (2012). Face distortion aftereffects in personally familiar, famous, and unfamiliar faces. *Frontiers in Psychology*, 3(AUG). <https://doi.org/10.3389/fpsyg.2012.00258>
- Weber, E. H., & Ross, H. E. (1978). *The sense of touch*. Academic Press for [the] *Experimental Psychology Society*.
- Webster, M. A., & MacLin, O. H. (1999). Figural aftereffects in the perception of faces. *Psychonomic Bulletin and Review*, 6(4), 647–653.

<https://doi.org/10.3758/BF03212974>

- Weinstein, S. (1968). *Intensive and extensive aspects of tactile sensitivity as a function of body part, sex and laterality. The skin senses.*
- Wilson, B. A., Cockburn, J., & Haligan, P. W. (1987). *Behavioural Inattention Test.* Thames Valley Test Company.
- Woodward, J. (1982). Single Finger Extension: For a Theory of Naturalness in Sign Language Phonology. *Sign Language Studies*, 1037(1), 289–304.
<https://doi.org/10.1353/sls.1982.0021>
- Woolsey, C. N., Marshall, W. H., & Bard, P. (1942). Representation of cutaneous tactile sensibility in the cerebral cortex of the monkey as indicated by evoked potentials. *Bulletin of the Johns Hopkins Hospital*, 70, 399–441.
- Wu, C. W. H., Seo, H.-J., & Cohen, L. G. (2006). Influence of Electric Somatosensory Stimulation on Paretic-Hand Function in Chronic Stroke. *Archives of Physical Medicine and Rehabilitation*, 87(3), 351–357.
<https://doi.org/10.1016/j.apmr.2005.11.019>
- Wu, C. W. H., van Gelderen, P., Hanakawa, T., Yaseen, Z., & Cohen, L. G. (2005). Enduring representational plasticity after somatosensory stimulation. *NeuroImage*, 27(4), 872–884. <https://doi.org/10.1016/j.neuroimage.2005.05.055>
- Wunderlich, G., Knorr, U., Herzog, H., Kiwit, J. C. W., Freund, H. J., & Seitz, R. J. (1998). Precentral glioma location determines the displacement of cortical hand representation. *Neurosurgery*, 42(1), 18–27. <https://doi.org/10.1097/00006123-199801000-00005>
- Yau, J. M., Celnik, P., Hsiao, S. S., & Desmond, J. E. (2014). Feeling Better: Separate pathways for targeted enhancement of spatial and temporal touch. *Psychological Science*, 25(2), 555–565.
<https://doi.org/10.1177/0956797613511467>
- Ziemann, U. (2001). Modulation of practice-dependent plasticity in human motor cortex. *Brain*, 124(6), 1171–1181. <https://doi.org/10.1093/brain/124.6.1171>