

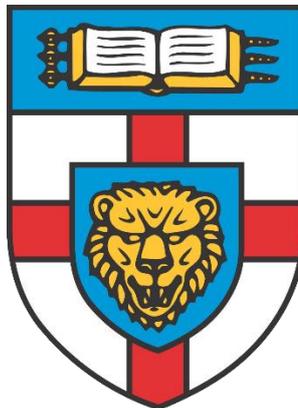
Cognitive mechanisms underlying body representation.
A study on body metrics and body perception.

Pietro Caggiano

Goldsmiths College

University of London

Department of Psychology



Submitted in fulfilment of the requirements for the degree of

Doctor of Philosophy in Psychology

MAY 2020

Declaration of Authorship

I, Pietro Caggiano, hereby declare that this thesis and the work presented in it is my own.

Where I have consulted the work of others, this is always clearly stated.

18/05/2020

Acknowledgments

I would like to express my sincerest gratitude to my supervisor Dr. Gianna Cocchini. Carrying out a part-time self-funded PhD has not been an easy task, without her support, thoughtful advice, guidance and help this would not have been possible. I am grateful for her constant encouragement which allowed me to grow both professionally and as a person. I would like also to thank Dr Jose Van Velzen for her advice and positive feedback on setting up my first EEG study and Dr Giordana Grossi who provided insightful comments on the preliminary EEG data. I thank Laura Mora, a friend and a companion in this journey. I will never forget our memorable trips to ‘sunny’ Edinburgh and Milan. A special thank you goes to Roberta Carugati with whom I shared many experiences. She has always had wise and encouraging words, especially when things were not going the way I would expect. Most importantly, a warm thank you goes to my mum and dad, Elvira and Carlo, and my brother Marco. It is thanks to your love and support that I have been able to follow and achieve my aspirations. Lastly, I would like to thank my partner Angela, I will never be able to thank you enough for all your support, patience and love. I owe you many weekends spent at home because I had to concentrate on my research. A heartfelt thank you!

Abstract

Our body is an essential component of our sense of self; it is not just a means through which we passively experience the world, but we actively use it to act *on* and interact *with* the world around us. Because of such ‘intimate’ relationship, it is natural to assume a relatively accurate perception of its size and the relative proportion of its parts. Surprisingly, this seems not to be the case. A growing body of research indicates that the way we represent the size and proportion of our body is dramatically and systematically distorted. The present work is an attempt to understand from where these distortions may arise. Starting from the classic distinction between the *body schema* and the *body image*, the focus of this thesis is to investigate the potential interaction between these two components, which has often been implicitly assumed but rarely explicitly assessed. The results obtained, by means of implicit and explicit quantitative measures, highlighted a *functional* dimension of the body representation. Event-related potential technique has been implemented to evaluate the effect of the object-body part relationship on the modulation of N2-P3 complex in parieto-occipital areas. Electrophysiological data indicated that body parts, coded as effectors, intrinsically carry information about their functional role. Furthermore, by actively manipulating the ‘action’ component in a further study, findings indicated that modification in the *body schema* were reflected into the more conscious representation of the *body image*. Lastly, the study on patients with Personal Neglect (PN) showed that these patients represent the size of their contralesional hand, quantitatively and qualitatively, differently from patients without PN and healthy controls. The results provided further insight into the impact of hemiplegia and personal neglect on the representation of the hands’ size, indicating that bottom-up and top-down processes can differentially impact on the body representation.

Parts of this work have been disseminated as the following:

Manuscripts published in peer-reviewed scientific journals:

Caggiano, P., & Cocchini, G. (2020). The functional body: does body representation reflect functional properties? *Experimental Brain Research*, 238(1), 153-169.

Caggiano, P., & Jehkonen, M. (2018). The “neglected” personal neglect. *Neuropsychology Review*, 28, 417-435.

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.

Manuscripts under review:

Caggiano, P., Carlacci De Mattia, L., & Cocchini, G. (submitted for publication). Object use modulates body representation: evidence of “functional” priming on body parts recognition. *Acta Psychologica*.

Caggiano, P., Veronelli, L., Mora, L., Arduino, L.S., & Cocchini, G. (submitted for publication). The downsized hand in personal neglect. *Journal of Clinical and Experimental Neuropsychology*.

Conference proceedings:

“Evidence of "functional" priming on body part recognition”, Body Representation Network, 5th July 2019, Milan (Italy)

“How do I look like? An insight into the mental representation of the body”, Body Representation Network, 29th June 2018, Edinburgh (UK)

“The downsized hand in Persona Neglect”, The British Neuropsychological Society Spring Meeting, 26th-27th April 2018, London (UK).

“Personal neglect following unilateral right- and left-brain damage ”, 2nd Word Conference on Psychology and Sociology, 27th -129th November 2013, Bruxelles (Belgium).

Table of Contents

Chapter 1 – <i>Building blocks of body representaion</i>	11
1.1 Introduction	11
1.2 Somatosensory System.....	13
1.2.1 Mechanoreceptors Mediate Touch and Proprioception.....	14
1.2.2 Ascending Somatosensory Pathways.....	16
1.2.3 The Organization of Somatosensory Cortex.....	19
1.3 Motor system.....	20
1.3.1 Descending motor pathways.....	21
1.3.2 The Organization of the Motor cortex	22
1.4 Visual System.....	24
1.4.1 Visual Body-selective areas.....	26
Chapter 2 - <i>The multiple concepts of the body representation</i>	30
2.1 Historical background	30
2.2 The need for clarity	34
2.3 Evidence in support of the dyadic model	36
2.4 Triadic model	44
2.5 Body metrics.....	48
2.6 The need for integration	53
Chapter 3 - <i>Research project structure</i>	57
3.1 Study rationale.....	57
Chapter 4 - <i>The ‘steady state’ of body representation</i>	63
STUDY 1	63
4.1 Overview	63
4.2 Introduction	64
4.3 Experiment 1a - Localization of body landmarks on real scale	68
4.3.1 Methods and procedures	68
4.3.2 Results.....	74
4.3.3 Preliminary discussion.....	77
4.4 Experiment 1b - Localization of body landmark in inverted position.....	79
4.4.1 Methods and procedures	79
4.4.2 Results.....	80
4.4.3 Preliminary Discussion	84
4.5 Experiment 1c - Localization of body landmark on elevated positions	86
4.5.1 Methods and procedures	86
4.5.2 Results.....	88

4.5.3 Preliminary Discussion	91
4.6 Experiment 2 - Depictive task for own and prototypical body	92
4.6.1 Methods and procedures	92
4.7 Discussion and Conclusion	97
STUDY 2	101
4.8 Overview	101
4.9 Introduction	102
4.10 Experiment 3 – Functional priming task	104
4.10.1 Methods and procedures	104
4.10.2 Results.....	107
4.10.3 Preliminary discussion.....	110
4.11 Experiment 4 – Functional priming task (ERP analysis)	112
4.11.1 Methods and procedures	112
4.11.2 Results.....	113
4.12 Discussion and Conclusions	120
Chapter 5 - Modulation: do actions shape body representation?	125
STUDY 3	125
5.1 Overview	125
5.2 Introduction	125
5.3 Experiment 5 – Localization task following motor training in different spatial locations	129
5.3.1 Methods and procedures	129
5.3.2 Results.....	132
5.3.3 Preliminary discussion.....	139
5.4 Experiment 6 – Arm bisection task following motor training with different arm segments	142
5.4.1 Methods and procedures	142
5.4.2 Results.....	146
5.4.3 Preliminary discussion.....	148
5.5 Experiment 7 – Functional priming task following motor training with different body parts.....	151
5.5.1 Methods and procedures	151
5.5.2 Results.....	153
5.6 Discussion and Conclusion	157
Chapter 6 - Personal neglect: a body representation disorder	160
STUDY 4	160
6.1 Overview	160

6.2 Introduction	161
6.3 Experiment 8 – Apertures task	164
6.3.1 Methods and procedures	164
6.3.2 Statistical analysis.....	167
6.3.3 Results.....	168
6.4 Discussion and Conclusion	176
Chapter 7 - <i>General discussion</i>	180
7.1 Summary of main findings	181
7.2 Function, integration and construction of the body representation(s).....	187
7.3 Limitations.....	193
7.1 Concluding remarks	194
References	197

List of Figures

Figure 1.1 Somatic sensory receptors	15
Figure 1.2 Schematic representation of dermatomes.	16
Figure 1.3. Schematic representation of the dorsal column–medial lemniscal System (in red) and the anterolateral system (in black).....	18
Figure 1.4. a) Primary motor cortex and b) primary somatosensory cortex.....	23
Figure 1.5. Visual areas of the human cerebral cortex.....	26
Figure 1.6. Body- and face-selective regions of the human visual cortex.	27
Figure 2.1 Schematic representation of Dijkerman and de Haan’s neuroanatomical model	36
Figure 2.2. Triadic cognitive-neuropsychological model of body representation (modified from Sirigu et al., 1991).....	44
Figure 2.3. Model of somatoperceptual information processing	50
Figure 2.4. Schematic depiction of body schema/body image interactions.....	54
Figure 4.1. Schematic sketch of the experimental setting.....	71
Figure 4.2. Under/overestimation in perceived body parts’ length.....	76
Figure 4.3. Schematic sketch of the experimental setting.....	80
Figure 4.4. Under/overestimation in perceived body parts’ length.....	83
Figure 4.5. Schematic sketch of the experimental setting.....	87
Figure 4.6. Under/overestimation in perceived body parts’ length.....	90
Figure 4.7. Types of stimuli adopted in the Experiment 2.....	93
Figure 4.8. Under/overestimation in perceived body parts’ length.....	97
Figure 4.9. Stimuli (objects and body parts) presented during the task.....	105
Figure 4.10. Example of <i>Related</i> condition. Response buttons were counterbalanced across subjects.	106
Figure 4.11. Participants’ performance (average and error standard) on the Priming task in terms of ACC, RLs and speed-accuracy trade off.....	109
Figure 4.12. Grand average waveforms for 19 participants.....	115
Figure 4.13. Grand average waveforms for 19 participants.....	119
Figure 5.1. Schematic representation of training sessions.	131
Figure 5.2. Under/overestimation in perceived body parts’ length.....	134
Figure 5.3. Differences between post-training and pre-training %BPEs.	136
Figure 5.4. Differences between post- and pre-training body part ratios.....	138
Figure 5.5. Schematic representation of the trainings involving distal and proximal movements.....	145

Figure 5.6. Perceived position of the middle point between the tip of the middle finger and the elbow.	147
Figure 5.7. Schematic depiction of the motor training session.	153
Figure 5.8. Participants' performance (average and standard error) following: a) HAND training on the left column, b) FOOT training on the right column.	156
Figure 6.1. Schematic representation of the apertures task. Participants were asked to imagine whether the palm of their hand, indicated by the arrows, could fit into a series of vertical apertures.	168
Figure 6.2. Superimposition of the right-hemispheric lesions for the two patient groups.	169
Figure 6.3. Graphic representation of both left and right hands distortion for the three groups.	173
Figure 6.4. Percentage difference (\pm SE) between left and right hands for the three groups.	174
Figure 6.5. Individual <i>delta</i> values for a) PN- group and b) PN+ group.	175

List of Tables

Table 4.1. Body parts that participants were asked to locate.	72
Table 4.2. Length of body segments.	73
Table 4.3. Results of two-tailed t-tests comparing percentage of distortion (bpE) with 0 (no distortion).	74
Table 4.4. Two-tailed t-tests results comparing %BPE with 0.	81
Table 4.5. Two-tailed t-tests results comparing %BPE with 0.	88
Table 4.6. Results of two-tailed t-tests comparing transition points with 0 for Own body and Avatar.	96
Table 5.1. Two-tailed t-tests results comparing %BPE with 0.	133
Table 5.2. Two-tailed t-tests results comparing % ratio aspects with 0.	137
Table 6.1. Demographic and neurological information of 11 right brain-damaged patients.	165
Table 6.2. Assessment for personal and extrapersonal neglect.	170
Table 6.3. Correlation between LH performance and demographic/assessment scores variables	171

Chapter 1

Building blocks of body representation

“...the I that I think is distinct from the I that it, itself, intuits...; I am given to myself beyond that which is given in intuition, and yet know myself, like other phenomena, only as I appear to myself, not as I am...”

Immanuel Kant, Critique of Pure Reason

1.1 Introduction

Our body is an essential component of our sense of self thus, it is not surprising that the way we represent our body has sparked an increasing research and debate in cognitive psychology and neuroscience. Body representation is a complex concept not easy to delineate. Generally speaking, it can be defined as a multidimensional construct that includes perceptual, cognitive, emotional and behavioural aspects towards the body. It refers to a complex function of synthesis that allows us to recognize our body as a whole, to identify the morphology, the relationships between the single parts and the changing position in space (Paillard, 1999). The successful interaction with the surrounding space, is closely linked to the ability to correctly localize stimuli located in the external space and their relationship with the spatial position of one's body.

The long-lasting epistemological debate in psychology, according to which the object of study is also the subject investigating it (the mind), appears to be even more evident when thinking about body representation. In fact, there is no doubt that our body, pre-reflexive¹ in nature, is the object of direct perception by which we experience reality

¹ In the field of phenomenology, pre-reflexive self-consciousness is defined as the immediate and first-personal givenness of experience. It refers to an implicit awareness rather than an explicit form of self-consciousness. The pre-reflective self-consciousness is not the result of active introspection and is present any time “I” am living through or undergoing an experience (e.g. when “I” am consciously perceiving the world or remembering a past event). In this sense, pre-reflective self-consciousness is pre-reflective because

in a *first-person* perspective, we feel our sensations “from the inside”. Similarly, it is also true that our body is a vehicle *for* perception. It is a physical object, like any other, subject to external forces that can be experienced in a *third-person* perspective allowing us to cognitively reflect “from the outside” on our body as a biological object. Such duality results in a constant cyclic exchange of information by which sensory input and perceptual experience inform and construct representations of the body and, at the same time, these body representations mediate and influence perception.

The perceptual experience starts with *somatosensation*, the basic sensory mechanisms underlying the bodily senses (i.e. touch, pain, proprioception). Different sub-modalities play different roles in the updating and feeding different aspects of body representation.

The first part of this dissertation will guide ‘from the body (as a physical object) to its representation(s)’. To this aim, two introductory chapters will set the ground to interpret the novelty of the data reported in the experimental section of this thesis. The current chapter (Chapter 1) will provide a brief overview on the building blocks and neural substrates that contribute to the body representation: i) somatosensory system, ii) motor system and iii) visual system. In the second part of the introduction (Chapter 2), a more detailed discussion about the history and recent approaches and models of body representation will be presented with a critical evaluation of some outstanding points in literature.

The study rationale will be then set out. Chapter 3 will introduce the study rationale with a detailed guidance on how the experimental section has been developed and structured. Chapters 4, 5 and 6 constitute the “core” of the present work and collectively refer to the experimental section of the thesis.

it is an awareness we have before we do any reflecting on our experience (Stanford Encyclopaedia of Philosophy, 2019).

Chapter 4 will aim at setting a baseline of how the body is represented and perceived. The hypothesis according to which the body representation may reflect *functional* properties will be directly explored. Such hypothesis will be further tested in Chapter 5 where the effect of movements and posture on body representation will be assessed. Lastly, in Chapter 6 the focus will shift on a particular neuropsychopathological condition, Personal Neglect, which recent literature has suggested to be linked to a primary disruption of body representation.

The final chapter (Chapter 7) will provide a closure to the present work by summarising the findings from the studies reported in the previous chapters of this dissertation; conclusions will be drawn, and future direction critically outlined.

1.2 Somatosensory System

The somatosensory system mediates bodily sensations through somatic information provided by specific receptors distributed throughout the body. Generally speaking, the initial stage of sensing occurs through sensory receptors that performs a *sensory transduction* of physical events into electrical signals. Critically, an evoked sensation depends on the sensorial organ and not on the stimulation mode itself (Norrzell, Finger, & Lajonchere, 1999). The same stimulation, applied to different nervous fibers, will produce a different sensation. In other words, it is the type of fibre and the cortical area the fibre is connected to, and not the stimulation by itself, that determines the type of sensation evoked.

The somatosensory system consists of a variety of specialized receptors which underlie various somatosensory sub-modalities. Three subsystems mediate different types of information: exteroceptive, interoceptive and proprioceptive. *Exteroception* is the sense of direct interaction with the external environment that occur mainly by touch which includes sensations of contact, pressure, stroking, motion, and vibration, and is used to identify objects. While some touch sensations originate from passive contact (i.e.

pressure), others involve an active motor component (i.e. stroking, tapping, grasping) whereby a part of the body is moved against another surface or organism. The sensory and motor components of touch are closely connected anatomically in the brain and are important in guiding behaviour. Exteroception also includes the thermal senses of heat and cold and the sense of pain (nociception). *Proprioception* is the sense of oneself. Receptors in skeletal muscle, joint capsules, and the skin enable us to have conscious awareness of the posture and movements of our own body. *Interoception* refers to the perception of our internal state and defines the sense of the physiological condition of various body tissues (Sherrington, 1906). For the purpose of the present project, the discussion will focus on touch and proprioception.

1.2.1 Mechanoreceptors Mediate Touch and Proprioception

Touch refers to the particular exteroceptive sub-modality by which contact with the body is perceived consciously. A particular class of sensory receptor respond to external stimuli that physically deform the tissue in which they reside and therefore their receptive surface. The mechanical distension, such as pressure on the skin or stretch of muscles, is sensed by specialized receptors and transduced into electrical energy by the physical action of the stimulus determining the type of stimulus detected by the neuron.

Eight types of mechanoreceptors are located in the skin that are responsible for the sense of touch (Figure 1.1). The glabrous skin contains four kinds of mechanoreceptors that can be divided according to where they are located (deep receptors and superficial receptors) or their adaptation capacity (slowly adapting and rapidly adapting). Meissner corpuscles and Merkel cells are both situated in the superficial layers of the skin while Pacinian corpuscles and Ruffini endings are deep receptors. Two of these, Merkel cells and Ruffini endings are slowly adapting receptors because they continue to fire in response to steady pressure on the skin. Meissner and Pacinian corpuscles are rapidly adaptive receptors with a high sensitivity (low threshold). They are activated when light

touch is delivered and rapidly generate action potentials, which quickly decrease and eventually disappear if pressure is maintained constant.

Hairy skin contains all of the mechanoreceptor described except the Meissner corpuscle with some other types of receptors. The hair follicle afferents have a function similar to that of Meissner's and innervate 10 to 30 hairs spread over an area of about 2 cm and they are sensitive to hair movement but not to static pressure. Other mechanoreceptors are the field receptors, which are very sensitive to skin movement, and low-threshold mechanoreceptors innervated by C fibers that respond to slow stroking of the skin.

Figure 1.1 Somatic sensory receptors

From Kandel et al. (2013)

Crucially, the distribution of these receptors differs across various body parts, resulting in a difference in sensory acuity. For example, the fingertips present a high concentration of Merkel's and Meissner's corpuscle and have the smallest receptive fields, making this body part one of the most sensitive in the body.

While mechanoreceptors in the skin mediate touch, mechanoreceptors in muscles and joints play an important role in the sense of the static position (*staticsesthesia*) and motor control (*kinesthesia*). These receptors include two types of muscle-length sensors, the

type I and II muscle spindle endings, the Golgi tendon organ and the joint-capsule receptors. The muscle spindle consists of a bundle of thin muscle fibers that provide information about changes in the length of the muscle. The Golgi tendon organs are located between skeletal muscle and tendons and sense the level of muscles contraction while the joint-capsule receptors transduce the flexion and extension of articulation. Interestingly, joint receptors play a very little role in conscious postural sensations of joint angle, the perception of the angle of the elbows or knees depends on afferent information provided by the muscle spindle receptors as well as efferent motor commands.

1.2.2 Ascending Somatosensory Pathways

Sensory information reaches the central nervous system through the 31 spinal nerves. The neural fibers that carry information from cutaneous receptors and other somatosensory receptors gather together in nerves and enter the spinal cord via the dorsal roots. The area of the body that is innervated by the left and right dorsal roots of a given segment of the spinal cord is called a *dermatome*, whereas the muscles innervated by the same nerve constitute a *myotome* (Figure 1.2). Somatosensory information ascends from

Figure 1.2 Schematic representation of dermatomes.

each side of the body to the cortex over two major pathways: *the dorsal-column medial-lemniscus system* and the *anterolateral system*. The dorsal-column medial-lemniscus system carries information mainly about touch and proprioception, while the anterolateral system is mainly dedicated to pain and temperature information.

The Dorsal Column–Medial Lemniscal System

The Dorsal Column–Medial Lemniscal tract (Figure 1.3), is characterized by three stages of transmission. The first set of neurons are the sensory neurons that enter the spinal cord via a dorsal root, ascend ipsilaterally in the dorsal columns and synapse in the dorsal column nuclei of the medulla. At this stage, the axons of dorsal column nuclei neurons decussate in the medial lemniscus, the homologous projection from the trigeminal nuclei join this tract and ascend to the thalamus.

The thalamus consists of different nuclei that have distinct connections to the cortex depending on the type of sensory information they process. The relay of the somatosensory information from the periphery to the somatosensory cortex occurs in the ventral posterior section of the thalamus. This part is composed by two nuclei: the ventral posterolateral nucleus (VPL) and the ventral posteromedial nucleus (VPM). The VPL receives fibers from the dorsal column nuclei and the VPM receives inputs from the trigeminal nerve fibers.

At this stage, a somatotopic organization can be already observed. The fibers carrying information from the lower body are located laterally and those carrying information from the upper body and face are located more medially (Lenz, Dostrovsky, Tasker, Yamashiro, Kwan, & Murphy, 1988). Most neurons of the ventral posterior nucleus project to the primary somatosensory cortex (SI); others project to the secondary somatosensory cortex (SII) or the posterior parietal cortex. Furthermore, within the dorsal column nuclei different somatosensory sub-modalities are segregated. In the rostral third of the dorsal column nuclei, nearly the 75% of neurons receive sensory information from muscle afferent while in the middle third, almost the 90% of neurons are involved in the

processing of tactile inputs (Kandel, Schwartz, Jessel, Siegelbaum, Hudspeth, & Mack, 2013).

The anterolateral system

In the anterolateral system (Figure 1.3.), most dorsal root neurons of the anterolateral system synapse as soon as they enter the spinal cord. The axons of most of the second order neurons decussate and then ascend to the brain in the contralateral anterolateral portion of the spinal cord. The anterolateral system comprises three different tracts: the *spinothalamic tract*, which projects to the ventral posterior nucleus of the thalamus; the *spinoreticular tract*, which projects to the reticular formation (and then to the parafascicular nuclei and intralaminar nuclei of the thalamus); and the *spinotectal*

Figure 1.3. Schematic representation of the dorsal column–medial lemniscal System (in red) and the anterolateral system (in black).

From Kandel et al. (2013)

tract, which projects to the tectum. The information that reaches the thalamus is then projected to SI, SII, posterior parietal cortex, and other brain areas.

1.2.3 The Organization of Somatosensory Cortex

The somatosensory cortex is divided in two major parts, the primary somatosensory (SI) and the secondary somatosensory cortex (SII), both situated in the anterior portion of the parietal cortex. The SI consists of four subdivisions, Brodmann's areas 3a and 3b, located in the posterior bank of the central sulcus, and Brodmann's areas 1 and 2 located on the surface of the postcentral gyrus and receive projections from the thalamus. While areas 3a and 2 are involved in the encoding of information concerning limb position and deep bone and muscle, areas 3b and 1 are responsible for cutaneous sensation (Geyer, Schleicher, & Zilles, 2000). These areas project to the postcentral gyrus and the intraparietal sulcus, of particular interest are the projections to Brodmann's area 5, which integrates the sensory signals and transmits them to the premotor cortex so that the somatosensory information can be used for movement coordination.

In 1937 Penfield and Boldrey, by means of direct stimulation of SI in awake patients, noted that when stimulation was applied to different regions of the postcentral gyrus, the patients reported somatosensory sensations to specific parts of their body (Penfield & Boldrey, 1937; Penfield & Rasmussen, 1952). It turned out that the relation between the site of stimulation and the part of the body in which the sensation was felt, resulted in the SI being somatotopically organized according to a map of the body now commonly known as the *somatosensory homunculus* (Narici, Bordini, & Cerretelli, 1991; Penfield & Rasmussen, 1952, Penfield & Boldrey, 1937) (Figure 1.4). A peculiar feature of the somatosensory map is the relative size of the different body portions represented in SI is not a function of the actual body part size but rather of the sensitivity to tactile stimuli in that area. The more sensitive a body part is (e.g. hands), the larger is its cortical representation.

The **secondary somatosensory cortex (SII)** located in the postcentral gyrus ventral to SI. Despite evidence suggesting the presence of direct thalamocortical projections to SII (Chakrabarti & Alloway, 2006; Kwegyir-Afful & Keller, 2004; Murray, Zhang, Kaye, Sinnadurai, Campbell, & Rowe, 1992; Turman, Ferrington, Ghosh, Morley & Rowe, 1992; Zhang, Zachariah, Coleman, & Rowe, 2001), SII receives most of its input from SI, hence the reason why it is named secondary somatosensory cortex. This area is reciprocally and somatotopically connected with the SI via ipsilateral and contralateral corticocortical connections (Burton, 1986; Gardner & Kandel, 2000; Jones, 1986; Barba, Frot, & Mauguier, 2002; Manzoni, Barbaresi, & Conti., 1984). The SII also presents a somatotopic map however, the correspondence between body parts and cortical areas is not as precise and straightforward as in SI. While the direct stimulation of a particular portion of the SI leads to a sensation that arises from the corresponding body part, a stimulation of adjacent SII leads to a sensation that extends outside the corresponding area (Mazzola, Isnard, & Mauguière, 2006).

The study of the information flow from early sensory to motor areas, highlighted the existence of 62 pathways linking 13 cortical areas in the somatosensory/motor system (Friedman, Murray, O'Neill, & Mishkin, 1986) and in addition to the connections between SI and SII, direct and indirect links have been observed between, the supplementary motor area and the primary motor area (M1) (Felleman & Van Essen, 1991).

1.3 Motor system

Humans acquire spatial knowledge directly via the sensorimotor system that operates as they navigate the external environment. This system monitors the external world and the consequences of its own actions and acts accordingly. In order to do so, a *sensory feedback* mechanism is used so that the motor output is guided by sensory inputs. The sensorimotor system is extremely complex. It describes the sensory, motor, and central integration and processing components involved in maintaining posture during bodily movements. The process of maintaining functional joint stability is accomplished

through a complementary relationship between static components such as ligaments, joint capsule, cartilage, friction, and the bony geometry within the articulation and dynamic components that arise from feedforward and feedback neuromotor control.

Proprioceptive information conveyed by mechanoreceptors (previously described) is the major “guide” of the sensorimotor system. It provides conscious sensation of three major submodalities: joint position sense, kinesthesia, and the sense of resistance or heaviness.

1.3.1 Descending motor pathways

Neural signals are conducted from the primary motor cortex to the motor neurons of the spinal cord over four different pathways. Two pathways descend in the dorsolateral region of the spinal cord, and two descend in the ventromedial region of the spinal cord.

1.3.1.1 The Dorsolateral tract

The pathway that descends from the cortex to the contralateral side of the spinal cord is the **dorsolateral tract**, which is divided into the *dorsolateral corticospinal tract* and the *dorsolateral corticorubrospinal tract*. The first decussates at the level of the medullary pyramid and controls distal muscles of the wrist, hands, fingers, and toes. The second, descends from the cortex, synapses and decussates at the level of the red nucleus and it then descends through the medulla, where some axons terminate in the nuclei of the cranial nerves and some others continue through the spinal cord motor neurons controlling the movement of the forearms, hands (but not the fingers), and feet.

1.3.1.2 The Ventromedial tract

The other descending pathway is the **ventromedial tract** also divided in two subdivisions: *ventromedial corticospinal tract* and *ventromedial cortico-brainstem-spinal tract*. The first division is a more direct pathway that descends ipsilaterally from the cortex and innervates the interneuron circuits in several spinal sections on both sides of the spinal gray matter. The second pathway projects to the brain stem and has multiple connections with a number of structures within the brain stem. Some axons then descend

bilaterally the spinal cord carrying signals from both hemispheres and controlling the proximal muscles of the trunk and limbs.

1.3.2 The Organization of the Motor cortex

The functional anatomy of the precentral motor areas is more complex and less straightforward than the somatosensory cortex. According to Brodman's classification, the precentral cortex is subdivided into caudal (area 4) and rostral parts (area 6). These two regions are functionally distinct motor areas, the caudal region that, in humans, is located in the dorsal portion of the frontal lobe, just before the central sulcus, is called **primary motor cortex (M1)** and provides the input that control simple motor actions. The rostral region, called *premotor cortex (PMC)* is more involved in high-order aspects of motor control.

M1 receives direct and indirect inputs from multiple cortical and thalamic areas, including premotor, executive, and sensory centers (Asanuma & Hunsperger 1975; Cicirata, Angaut, Cioni, Serapide, & Papale, 1986; Horne & Tracey 1979; Muakkassa & Strick 1979; Porter & White 1983; Reep, Goodwin, & Corwin, 1990). Similarly to the SI, M1 is somatotopically organized (*motor homunculus*) (Penfield & Rasmussen, 1952) (Figure 1.4) and the areas responsible for the perception of touch in the somatosensory homunculus are located mostly adjacent to the areas responsible for body parts movements in the motor homunculus. This somatotopic correspondence between the two maps highlights the existence of close somato-motor functional relationships (Gallace & Spence, 2008). Recent studies have confirmed M1's somatotopic organization but, interestingly, its organizing principle differs from SI. In fact, while the receptive field of each neuron of SI corresponds to a relatively well-defined portion of the skin (Blankenburg et al., 2003), the map in M1 is not discrete and neatly segmented as in SI so that the motor representations of the different body parts overlap. M1 seems to be organized for representing muscle groups and patterns of movement rather than

individual muscles (Lemon, 1988). It has been shown that stimulation of the M1 rather than eliciting the contractions of individual muscles, it elicits complex movement responses, which often involved several groups of muscles functionally related (Graziano, 2009). Critically, muscles are grouped together to form functionally coherent units (Hlušík, Solodkin, Gullapalli, Noll, & Small, 2001), resulting in the overlap in the cortical areas of adjacent body parts (Rathelot & Strick, 2006).

Movements of the contralateral body can be elicited not only by electrical stimulation of the M1, but also by stimulation of the *supplementary motor area* (SMA). This area contains a less fine detailed motor map of different body parts than that of the M1, also lacking the enlarged distal arm and hand representation seen in the primary motor cortex.

There is currently controversy over how many cortical motor areas exist. For the purpose of present discussion, a description of cortical areas that are conventionally considered motor areas (involved in movement planning and/or execution) is provided. The PMC occupies the part of lateral Brodmann area 6 and is divided into a ventral (PMCV) and a dorsal (PMCD) segment. The latter is further divided into a rostral (PMCDr) and a caudal (PMCDc) portion (Barbas & Pandya 1987). The SMA (medial area 6)

Figure 1.4. a) Primary motor cortex and b) primary somatosensory cortex.

consists of two functional regions: a caudal region called SMA proper and a more rostral region called pre-SMA.

Although the number of subdivision of the motor cortex would appear superfluous for this dissertation, it is important to consider the complexity of the motor action which requires the integration of somatosensory and visual information, but also multiple operations involving the selection, timing, planning, and execution of the action in response to external stimuli and internally generated needs.

1.4 Visual System

So far it has been discussed how the somatosensory and motor systems provide information about our own body. However, a dissertation on body representation would be incomplete without incorporating the visual system. At first glance, the visual cortical processing may seem to not necessarily include body representations, as it provides direct information about the structure and position of external stimuli. Nevertheless, visual input about the observer's body is an important source of information, both during the guidance of movements and for perceptual awareness and recognition of our, and others, body. Considering that vision is an extremely complex process which requires multiple stages of information processing, the fine details of this mechanism will not be discussed as this is beyond the purposes of the present work.

The retina-geniculate-striate system is the major visual pathways that from the eyes carries information to the **primary visual cortex** (V1) through the lateral geniculate nuclei. The first stage of visual processing occurs in the primary visual cortex, also known as striate cortex, located in the posterior region of the occipital lobes, where neuronal responses can discriminate small changes in visual orientations, spatial frequencies and colors. V1 is divided up into six distinct layers, each comprising different cell-types and functions. Layer IV is the location that receives information from the lateral geniculate. The areas surrounding V1 are referred to as extrastriate cortex. Direct feedforward projections from V1 to other visual areas of the extrastriate cortex originate mainly in

layers II and III and terminate mainly in layer IV of the target cortical areas (Purves, et al. 2012). The secondary visual cortex (V2) is the first region of the visual association area and, as such, responds to more complex properties of visual stimuli. From there, the visual information is progressively processed from other areas of the association cortex (i.e. V3, V4 and V5) (Figure 1.5). Critically, as one moves up this visual hierarchy, the neurons have larger receptive fields and the stimuli to which they respond are more specific and complex (Zeki, 1993). However, pathways are not exclusively serial. In fact, higher-order areas provide feedback to the lower-order areas from which they receive input. In this way neurons in higher-order areas, sensitive to the global pattern of sensory input, can modulate the activity of neurons in lower-order areas that are sensitive to local detail (Kandel et al., 2013).

Classically, two major pathways have been identified that functionally link the striate cortex to the extrastriate areas: the dorsal and the ventral stream (Ungerleider & Mishkin, 1982). The first stream travels from V1 to the posterior parietal lobe and it is thought to be involved with perceiving motion and spatial relationships between objects. The second stream projects from V1 to the inferior part of the temporal lobe and it is thought to carry information involved with object's form and recognition. Of particular interest are the lateral and ventral occipitotemporal cortices (LOTc, VOTc) which seem to play a role in higher-level body-related cognition in humans (Downing, Jiang, Shuman, & Kanwisher, 2001). So far, it has been highlighted that one of the most robust organizational principles in the brain is the topographic mapping of the body in the somatosensory and motor systems. However, LOTc and VOTc contain regions that not only respond preferentially to pictures of human bodies and faces (Kanwisher, McDermott, & Chun, 1997; Peelen & Downing, 2007), but also to individual body parts such as hands and torsos (Bracci, Ietswaart, Peelen, & Cavina-Pratesi, 2010; Op de Beeck,

Brants, Baeck, & Wagemans, 2010; Orlov, Makin, & Zohary, 2010). This seems to suggest the presence of a body map also at a visual level.

Figure 1.5. Visual areas of the human cerebral cortex.

The blue arrow indicates the dorsal stream, the green arrow the ventral stream of vision.

Modified from Pinel 2010.

1.4.1 Visual Body-selective areas

Similarly to faces, human bodies possess a peculiar configuration and, more importantly, convey socially meaningful cues. The visual perception of human body is a critical component of the ability to identify and interpret the actions and intentions of other people. It is therefore not surprising that, over the last decade, neuroimaging studies have identified two brain regions of the extrastriate visual cortex that are highly sensitive to the perception of human bodies and body parts. These two regions selective for body visual processing are the *extrastriate body area* (EBA) (Downing et al., 2001) on the lateral surface of the occipitotemporal cortex and the *fusiform body area* (FBA) (Peelen & Downing, 2005) found in the medial fusiform gyrus, which partially overlaps with fusiform face area (Figure 1.6). Both regions respond to visual appearance of bodies and body parts relative to faces, objects and a large number of other visual categories (Downing, Chan, Peelen, Dodds & Kanwisher 2006). Whereas activation in EBA is a direct function of the amount of body visible (e.g., greater for whole body and less for a single arm), FBA appears not to distinguish single body parts (e.g., arm) from the whole

body (Taylor, Wiggett, & Downing, 2007). This finding suggests that these two body-selective regions contribute differently to processing body-related information.

Figure 1.6. Body- and face-selective regions of the human visual cortex.

From Peelen & Downing, 2008

Evidence of the critical role of EBA body processing has been provided by Urgesi and colleagues (2004) who showed that the modulation of this area, 150–250 msec after stimulus onset by means of TMS, impairs individuals' perceptual discrimination on a delayed match-to-sample task for full bodies and body parts, but not for face or object parts (Urgesi, Berlucchi, & Aglioti, 2004; Urgesi, Calvo-Merino, Haggard & Aglioti, 2007; Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009). Furthermore, although lesions that selectively affect the EBA are relatively rare, a study conducted on a large sample of stroke patients (Schwoebel & Coslett, 2005) showed disrupted semantic and structural body representations associated with lesions of the left temporal lobe.

Although the anatomical evidence from this study was not precise enough to determine whether this specifically involved the EBA or the FBA, more recent fMRI studies highlighted how distinct sub-clusters of voxels within the EBA territory show a clear preference for different visually presented body parts (Schwarzlose, Baker, & Kanwisher, 2005; Bracci et al., 2010; Orlov et al., 2010; Weiner & Grill-Spector, 2010) providing evidence for a systematic topographic organization of body parts in the visual cortex. Additionally, it has been shown that the execution of (unseen) movements with

different body parts activates EBA (Astafiev, Stanley, Shulman, & Corbetta, 2004) and, more interestingly, the movement of specific body parts, partially overlap with the body parts represented within the visual body map (Orlov et al., 2010). This motor-driven activation seems to suggest that visual and motor-related information converge within the occipito-temporal cortex (OTC) in a body part specific manner. It has also been suggested that EBA activation could occur through *corollary discharge*; signals from motor areas that dynamically update the body representation in the EBA and adjust for sensory input resulting from the movement (Peelen & Downing, 2007).

In line with this hypothesis, other studies have shown that body parts are semantically coded as motor effectors (Bracci, Cavina-Pratesi, Ietswaart, Caramazza, & Peelen, 2011; Bracci, Caramazza, & Peelen 2015), suggesting that the action-relatedness of a given body part is a fundamental organizational principle in the occipito-temporal pole (Bracci & Peelen 2013; Bracci et al., 2015; Lingnau & Downing, 2015).

Adding to the functional imaging and brain stimulation evidence, EEG (Thierry, Martin, Downing, & Pegna, 2006) and intracranial studies (Pourtois, Peelen, Spinelli, Seeck, & Vuilleumier, 2007) have identified a body-specific Event-Related Potential (ERP) that appears as a cortical negative potential peaking around 190 msec after stimulus onset (i.e. body-N190). Source localization analysis (Thierry et al., 2006; Giabbiconi Jurilj, Gruber, & Vocks, 2016) and intracranial recordings (Pourtois et al., 2007) pinpointed EBA as neural generator of this component with ERPs identified bilaterally over the occipito-temporal electrodes (PO7, PO8, P7, P8, P9, P10). Moreau and colleagues (2018) used a set of stimuli subdivided according to the amounts of visible body information (i.e. finger, hand, arm, body) and a hierarchically-matched set of whole-tree and tree-part stimuli (leaves, leaf clusters, branches, tree), to identify band-specific changes in post stimulus EEG power associated with the processing of body-related visual stimuli. The authors reported that body and body-part stimuli generated specific EEG

activity not only in time domain (ERP), but also in the time–frequency domain (Moreau, Pavone, Aglioti, & Candidi, 2018). In particular, the authors observed that theta synchronization increased for hand and arm images compared to other body-part (fingers), full body images and non-body control stimuli (i.e. whole-tree/tree-parts) over occipito-temporal cortices. The authors argued that this modulation further supports the categorical organization of neural responses to human effectors in the visual system as reported in previous studies (Bracci et al., 2012; Lingnau & Downing, 2015).

In this chapter, it has been shown how different sensory modalities and the information computed in different cortical areas may contribute to the bodily experience. It should be appreciated that when looking in isolation at the contribution of *a* sensory modality or *a* specific cortical area, it would not be possible to fully understand how complex body representation(s) may arise. Different models have been proposed to explain the nature of body representation(s) and the processes involved in its construction. This will be the topic of the next chapter.

Chapter 2

The multiple concepts of the body representation

2.1 Historical background

Body representation is a complex concept not easy to delineate. Generally speaking, it can be defined as a multidimensional construct that includes perceptual, cognitive, emotional and behavioural aspects towards the body. It refers to a complex function of synthesis that allows us to recognize our body as a whole, to identify the morphology, the relationships between the single parts and the changing position in space (Paillard, 1999). Successful interaction with the surrounding space is closely linked to the ability to correctly localize stimuli located in the external space and their relationship with the spatial position of one's own body. To better understand the current perspectives about body representation it is fundamental to provide an outlook on how such concept has developed over the centuries.

In 1551, the French surgeon Ambroise Parè for the first time reported, in his book *La Manière de Traicter les Playes Faictes tant par Hacquebutes que par fleches...* (1551), cases of amputee patients showing a ‘curious syndrome’, where they were experiencing amputated limbs as still present. Three centuries later, in 1871, Silas Weir Mitchell provided the first clear clinical description of such syndrome introducing the definition “*phantom limb*”. Such phenomenon was (and still is) described as a persistence of conscious perception of a limb despite its amputation or, more rarely, its congenital absence (Denes & Pizzamiglio, 1996). Since the time of Mitchell’s original description,

there have been numerous clinical cases reporting the phantom limb, which led almost all neurologists to consider the existence of a mental model of the body that, despite the loss of a limb (or body parts), remains unchanged. However, until the end of the XIX century, body awareness was considered as being mostly based on vague and diffuse internal (e.g. muscles) and external (e.g. skin) sensory impressions that were classified with the term ‘cenesthesia’ (from the greek: *koinos*, ‘common’, *aisthēsis*, ‘sensation’).

Pierre Bonnier in his *The aschématie*, published in 1905, coined the term “*schema*” to denote the internal representation of the body, referring to the ability to orient ourselves in space, and to take into account the localization of the different parts of our body. In Bonnier’s view (1905), the *schema* is a ‘topographic configuration’ concerning the orientation and position of the body and its parts, their volumetric properties and localization of sensory inputs. So, the body becomes the mean by which we build a ‘sense of space’ and, therefore, develop the consciousness of occupying a precise and personal space.

Arnold Pick, in his studies on autotopagnosia and phantom limb (Pick, 1908, 1915), adopted the term *body schema* and spoke about the ‘awareness of having a body’ as a key component of the body representation. Pick suggested the existence of multiple *schemata* to refer to the different modalities and body parts from where the sensory inputs came from, and stressed the importance of the "spatial images of the body " (Pick, 1908) as an essential framework for the consciousness of the body (Pick, 1915).

However, the most influential and cited authors regarding the formulation of a new concept of *body schema* are Head and Holmes (1911). The authors proposed the existence of two types of *body schema* which are distinguished from the *body image*. Head and Holmes (1911) stated that the movement and position of the body, coming from proprioceptive and kinaesthetic afferent impulses, remain unconscious until this information is ‘computed’ by a central system which constantly compares, elaborates,

records and adds the new information to the pre-existing schemata, in a constant and dynamic integration:

“... resulting from previous postures and movements [...] against which all subsequent changes of posture are measured before they enter consciousness [...] By means of perpetual alterations in position we are always building up a postural model of our selves which constantly changes. Every new posture or movement is recorded in this plastic schema, and the activity of the cortex brings every fresh group of sensations evoked by altered posture into relation with it...” (Head & Holmes, 1911; pp. 186-189).

This definition describes what the authors called “combined standard” model or “postural schema”. Such schema is distinguished from a second “superficial” schema derived from cutaneous afferent impulses signalling the location of tactile stimuli on the surface of the body:

“... In the same way, recognition of the locality of the stimulated spots demands the reference to another “schema” [...] This faculty of localization is evidently associated with the existence of another schema or model of the surface of our bodies...” (Head & Holmes, 1911; pp. 186-189).

According to Head and Holmes (1911), these schemata are independent from, though related to, a conscious ‘image’ of the body, considered to be an integrated and multimodal top-down cognitive representation, binding together visual, tactile and motor information (Gallagher, 1989; Head & Holmes, 1911). So, in the early 1900s while the concept of *body schema* was taking a more detailed and articulated shape, the notion of

body image was still rough and vaguely defined. Moreover, the two concepts were often used interchangeably leading to conceptual confusion (Gallagher, 1986).

In the mid-1930s Paul Schilder (1935) offered an exhaustive and influential definition of the *body image*:

“The picture of our own body which we form in our mind, that is to say, the way in which the body appears to ourselves [...] We call it body schema of our body or bodily schema [...] The body schema is the tri-dimensional image everybody has about himself. We may call it ‘body-image’ ”.
(Schilder, 1935, p.11).

Schilder’s merit relies on his ability to describe the concept of *body image* from a neurophysiological, neuropsychological, psychoanalytic and psychiatric points of view. Taking inspiration from previous studies about the idea of a subconscious *body schema*, in particular, the ‘postural’ schema described by Head and Holmes (1911), the authors highlighted the limitations of body representation reduced only to a sum of sensorymotor information. Therefore, alongside an “unconscious” *body schema*, a second representation as result of the subjective experience of the body must be considered. Based on Schilder’s suggestion, Jean Lhermitte (1942) empathized the role of the visual component of the *body image* making a distinction between a “perceptual” *body image*, based on sensory inputs, and “mnestic body images” (Lhermitte, 1942, p. 21) which refer to how we remember or believe the body is, according to the way our body is experienced in physical reality. The idea of an image based on mnestic processes was also retrieved by Fisher (1972):

“Body image [...] represents the manner in which a person has learned to organize and integrate his body experiences.” (Fisher, 1972, p. 113).

However, Fisher (1972) did not make a clear statement whether the *body image* is present to one's consciousness or not. The distinction between conscious and unconscious processes and the ambivalent use of the terms *body image* and *body schema* is what, according to Gallagher (1986), has caused considerable methodological and theoretical confusion (Gallagher, 1986) in the study of body representation.

2.2 The need for clarity

Consistent with classic accounts suggesting multiple representations of the human body, Gallagher (1986, 2005) has proposed a conceptual distinction between *body image* and *body schema* in order to better understand the complex dynamics of the bodily experience (Gallagher, 2005). According to Gallagher (2005), the *body schema* can be defined as an on-line dynamic representation of the body in space based on proprioceptive, somatosensory and motor information that works beneath our conscious awareness. Its main characteristic lies in the pivotal role that plays in 'guiding' the actions and maintaining the body posture. In this sense, *body schema* is involved in all those motor capacities, abilities and habits that do not require (necessarily) conscious monitoring of the state of the body. For example, riding a bike requires a heavy involvement of the *body schema* but, the intentional object of perception is not the body *per se* rather is the bike one intends to ride.

The *body image*, in contrast, consists of a conscious set of dispositions such as perceptions, attitudes and beliefs concerning one's own body (Gallagher, 2005). Compared to the *body schema*, it requires self-referential intentionality, so that the object of reflection is one's own body. Conscious awareness is necessary, for example, if one wants to describe the body (in conceptual/scientific terms) or reflect on his/her or other physical appearance.

Such distinction is not merely theoretical, it is also supported by empirical research strongly influenced by the introduction of the visual two-routes model initially proposed by Ungerleider and Mishkin (1982) and later revised Goodale and Milner (1992).

Dijkerman and de Haan (2007) took inspiration from Goodale and Milner's approach to explore the existence of separated cortical pathways for somatosensory information in terms of separated processing streams. The authors suggested that there are two separated, yet interdependent, somatosensory pathways: one responsible for tactile perception of external objects and the other involved in action-related processing. The model also distinguishes between somatosensory processing about the body (where you have been touched) and about external stimuli (e.g., surface features of objects). Dijkerman and de Haan (2007) also explored the neural substrates underlying these two routes and suggested that while the former is running from the anterior parietal cortex to the insula, through the secondary somatosensory cortex; the second involves a cortical pathway that originates in anterior parietal cortex and terminates in the posterior parietal cortex (see Figure 2.1). Crucially, the somatosensory system provides information not only about the external world but also about the body itself. The authors proposed that the pathway from the anterior parietal cortex to the insula may reflect the neural substrates of the perceptual representation of the body: the posterior parietal cortex encodes information about the metric of the body and the insula information relevant for the sense of ownership. The action-related pathway, on the other hand, codes for the body representation for action (i.e. motor programs and action execution). This model is at the base of the dyadic definition of body representation. From a methodological point of view, the dyadic model has proven to be relatively robust as it provided a framework to test its characteristics and study the dissociation between a body representation for action (*body schema*) and perception (*body image*). The dissociation *body image/body schema* has been grounded on dissociation reported in studies considering both neuropsychological conditions and healthy individuals. The most compelling evidence of the existence of two separate body representations comes from the double dissociation

observed between numbsense (disruption of *body image*) and deafferentation (ascribed to disruption of *body schema*) (Paillard, 1999).

Figure 2.1 Schematic representation of Dijkerman and de Haan's neuroanatomical model

Somatosensory pathways for action are indicated by dark grey boxes and broken lines. Somatosensory pathways for perception are indicated by light grey boxes. Somatosensory pathways for perceptual recognition are indicated by black lines
APC, anterior parietal cortex; SII, secondary somatosensory cortex; PPC, posterior parietal cortex.

From Dijkerman and de Haan (2007).

2.3 Evidence in support of the dyadic model

The condition of numbsense can be considered as the somatosensory equivalent of blindsight². Patients who have lost feeling in part (or all) of their body report that they are not aware of any tactile sensations. Nevertheless, when tactile stimuli are delivered on the insensible area, they are able to correctly point to where the 'unfelt' stimuli were delivered with above-chance performance. Critically, when asked, they can neither verbally localize it nor indicate the location on a pictorial representation of the body (Paillard, Michel, & Stelmach, 1983; Rossetti, Rode, & Boisson, 1995). The latter aspect

² ability of individuals suffering of cortical blindness, due to lesions in the striate cortex, to respond to visual stimuli in their scotomas even though they have no conscious awareness of the stimuli (Danckert & Rossetti, 2005; Weiskrantz, 2004).

is particularly interesting as it has been used as evidence of a deficit of *body image*, with a preserved *body schema* (Paillard, 1999). In fact, patients' localization ability seems to be based on proprioceptive information that enables body-oriented actions and localizes tactile stimuli on their bodies but this information is not translated into a perceptual representation of 'a body' so that patients fail to point the correct location onto a schematic drawing of a body. Furthermore, the lack of awareness of having been touched seems to suggest that the *body schema* operates underneath conscious awareness.

Cases of personal neglect have also been used to highlight such dissociation (i.e. disrupted *body image* and preserved *body schema*; Gallagher, 2005). Patients with personal neglect, fail to perceive or attend the contralesional side of their body. However, it has been reported that, in absence of hemiparesis, although they do not spontaneously move their neglected arm, they may unconsciously use it without being aware of it if the movement is directed towards the ipsilesional side (Ogden, 1996; Punt & Riddoch, 2006). Therefore, although awareness is absent, movements are still possible. Similar observations have been reported in test of hand grip in which patients, despite neglecting the left hand, show normal hand grip to reach the target object (Milner, 1998). Again, this evidence highlight how underneath consciousness, visual information about the target informs the motor system so that the hand is automatically shaped for a purposeful motor program even if the hand is not integrated into subjects' conscious *body image* (Gallagher, 2005).

Conversely, cases of deafferented patients have been used to demonstrate instances of intact *body image* and impaired *body schema* (Cole & Paillard, 1995; Gallager & Cole, 1995). In deafferentation, patients have no proprioceptive information and no sense of touch in different body parts (or full body), depending on the level where the deafferentation occurred. Yet, thermal sensation and nociception is preserved as well as motor functions and the vestibular sense of balance. Nonetheless, the 'implicit' sense of

bodily posture seems to be missed; without visual feedback, patients cannot correctly locate their limb position in space. This disturbance is so severe that the patient reported by Gallagher and Cole (1995) had to develop visual based strategies as a substitute of proprioception to guide her movements. Gallagher and Cole (1995) argued that in these instances the *body schema* is disrupted and therefore, compensated by a reflexive, conscious use of *body image*. It is intriguing to note that in this circumstance, due to altered *body schema*, different weight is given to the type of information used to guide movements; proprioception plays an important role in actions, but it has been taken over by vision (de Vignemont, 2010). This aspect is particularly relevant for the purpose of the presents work and it will be further discussed in next sections and chapters.

More recently, Anema and colleagues (2009) reported what is probably one of the most compelling evidence of dissociation between *body schema* and *body image*. The authors described a double dissociation for action and touch in localization tasks in two stroke patients with intact basic somatosensory processing. Both patients were able to perceive tactile stimuli delivered on their contralesional hand and arm; however, one patient failed to accurately localize tactile stimulations on his own hand, but he was able to indicate the stimulated side on a pictorial representation of his hand. On the contrary, the other patient failed to localize tactile stimulations when asked to point to the stimulated side on a pictorial representation of the hand, but not to her own hand (Anema et al., 2009).

The neuropsychological evidence of a functional dissociation between *body schema* and *body image* provides valuable insight into the study of body representation. However, methodological aspects and other, possible, cognitive and physical factors associated with the complexity of neuropsychological disorders, pose a relative limitation to the full generalization of the findings. To further probe and validate the existence and relative independence of *body schema* and *body image*, studies on healthy individuals have been

conducted more recently. The Rubber Hand Illusion (RHI) paradigm has been widely used to explore body representation in healthy individuals (Botvinick & Cohen, 1998; Costantini & Haggard, 2007; Tsakiris & Haggard, 2005; Kammers, de Vignemont, Verhagen, & Dijkerman, 2009; Kammers, Kootker, Hogendoorn, & Dijkerman, 2010).

In the classic RHI paradigm, participants sit in front of a table with their arm concealed from sight behind a screen and a dummy rubber hand is placed in a plausible posture in front of them. Participants are asked to look at the hand while the experimenter, with two paintbrushes, simultaneously strokes both the participant's hand and the fake hand. Strokes can be synchronous or asynchronous (i.e. there is a temporal delay between the touch on the two hands resulting in a mismatch between the visual and the tactile information). In the synchronous condition (i.e. without temporal delay) the visual information modulates the proprioceptive input to the point that participants not only feel that the touch is actually occurring at the location of the rubber hand but also that the rubber hand is their own hand (Botvinick & Cohen, 1998). Interestingly though, for the RHI to occur, temporal synchronicity is not the only factor involved, spatial compatibility and configuration also come into play. Tsakiris and Haggard (2005) showed that in conditions in which the dummy hand was either rotated of 90° or its laterality was not congruent to the real hand, participants did not experience the illusion even if the touches were delivered synchronously. Similarly, the proprioceptive drift did not occur also when a neutral object (a wooden stick) was used instead of the rubber hand.

In another study, to assess more in detail on which components of the body representation the RHI impact on, Kammers and colleagues (2009) developed an experimental design where participants had to indicate the felt position of their unseen stimulated hand by providing both verbal responses and motor responses. This allowed the authors to differentiate and compare performances in two tasks (motor and perceptual) and test whether the RHI had a selective effect on the perceptual localization task (*body*

image) and/or on the motor localization task (*body schema*). In their study, after synchronous (or asynchronous) stimulation, participants could no longer see the rubber hand, nor their own hands and an experimenter moved his own finger on a board placed above the table. Participants were asked to stop the experimenter when they judged the experimenter's finger to be at the location that corresponded to their own (left or right) index finger. After the perceptual judgement, participants had to provide a set of motor responses in order to reach the stimulated hand with the contralateral hand and reach the contralateral hand with the stimulated hand. Then the perceptual task was performed again. In a second experiment, the perceptual task consisted in verbally choosing a stick (out of three) that matched the distance between two hands, while in the motor task participants had to grasp a stick at the two ends with both index fingers of their hands. The authors consistently found that the proprioceptive drift occurred for the perceptual response, but not for the motor responses in line with the hypothesis according to which the two body representations, are characterized by a different weighting of the sensory information.

Interestingly, in the first experiment the authors reported modulation of RHI on the perceptual judgment task after the motor responses. Specifically, after the two reaching responses with the stimulated hand, the strength of the illusion on the perceptual judgment was significantly reduced when compared to the first perceptual judgment (prior the motor tasks), suggesting that the kinesthetics and proprioceptive inputs associated with the pointing reduced the proprioceptive drift, compared to its original amplitude. Albeit the change in the amplitude drift was still significantly different from the actual location of the hand. This aspect is of particular interest as it clearly suggests that, even if visual information is predominantly responsible for *body image* while the *body schema* is mainly based on proprioceptive information, the two components interact and reshape each other. The weight of different type of input (e.g. visual, proprioceptive etc.) may depend on the

context or task demands and is crucial to maintain some coherence between the body, as we perceive it (i.e., *body image*) and the actions that we perform with it (i.e., *body schema*). In this sense, the relative weighting of proprioception and vision depends on what information is the most ‘reliable’ for each type of body representation (Welch & Warren, 1986). Following this line of thought, it would, therefore, be possible to induce a modulation of the *body schema* through the RHI paradigm. In a modified version of RHI paradigm, Kammers, Kootker and colleagues (2010) used a dummy hand designed with different postures as if it was about to grasp an object. Participants also had to maintain a fixed grip posture with their hand, which could have been congruent or incongruent with the rubber hand grip width (located on top of their actual hand). Participants were asked to grasp an object after the delivery of strokes (synchronous and asynchronous) on both index and thumb fingers. Interestingly, the seen rubber grip aperture influenced the participant’s maximum grip aperture during the grasping trajectory after synchronous stimulation. In other words, subjects opened their thumb and index finger wider when they experienced the illusion of ownership for the RH with a larger grip aperture. Quite surprisingly, this result was in contrast with the authors’ initial hypothesis. In fact, since the motor program would require incorporating additional ‘opening’ of the perceived starting grip aperture, grasping responses should have been larger when participants viewed a rubber hand with a small grip aperture. Critically, the position of our hands is based on the combination of both visual and proprioceptive information (van Beers et al. 1999, 2002). The authors, therefore, speculated that the effect can be explained as the result of a modulation of visual information (visible grip posture) over the proprioceptively perceived hand configuration. Indeed, as consequence of the illusion, participants incorporated the rubber hand (as if it were their own) and shaped their hand according to the visible grip aperture, indicating that the *body schema*

(motoric information) is sensitive to visual information associated with the RHI (Kammers, Kootker, et al., 2010).

To further highlight the interaction between *body image* and *body schema*, bodily illusions, such as the Pinocchio Illusion are particularly effective. This illusion was firstly reported by Lackner (1988) who induced an illusionary sensation of movement of the arm by vibrating alternatively the biceps brachii, or the antagonist muscles of blindfolded participants. The curious effect occurred when Lackner asked participants to touch their nose (he also tested the effect on other body parts) during the vibration. As a consequence of a conflict between erroneous proprioceptive information (the illusionary displacement of the arm) and accurate tactile information (contact between the finger and the tip of the nose), participants experienced a vivid sensation of their nose increasing in length (almost 30 cm).

It has been recently shown that this illusion can influence subjects' estimation of tactile length (de Vignemont, Ehrsson, & Haggard, 2005). After asking blindfolded participants to grasp the tip of their left index finger with the right hand, the proprioceptive illusion of finger elongation was elicited through right-arm biceps vibration. During the illusion, participants estimated the distance between two simultaneous tactile contacts on the left finger. Participants reported that the tactile distance was bigger when the touched body part felt elongated compared to the control condition when no illusion was present. This result shows that the modulation of touch is linked to the perceived index-finger size induced by tendon vibration. Thus, it suggests again an interaction between the two representations and/or a dynamic recruitment of one or the other body representation, depending on the type of task required and/or the weight accorded to the current sensory information.

Altogether, these findings suggest that the bottom-up coupling between visual and tactile stimulation is a necessary, but not sufficient, condition to evoke such an illusion.

In fact, the illusion is clearly modulated by both sensory information (bottom-up) and existing internal representations of the body (top-down) (Costantini & Haggard 2007). When the rules of this body representation are violated, as in the case of an incompatible posture of the rubber hand or an incongruence of the fake hand laterality, the illusion is broken.

At this point, it is possible to appreciate how the literature offers a consistent body of evidence that supports the existence of two separated body representations: the *body image* and *body schema*. There is a quite large consensus that the *body schema* presents some clearly defined features: it represents both position and configuration of the body as a three-dimensional object in space (Macaluso & Maravita, 2010); it is pre-conscious or, at least less accessible to consciousness (Gallagher, 1998, 2005; Longo, 2016); it is highly dynamic and characterized by a short-term plasticity and reorganization (Maravita & Iriki, 2004). On the other side, the *body image* has been described as a conscious perceptual representation of the body. It is less flexible and characterized by long-term plasticity. However, it is susceptible to changes and illusion as demonstrated by the RHI and Pinocchio Illusion (Lackner, 1988; de Vignemont et al., 2005).

While there is a coherent and structured definition of the *body schema*, the construct of *body image* remains slightly controversial because it lacks of a unifying clear definition. The concept of *body image* is too heterogeneous and has been used as a ‘container’ for all that the *body schema* is not. The following passage may help to understand this point:

“The body schema consists in sensorimotor representations of the body that guide actions. The body image groups all the other representations about the body that are not used for action, whether they are perceptual, conceptual or

emotional (body percept, body concept and body affect)” (de Vignemont, 2010, p. 670)

2.4 Triadic model

Originally proposed by Sirigu and colleagues (1991), the triadic model (Figure 2.2) was an attempt to better define the *body image* and frame it within more functional boundaries. In this model, the *body image* is split up in two sub-components (Schwoebel, & Coslet, 2005; Buxbaum & Coslet, 2001; Sirigu, Grafman, Bressler, & Sunderland, 1991): the *visuo-spatial representation* (or *map*) and a *semantic and lexical representation* of the body. The first component, consists of a structural descriptions of the body and its parts, which defines the relationships between body parts in a perceptual non-verbal format that takes into account the configuration of each body part in respect to the whole body (i.e. their boundaries, their proximity and their position relative to each other). The *semantic/lexical* component, refers to the conceptual and linguistic knowledge we have about how a “standard” body should look like and the shape, the location of each

Figure 2.2. Triadic cognitive-neuropsychological model of body representation (modified from Sirigu et al., 1991).

part within the configuration of the whole body and their function (Kemmerer & Tranel, 2008).

Several studies have reported patients with selective impairment of the *semantic/lexical knowledge* of the body while other semantic domains remained unaffected (Dennis, 1976; Laiacona, Allamano, Lorenzi, & Capitani, 2006; Suzuki, Yamadori, & Fujii, 1997). For example Dennis (1976) reported a patient who had difficulties in pointing to body parts on her body on verbal command, but when the body part was presented visually (indicated on a schematic image of a body) she had no difficulties in pointing at the corresponding body part. The different semantic domains within the *body image* can be appreciated by the case described by Suzuki and colleagues (1997). The authors noted that when the patient was asked to point to a body part named verbally (i.e. point at your foot) he was unable to perform the task. However, if the same body part was described in terms of functional characteristics (i.e. point at the body part that you use for kicking) the pointing was successful. The fact that the semantic knowledge about body parts follows functional principle is also supported by a study on healthy participants by Reed and colleagues (2004). The authors found that when participants categorize a series of body parts, they did so in such a way that body parts were grouped into clusters that identified the functional characteristic of body parts rather than, for example, their shape or size. These evidences suggest the existence of specific lexico-semantic information about bodies, but what about the non-verbal structural description of the body? Again, research conducted in the field of neurology and neuropsychology comes into play. Several studies have shown that knowledge of body topology can be doubly dissociated from semantic knowledge in patients (Benedet & Goodglass, 1989; Schwoebel & Coslett, 2005). The most striking evidence comes from patients with autotopagnosia as described in Sirigu and colleagues (Sirigu et al., 1991). The authors reported a patient who was unable to answer questions assessing knowledge of the spatial relations between body parts but,

could answer questions assessing functional knowledge about body parts. More in detail, the authors tested the patient's ability to localize body parts on her own body, the experimenter's body or a doll's body under verbal instructions ("point to the knee") or visual cues ("touch on your body the body-part the experimenter is touching on himself"). While the patient was unable to point to any body part in any condition, under both verbal and visual commands, she was able to correctly point to inanimate objects' parts (i.e. telephone, table, blouse, truck) indicating that the localization problem was specific to body parts and not associated with a more general inability to "analyse a whole into its parts" (De Renzi & Scotti, 1970; Poncet, Pellissier, Sebahoun & Nasser, 1971). Interestingly, the authors noted that, in regard to body pointing, patient's movements followed two types of errors: contiguity and functional errors. The former consisted in the patients pointing to body parts close to the target one (e.g. the lower arm for the elbow), the latter consisted in pointing to a body-part similar in semantic/functional terms (e.g. the joints, the knee for the elbow). Nonetheless, when they tested the ability to verbally name body-parts and their function, this appeared to be intact even though the capacity to describe the position was impaired. Similar cases of patients showing body-specific topological deficits on their body, other and body prototypes have been reported (Buxbaum & Coslett, 2001; Ogden, 1985; Semenza, 1988).

A major study on a relatively large group of brain damaged patients has been conducted by Schwoebel and Coslett (2005) to test the dissociation of body representation components proposed by Sirigu et al. (1991). In order to do so, the two authors asked patients to perform on a series of tasks specifically designed to target the three components of body representation: *body schema*, *visuo-spatial map* and *semantic knowledge*. To assess the *body schema*, two tasks were used: a motor imagery task where patients were asked to imagine performing four different movements with both the ipsilesional and contralesional hand, and to identify if the hand presented in a picture was

a left or a right one (Hand Laterality Task; Parsons, 1987a, 1987b). The *visuo-spatial map*, was tested by means of two localization tasks that consisted in pointing to the actual own body-part corresponding to the one shown on a picture and, to indicate on a body map the body part that corresponded to the one where they had been touched. A matching task, that required participant to pair pictures according to their functional similarities (e.g. the elbow and the knee), or to the cultural association with clothes/objects (e.g. foot and shoe), was used to assess the body *semantic knowledge*.

The findings highlighted a strong correlation, between the performances on the matching tasks as well as between the tasks targeting the *visuo-spatial map*. The dissociation, and relative independence of the *semantic knowledge* and the *visuo-spatial map* representations, was evidenced by the absence of correlation between the scores on the tasks selectively targeting these two components. Furthermore, lesion analysis showed that different brain regions were associated with defective performances on specific tasks. For example, the dorso-lateral frontal and posterior parietal cortices correlated with impaired performances on the *body schema* tasks. Deficits on the semantic tasks were associated with more temporal lesions (particularly the left lobe), while left parietal lesions were more relevant for visuo-spatial map deficits.

Additional evidence on the neural substrates of body structural description has been provided by fMRI studies (Corradi-Dell'Acqua, Hesse, Rumiati, & Fink, 2008; Corradi-Dell'Acqua, Tomasino, & Fink, 2009; Felician et al., 2004). In line with the clinical literature, a study on healthy participants showed a critical involvement of the left intraparietal sulcus during the estimation of the true distance between body parts images, but not for inanimate objects (Corradi-Dell'Acqua et al., 2008). Similarly, a study by Felician and colleagues (2004) also showed of the activation of the left superior parietal cortex when participants were asked to point to parts of their body.

Overall, these results support Sirigu and colleagues' model and in particular show that the semantic/lexical and structural knowledge of the body are coded in separate representations that have their own neural correlates.

2.5 Body metrics

One critical topic in body representation literature concerns body size representation. At first glance, this aspect seems to be relatively simple and straight forward. When considering the proportions of our bodies, the quantity of visual information relative to body size seems obvious: we constantly see human bodies around us and we often look at ourselves in the mirror. Furthermore, from a practical point of view, knowing the dimensions of one's own body is critical to plan actions and navigate through space. It is not surprising then, that for long time it has been generally assumed that the perceived relationship between body parts size and metric information about the body is relatively accurate (Soechting, 1982; van Beers, Sittig, & van der Gon, 1998). Yet, it has been recently showed that healthy individuals misestimate both size and shape of their body parts (Caggiano & Cocchini, 2020; Peviani, Melloni, & Bottini, 2019; Sadibolova, Ferrè, Linkenauer, & Longo, 2019; Stone, Keizer, & Dijkerman, 2018; Linkenauer et al, 2015, Fuentes, Longo & Haggard, 2013; Longo, 2016; Mora, Cowie, Banissy, & Cocchini, 2018). Intriguingly, the origin of these distortions has not been clearly identified yet, sparking a vivid debate.

To tackle and solve the issue of body metrics, Longo and colleagues (2010) have proposed a new model³ (Figure 2.3) which includes an additional body representation specifically dedicated to information relative to body metrics and size: the *body model* (Longo, Azañón, and Haggard 2010). In their model, the authors argued that in order to localize a stimulus on the body, the tactile information, which is firstly coded within the

³ The model has been recently reviewed and updated to include a fourth (offline) body representation of the most plausible spatial locations for a given touch: *postural prior*. According to the authors, this representation interacts with the *postural schema* to produce an accurate and quick response for the localization of touch in space (Tamè, Azañón, & Longo, 2019).

neural somatotopic map, must be coupled with a representation of the body surface that the authors called *superficial schemata*. The multisensory integration of afferent and efferent information to and from the periphery (i.e. proprioception, touch, and movement) provides information about body posture, including signal from joint angles and the relative flexion or extension of each joint and muscles (Proske & Gandevia, 2012). Crucially though, there is no direct information from the periphery to the cortex that informs the brain about either the absolute location of a body part in space or its shape and size. Nevertheless, this type of information is essential for the successful motion in space and interaction with the external environment. So, according to the authors, proprioceptive signals need to be linked with the *body model* which contains a representation of body parts' size and shape (Longo et al., 2010). The authors ground their assumption of the existence of the *body model* on evidences coming from the Weber illusion (Weber, 1834).

Put it simply, the Weber's illusion consists in individuals perceiving the distance between two tactile stimuli on a single skin surface to be larger on regions of high tactile sensitivity (the hand) than those with lower acuity (the forearm) (Anstis, 1964; Goudge, 1918; Weber, 1834; Weinstein, 1968). This effect indicates that receptive fields, across a body part, can influence tactile size perception and suggest a potential correlation between the skin surface and the relative size of the somatosensory homunculus (Penfield & Boldrey, 1937; Penfield & Rasmussen, 1952). Yet, it has been estimated that the degree to which individuals experience a change in tactile size is only a fraction (10%) of what would be expected if perceived tactile size was derived exclusively from differences in tactile receptive field size (Taylor-Clarke, Jacobsen, & Haggard, 2004). This highlights that only a partial re-scaling occurs between the cortical areas and the representation of the corresponding body part. Because of this, Longo and colleagues reasoned that there must be a compensatory mechanism that decreases the tactile size discrepancies to reach

a percept of size closer to objective size. As mentioned, because there are no afferent signals, that directly specify bodily size or shape, this mechanism must rely on a pre-existing representation of the actual metric properties of the body: the *body model*.

Figure 2.3. Model of somatoperceptual information processing

Diamonds indicate inputs, ovals indicate body representations, rectangles indicate perceptual processes.

From Longo, Azañón, and Haggard (2010)

To test their assumption, Longo and Haggard (2010) developed a localization task paradigm to assess the perceived size and configuration of the hand. Participants were asked to indicate the perceived location of specific landmarks (tip of fingers and knuckles) on their hand concealed from sight. The authors reported a highly distorted and stereotyped pattern of distortion in which participants overestimated the width of the hand and underestimated of the length of fingers. However, when they assessed perceived hand size with a template-matching task (i.e., participants have to select, among of a series of hands of different size, the one most similar in shape/size to theirs), participants were more accurate (Longo & Haggard, 2010). The authors reasoned that, because the localization task would exclude the engagement of the *body schema* (due to type of pointing and input modality) while the template matching task, involves the *body image*

(perceptual), the different performances on the two tasks and the extent of distortions must involve a third representation. The motivation the authors adduce for distinguishing between these representations is that, the *body model* shows large distortions which, arguably, do not appear to characterise the *body image* (Longo, 2016).

A similar paradigm had also been used to test body metric for the whole body (Fuentes et al., 2013). Participants were asked to locate, on a computer screen, a series of body parts. The distances between pairs of points indicated were calculated to obtain the participants' represented body silhouette. The results showed an overestimation of the length of their upper arms, relative to their height and an underestimation of the lengths of lower arms and legs which, the author interpreted as the result of the participants accessing an internal representation of body metrics (*body model*).

In light of the body of evidence reported, the *body model* appears to be able to explain the evidence reported above; however, it is not exempt from critics. The assumption of the existence of an additional body representation specific for bodily size seem to raise more questions rather than answers. According to the model proposed by Longo and collaborators, the *body model* does not receive any direct sensory information; sensory signals are referenced to this stored representation of body size and shape. In this instance, the first question would be from where such representation would originate and crucially, how it can be updated. Even if one would assume that such representation is innate, the latter aspect has an essential practical implication. It is evident, beyond doubt, that over time our bodies change in size and shape, this consideration makes difficult to understand how the *body model* would take into account such changes if there were no direct input available. Furthermore, the findings from the localization tasks show a cogent distortion of the represented body sizes. It seems rather questionable, if not counterproductive, for our cognitive system to have a dedicated body metrics representation that is dramatically distorted. In other words, if the *body model* is meant to

compute information about size and shape, it becomes unclear how it can fulfil its functional purpose and enable effective motor actions if representation of body parts' size is not accurate.

An alternative explanation has been proposed by Linkenauer and colleagues (2015). In a series of experiments the authors asked participants to estimate the size of specific body parts by using their hand length, foot length or a non-corporeal object as a metric. The authors found that individuals overestimated their forearm lengths and the length of their body (relative to the head) and argued that the perceived size of their own body parts depends on tactile sensitivity and physical size. In other words, the *reverse distortion hypothesis* suggests that bodily areas with lower numbers of tactile receptive fields are represented larger than the more sensitive body part in order to compensate for the lack of cortical resolution (Linkenauer et al. 2015; Sadibolova et al., 2019). Furthermore, given an equal degree of sensitivity, body parts that are physically larger will be less distorted (i.e. legs will be less distorted than arms because already physically large).

However, the combined effect between the body part's actual dimension and tactile acuity does not fully account for the data reported in a recent study by Peviani and collaborators (2019). The authors assessed the metric representation of five different body parts by means of a Line Length Judgment task (Longo & Haggard, 2010) in which participants had to determine whether the length of vertically or horizontally oriented lines was shorter or longer compared to a specific body part serving as a reference. The reference used in the experiment were either the hand, the foot, the nose, the lips or the dorsal portion of the neck. For each body part, participants had to compare the lines to either the width or the length of the body parts. Despite the difference in their physical size, results showed a similar underestimation of the hand, foot, lips and partially of the nose. Conversely, the dimension of dorsal portion of the neck was more accurately

estimated. Critically, these findings seem not consistent with the *revert distortion hypothesis* and suggest that when estimating our own body parts, multiple sensory information (more than tactile acuity) is involved in higher-level representations. The author argued that because hands, feet, lips and the nose are readily available to vision on daily basis, compared to the dorsal portion of the neck that is concealed from sight, the visual information is weighted more in the building up the mental representation of these body parts and elicit larger distortions (Peviani et al., 2019).

2.6 The need for integration

The concept of assigning different weights to different sensory modalities for the structuring of body representation has been further explored by Pitron and colleagues (2017, 2018). The authors have recently put forward a new theoretical model which, based on the classic distinction offered by the dyadic model (Dijkerman & de Haan, 2007; Gallagher, 2005; Paillard, 1999), posits that the *body schema* and the *body image* are intertwined and they modulate each other's content (Figure 2.4). The *co-construction model* is grounded on the review of several cases of bodily hallucinations, which, depending on the context, may affect only the *body image* or both the *body image* and the *body schema*. In a nutshell, the model suggests that the two body representations are clearly defined in respect to their function: the *body schema* holds information mainly for action and the *body image* holds information for perception. Nevertheless, in a process of *co-construction*, they reshape each other in order to minimize prediction error and increase their reliability (Pitron et al., 2017, 2018).

In the initial stage, the model assumes that inputs consisting of some a priori knowledge about the body and its constraints, and information coming from various sensory modalities, are at the base of body representation. This information updates two intermediate body sketches, which the authors define as *raw body schema* and *raw body image*. These are the result of the interplay between the sensory inputs, previous experience and expectations associated to internal and external demands. The *raw body*

schema, according to its nature, favours metrical information that is relevant for action while the *raw body image*, focuses on information about the outlines of the body part. Critically, at this stage, both sketches receive the same sensory inputs, but the weights ascribed to the inputs and different decision criteria differ according to the structure defined by prior knowledge and experience (Kammers, Mulder, de Vignemont, & Dijkerman, 2010). In a second step, the two raw representations are compared and averaged in order to obtain an output that is congruent, as much as possible, with the context demands. In this process, the construction of body representations never stops and it is continuously fed by new inputs.

In their model, the authors speculate that the *body schema* is built first (from both a phylogenetic and ontogenetic perspective) and thus, may work as a “prior” for the construction of the *body image* (see figure 2.4). In this view, the *body schema* has a more fine-grained spatial content that encodes information about the bodily properties required for planning and controlling action. On the other hand, the content of the *body image* is not as precise as the content of the *body schema*, but it carries information about more properties and, unlike the *body schema* it is concerned with the visual appearance of the body (greater weight is given to the visual information). The richness of *body image*’s content results in this representation being less accurate compared to the *body schema*. In

Figure 2.4. Schematic depiction of body schema/body image interactions.

other words, in the process of its construction, as the *body image* gains complexity and spatial richness, it loses its accuracy.

This passage may help to interpret the results from Peviani et al. (2019), who found that larger distortions occurred when visual information (*body image*) was more available. Similarly, the dissociation between the localization task and the template-matching task reported by Longo & Haggard (2010) can be the results of different weights influencing the output. It is possible that the *body image* is actually used in both tasks. The richness of the visual information made available by the hand templates (participants had to choose between pictures) minimize the incongruence between the two representations and prioritize the *body image*. Conversely, the absence of online visual information in the localization task increases ambiguity so that, somatosensory and pictorial information are weighted and compared to reduce conflict.

In light of this, it is therefore possible that a metric of the body is present in both the *body image* and the *body schema* and that the metric properties of the two representations can be differently affected and accessed to, possibly according to the different processing elicited by different contexts.

According to the Ockham razor principle, “*More things should not be used than are necessary*” (Encyclopædia Britannica, 2018). It is indeed tempting to split body representations in smaller and more specialized representations in order to account for all the possible combination in which body representation is disrupted. However, the risk of postulating additional body representations for each stage of the sensory processing and bodily disorders, leads to a multiplication, virtually to the infinite, of the number of levels of representations within our models instead of reducing them:

“[...] *there are so many bodily disorders, and therefore so many possible dissociations, that one would end up with an almost infinite list of body*

representations. Pushed to its limits, the dissociative principle would no longer make sense." (de Vignemont, 2010, p. 675).

In this chapter, it has been shown how studies reported double dissociations between the *body image* and the *body schema* in patients (Paillard et al, 1983; Rossetti et al, 1995; Anema et al, 2009; Brochier, Habib, & Brouchon, 1994; Halligan, Hunt, Marshall, & Wade, 1995) and healthy subjects (Kammers, Kootker, et al., 2010; Kammers et al., 2009). As it is true that these components dissociate, recent findings and models suggest that their interaction is not only possible, but also inevitable.

The present work is an original attempt to investigate the extent of this interaction. The research project's structure is outlined in the next chapter.

Chapter 3

Research project structure

3.1 Study rationale

As discussed in the previous chapters, the notion of the body representation has changed and developed throughout the centuries, and yet the very nature of such puzzling concept remains difficult to grasp. The distinction between *body schema* and *body image* helps to define the cognitive processes involved in the formation of the body representation. However, despite the common agreement on such distinction, a growing amount of evidence suggests how the clear distinction between the two concepts is actually rather blurred.

Bearing in mind the theoretical and functional efficacy of dividing the concept of body representation in *body image* and *body schema*, the aim of the present Ph.D study is to obtain a deeper understanding of the sense of the body representation. It will be systematically addressed the hypothesis according to which the *body schema* and *body image* are not independent one from the other, but they do interact.

The experience of the body in external space depends on sensorimotor expectations (*body schema*); however, this type of information needs to be integrated with information about the size and shape of the body segments (*body image*). Recent studies, however, have pointed out that the mental representation of metric properties of the body (such as body size and shape) are built upon somatoperceptive bottom-up information too, suggesting the multimodal and integrated nature of the *body image* (Longo et al., 2010). Thus, the conscious perceptual experience of the *body image* depends also on more

implicit information that may ultimately affect the conscious *body image*. This would result in possible different patterns of distortions that are specifically linked to distinct levels of information processing related not only to the visual domain.

The present work will systematically investigate the cognitive dimension of body representation through a series of eight experiments divided into three main chapters. The research project is motivated by a set of questions addressing three major topics at its core. The first concerns the ‘structure’ and the ‘standard’ of the bodily experience. The second revolves around the ‘structuring’ of the explicit experience of the body. The third and last one concerns the examination of pathological condition and whether this helps to better understand normal condition. Each topic is addressed specifically in each phase of the research project: chapters 4 and 5 of this work focus on the analysis of body representation in normal adult processes, whereas chapter 6 focuses on pathological distortions as seen in clinical population.

The current Ph.D project started with a fairly simple question: how do ‘normal’ individuals typically represent their own body? During the original planning and data gathering for the research project, a growing number of other labs have started to address this issue. Yet, the question from where information about the body metrics arise seems not easy to answer and a vivid debate is still ongoing. Therefore, the experimental section of this work shall begin in the most transparent and logical way: in the same way the Ph.D was originally approached.

Chapter 4 “*The ‘steady state’ of body representation*”. This chapter is an attempt to set a baseline of *how* the body is represented and perceived in a “default” mode, and it provides the first elements to understand the multidimensional reality of the body. In order to do so, two studies have been developed and carried out.

In *Study 1*, a crucial aspect of body representation literature, that only recently has gained a new momentum, is specifically addressed: body metrics and size.

In order to test the perceived size of body parts and overall body configuration in space, a modified version of the Body Image Task (Fuentes et al., 2013) was adopted. This was done to obtain a more precise measurement of the represented metric properties of the body. This study also aimed at overcoming few limitations (described in the following chapter), of current findings reported in the literature.

A set of four experiments examines the extent to which the body metrics representation might be affected according to specific conditions:

- ❖ *Experiment 1.a* – analysis of possible different patterns of distortion relatively to the body surfaces (frontal vs dorsal prospective views);
- ❖ *Experiment 1.b* – test of the inversion effect (upside down body: inverted) on the mental representation of the body (upright vs inverted);
- ❖ *Experiment 1.c* – test of possible variation in bodily distortion configurations according to the position of specific landmarks (head vs navel);
- ❖ *Experiment 2* – investigation of the visuo-perceptual component of the metric properties of body representation by means of a "depictive" psychometric task.

Building up from the result obtained in Study 1 and to further support a “functional body representational hypothesis”, the Study 2 tackles the functional component in the realm of visual body perception. Crucially, it is investigated the relationship between objects and effectors (body parts) by assessing whether recognition of specific body parts can be influenced by brief exposure of objects functionally related (in absence of actual motor actions). *Study 2* addresses the issue by means of two experiments:

- ❖ *Experiment 3* – test of existing functional links between specific objects and body parts;
- ❖ *Experiment 4* – by means of event-related potential technique (ERP), this experiment assesses the effect of the object-effector relationship on the modulation of N2-P3 complex elicited in parieto-occipital areas, specifically EBA.

At the end of the chapter, an alternative approach will be set out that could, possibly, reconcile apparently contrasting evidence in the most recent literature. It will be argued that the body representation cannot be fully understood without taking into consideration the close link between the body, as an object in space, and the functional role of some of its parts in performing motor actions. These findings will highlight the role of motor aspects of an object in influencing the recognition of its body effectors. It will be argued that bodily distortions may arise as result of a *co-construction* process between *body image* and *body schema* and therefore, do not require the postulation of other types of body representations. Patterns of distortions can be explained in terms of how information on different levels contributes to the content of the subjective experience of the body. In this sense, the conscious perception of our own body could be influenced, at least in part, by *body schema* information that, indirectly, shapes the mental image of our body.

In **Chapter 5** “*Modulation: do actions shape body representation?*”, the effect of movements and posture on the perceptual experience of the body will be further explored. Based on the results discussed in Chapter 4, a stronger focus will be put on the role of *body schema* to deepen the understanding of how this information contributes to the determination of perceptual consciousness and experience of the body, which defines the *body image*. *Study 3* addresses the issue by means of three experiments:

- ❖ *Experiment 5* – evaluated whether same actions performed in different portions of the space impact selectively on specific body segments;
- ❖ *Experiment 6* – investigated whether specific training sessions, involving different motor patterns, can differently modulate body metrics;
- ❖ *Experiment 7* - tested whether action performance with different body parts on the same object modulate the formation of a selective functional link between the objects and body parts used during the training.

At the end of this chapter, it will be argued that postural and motor actions of the *body schema* do, in fact, impact on the *body image* by working “behind the scene”. Performing an action with specific parts of the body and in some portions of the space implicitly structure the content of the *body image* both in terms of metric properties as well as visual recognition.

Chapter 6 “*Personal neglect a body representation disorder*”. A deeper insight into the structure and the functioning of the normal cognitive mechanism underlying the representation cannot be separated from the study of pathological conditions in which the body representation may be disrupted. As clearly stated by McCloskey (2001):

“complex systems often reveal their inner workings more clearly when they are malfunctioning, than when they are running smoothly.” (p. 594).

Therefore, this chapter addresses one of the numerous instances of a ‘disrupted’ body representation. The focus is on a particular neuropsychopathological condition in which patients show a particular pattern of symptoms that suggests not only an attentional disorder related to their body but a primary disruption of body representation: Personal Neglect. For this reason, a clinical sample has been considered for the last experiment:

- ❖ *Experiment 8* – test of the perceived hands' width of 11 patients with right hemisphere cerebral lesions (5 with personal neglect, 6 without personal neglect) and 12 healthy controls on a judgment of passability task.

In the concluding chapter (Chapter 7) all the arguments outlined throughout the previous chapters will be summarized by drawing together all the relevant points and set out possible future direction in the study of body representation.

Chapter 4

The 'steady state' of body representation

STUDY 1⁴

4.1 Overview

There is a growing interest in the distortions of body representation in healthy population and most studies have focused their attention on specific parts of the body, such as the hands. Only very few studies have considered the representation of the body as a whole. Findings, acquired by different means of assessment methods, are partially contrasting, leading to different interpretations. The present study aims to investigate which aspects of body representation can be preserved regardless of the method adopted and whether current and previous findings can be explained by a unique theoretical model. In Experiments 1a, 1b and 1c a modified version of the Body Image Task has been adopted to investigate body representations in real scale and the relationship of its parts under different conditions. The Experiment 2 investigated i) whether the pattern of distortions observed in the first experiments are maintained across different methods and ii) whether similar distortions can be generalized to stereotypical representations.

Overall, a consistent pattern of distortions was observed, whereby upper body limbs are underestimated and lower parts of the body are overestimated across all experiments and conditions. These findings are then interpreted as the result of a *functional*

⁴ Part of the data collected for the present study have been published in a first-authored paper (Caggiano & Cocchini, 2020).

relationship between body parts and daily actions, which underlie a close modulation of *body schema* and *body image*.

4.2 Introduction

As highlighted in Chapter 2, the notion of body representation has changed and developed throughout the years, and yet the very nature of this concept remains difficult to delineate. It has been discussed that the *body image* and *body schema* differ in terms of their level of access to consciousness and type of sensory input they rely on. The *body image* is a multidimensional construct that refers to the person's conscious perception and experience of the physical self in terms of its size, shape and physical composition (Longo, 2016; Gallagher, 2005). According to the triadic model, it can be further divided in two sub-components. The *body semantics* provides a description of the functional purpose of body parts and their categorical relationship whereas at a perceptual level, the visual and somatic information provides a structural description of the body (*visuo-spatial body map*) that metrically and spatially describes the relationships between body parts (Schwoebel & Coslett, 2005; Sirigu et al., 1991). The *body schema* instead, consists of more dynamic, action-based representation of body posture and configuration mainly based on kinematic and proprioceptive feedback that provides a representation of the body at each given moment during movement (Buxbaum & Coslett, 2001; Head & Holmes, 1911). Furthermore, while the *body image* is generally considered a relatively long-term stable representation, the *body schema* is characterized by a short-term plasticity and reorganization due to posture and orientation changes of the body in space (Dijkerman & de Haan, 2007; Longo, 2016). From this point of view, body configuration and metrics appear to be long-term properties of the body representation as, in 'normal' conditions, these properties tend to be rather stable with relatively slow changes over time. However, it should be taken into consideration, that there is not a clear-cut definition that provides a full account of the relationship between the different body representations (de Vignemont, 2010). Research on tool use has shown that, although the objective length

of the upper limbs remains stable, the subjective length of these body parts can be modulated following motor training (Pitron et al., 2018). For example, Cardinali and colleagues (2009) observed that after the use of a mechanical grabber, participants performed grasping movement (without the tool) as if their arms were longer. The authors suggested that the kinematic consequences of tool use lead to somatosensory changes in the *body schema* (Cardinali, Frassinetti, Brozzoli, Urquizar, Roy, & Farnè, 2009). Interestingly, the effect of tool use did not just modify the kinematic of the grasping movement, but also the subjective perception of the arm's length. When participants were asked to localize touches delivered on their elbow and middle fingertip, before and after tool use, the distance between the two landmarks increased, as if the arm was perceived as longer after tool use (Cardinali, Frassinetti, et al., 2009). Similarly, other studies have shown that the use of tools, as well as specific manipulations of body parts mobility, modulates the internal representation of body parts size (Canzoneri, Ubaldi, Rastelli, Finisguerra, Bassolino, & Serino, 2013; Sposito, Bolognini, Vallar, & Maravita, 2012; Bassolino, Finisguerra, Canzoneri, Serino, & Pozzo, 2015; Romano, Uberti, Caggiano, Cocchini, & Maravita, 2018). Furthermore, even in the absence of tools, extensive training can shape the metrics of the body representation. Cocchini and colleagues (2018) showed that magicians, using sleight of hand, are considerably better than naïve-to-magic controls in estimating their own finger lengths in a localization task. This evidence, along with some well-known body illusions (e.g., Pinocchio illusion; Lackner, 1988; Ramachandran & Hirstein, 1998), highlight that, under specific circumstances, the *body image* is rather malleable. It is therefore clear that subjective body metrics do not rely on a unitary mechanism but rather it is the combination of various factors. Afferent signals provide information about body posture and limb configuration; however, these signals do not relate directly to the actual length and width of specific body-parts. It follows that

the current body state must be inferred by stored representations of the body's metric properties (Berlucchi & Aglioti, 2010; Longo et al., 2010; Longo, 2016).

Although, as clearly outlined in Chapter 2, some studies showed that, under some circumstances, *body image* and *body schema* can be dissociated (e.g., Kammers et al., 2009; Botvinick & Cohen, 1998; Anema et al., 2009), these components are usually both impaired in the neuropsychopathological population (de Vignemont, 2010). These observations seem to suggest that a dialectic relationship between these two representations is essential for the successful interaction with the external environment; so that there is some coherence between the body, as we perceive it (i.e. *body image*) and the actions that we perform with it (i.e. *body schema*). According to the *co-construction model* (Pitron et al., 2018; Pitron & de Vignemont, 2017), *body schema* (for action) and *body image* (for perception) interact and reshape each other. This model claims that information coming from different sensory modalities determines the construction of body representation. However, this information is compared within a probabilistic model where one type of input may be predominant over another depending, for example, on the context or task demands.

Different factors can play different roles in determining the final representation and its related distortions (i.e., Sadibolova et al., 2019; Cocchini, Galligan, Mora, & Kuhn, 2018; Ambroziak, Tamè, & Longo, 2018; Tamè, Bumpus, Linkenauger, & Longo, 2017; Linkenauger et al., 2015; Fuentes et al., 2013; Longo & Haggard, 2010, 2012a, 2012b; D'Angelo et al., 2018). The majority of these studies shed light on different mechanisms involved in the representation of the hand or the face, which are very special parts of the body (Bruce & Young, 1998; Brozzoli, Ehrsson, & Farnè, 2014). It remains unclear how to extend these findings to the representation of the body as a whole, which has been the focus of interest of very few studies. Fuentes and collaborators (2013) presented scaled body parts (e.g., the head) on a computer screen and asked participants to judge the

relative location of the other parts. The authors found that the width of their shoulders and the length of their upper arms were overestimated, while the lengths of forearms and lower legs were underestimated. A different pattern of distortions has been found in more recent studies (Linkenauger et al., 2015; Sadibolova et al., 2019) where participants showed an overall overestimation when asked to judge body parts' length by inferring how many times a metric standard (an object or a body part) would fit into the body segment they were asked to estimate.

Therefore, while there is some evidence that supports that even healthy population tends to hold a distorted and malleable body representation, there are contrasting results which pose the question of why different patterns of distortion may arise. It has been suggested that the method adopted, either “metric” or “depictive”, may lead to different types of representation due to implicit or explicit (metric and depictive, respectively) access to the *body image* (Longo & Haggard, 2010).

The present study aimed at investigating the role of different factors affecting the body metric representation. In Experiment 1, a modified version of the Body Image Task (BIT) has been adopted to evaluate the relationship between real and represented body parts' location and measures. In the original version of the BIT, body parts are presented on a screen and are on scale. Because of this, it could be argued that participants may provide answers mainly based on a stereotypical logical relationship between the body part shown and those to be added resulting in a reduced self-specificity of the represented body parts. In fact, Fuentes et al. (2013) did not find any significant correlations between the perceived and true lengths for any body part. Also, by pointing on a computer screen, participants may not make any significant effort to represent their own body in the actual external space. Therefore, two critical manipulations were considered in the present experiment: the size and the location of the area onto which the BIT occurred. Specifically, participants were asked to perform the task in real scale to enhance the

correspondence between their actual and represented body parts' size. Furthermore, by means of a laser pointer, participants had to 'project' the position of the represented body parts in extrapersonal space. Because the sense of bodily experience occurs *in* space, it was predicted that such manipulation it might reveal distortions that reflect intrinsic 'functional' properties of body parts. Building on the results of Experiment 1, in Experiment 2, the metrics of specific body parts (i.e. arms and legs) were explicitly assessed by means of a depictive task. The aim was to test whether bodily distortions are consistent across different methods (metric and depictive) and whether the effect is individual-specific or more generalized to a prototypical body (own and avatar).

4.3 Experiment 1a - Localization of body landmarks on real scale

4.3.1 Methods and procedures

4.3.1.1 Participants

Sample size was determined by an a priori power analysis run with G* Power (Faul, Erdfelder, Buchner, & Lang, 2009), which considered the type of analyses required to assess: i) differences between real and represented body measures by means of t-tests; and ii) differences between represented body measures among different conditions by means of analysis of variance. Previous studies on body representation adopting a localization task that reported an averaged effect size for one sample t-test of 0.8 were also considered (i.e., Ganea & Longo, 2017; Mora et al., 2018).

The power analysis for one sample t-test with an effect size of $d = .8$, $\alpha = .05$, and power = .95 indicated an adequate sample of 23 participants.

The sample size was also calculated for a repeated measures design with two conditions and 12 body parts to estimate with an $\eta^2_{partial} = .1$, $\alpha = .05$ and power of .95. The average effect size reported in previous studies assessing differences in length

estimation across body parts was $\eta_{partial}^2 = .3$ (Linkenauger et al., 2015; Sadibolova et al., 2019). The analysis suggested a sample of 12 participants to obtain an appropriate effect.

Twenty-eight participants (16 females) took part in the first experiment; their age ranged from 20 to 26 years, with a mean of 23.6 years (SD = 3.5). All participants were right-handed (Edinburgh Inventory mean score = 0.95; SD= 0.11). The study was approved by the Goldsmiths Ethics Committee and it was carried out in accordance with the Declaration of Helsinki (BMJ 1991; 302: 1194). All participants gave informed written consent.

4.3.1.2 Body Image Task (BIT)

The experiment consisted of a modified version of the Body Image Task (BIT; Fuentes et al., 2013). Participants were asked to imagine their silhouette with their arm aligned with the body, as if they were standing against a white wall at 2 meters in front of them (see Figure 4.1). Given the type of paradigm adopted (i.e. pointing in real scale), a methodological consideration was made to avoid an explicit and direct correspondence between the participants' body parts and the location in which these should have been located was crucial. Therefore, to create some mismatch with the represented silhouette, participants performed the task while seating on a chair. Two conditions were considered. In the first condition (*Frontal View*) participants were asked to imagine themselves standing with their back against the wall. In the second condition (*Dorsal View*) participants were asked to imagine their own silhouette from behind (i.e. as if they were looking at their back). Each participant performed both conditions, which were counterbalanced across participants.

The purpose of asking participants to represent their own silhouettes in a *Frontal* and *Dorsal* views was based on two considerations. First, to test whether different patterns of distortion found, with a similar localization task paradigm, between the palmar or dorsal surface of the hands (Longo and Haggard, 2010) also applies for the representation

of the whole body. Second, because in the *Frontal* view the body parts' location is mirror-inverted - right is on the left and vice versa -, such condition was used to control for possible biases concerning whether participants were actually pointing to the body part asked as they have to make a conscious effort to imagine their left (or right) body parts on the opposite side in external space.

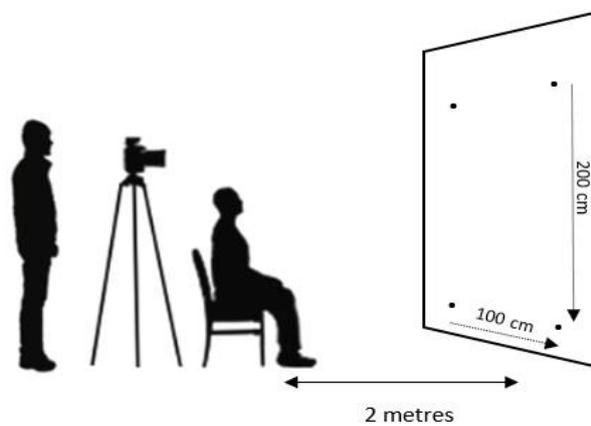
Four small black dots (150 mm of diameter) were placed on the wall in order to provide references for the four corners (frame reference points) of a rectangular frame (100x200cm) located at 9 cm from the floor. Participants, who were not aware of the actual distance between the dots, were asked to imagine their own silhouette within the frame and to indicate, by means of a laser pointer, a total of 17 body parts: 3 midline points, 8 landmarks for the arms and 6 landmarks for legs (see Table 4.1). Body parts were read aloud one each a time by the examiner and the participants had to locate the body parts by moving the wrist of the hand holding the laser pointer (participants were asked to maintain the hand still on their laps close to the torso). The three body midline points were read first then the others in pseudorandom order. The experimenter stood behind the participant's chair throughout the experiment to record each response taking pictures with a digital camera mounted on a tripod (see Figure 4.1).

The first location requested was always the navel. To avoid possible 'shift' of the imagined silhouette during testing, the perceived position of the navel was marked (with a small dot) on the wall and was used as visible landmark during the entire task. While the examiner marked the subjective position of the navel, participants were asked to close their eyes to avoid any reference (i.e. seeing the examiner close to the wall). Once the examiner was again standing behind the camera, participants were asked to open their eyes and indicate the other two midline landmarks (i.e., top of the forehead and the nose; their order was counterbalanced across participants) followed by the remaining body parts. These were not marked on the wall but the examiner recorded each response by

taking a picture with a Nikon Reflex D3100 mounted on a tripod located behind the participants. Both conditions (*Frontal* and *Dorsal* views) were repeated three times. Therefore, each of the 17 landmark locations was recorded 6 times (3 in *Frontal* and 3 in *Dorsal* view) for a total of 102 responses across both conditions.

Before leaving the experimental setting, a picture of each participant standing against the wall was taken and actual location of the navel was noted for later analyses.

Figure 4.1. Schematic sketch of the experimental setting.



The camera is positioned on a tripod behind the participant and it is aligned with the center of the wall frame.

From Caggiano and Cocchini, 2020.

4.3.1.3 Visuo-spatial estimation task

To assess general ability to perform spatial estimation, at the end of the modified BIT, each participant was asked to imagine a well-known object (i.e. a A4 sheet on landscape view) on the wall and to indicate its size by pointing to the four corners by means of the laser pointer. Finally, participants were asked to estimate a vertical line of 1 meter by indicating the two extremities.

Table 4.1. Body parts that participants were asked to locate.

BODY PARTS ASKED	ANATOMICAL POINT
<i>MIDLINE LANDMARKS</i>	
Navel	Umbilicus
Top of the forehead (hairline)	Middle point of frontal eminence
Nose	Tip of the nose
<i>ARM LANDMARKS</i>	
Corner of the right/left shoulder	Acromion
Right/Left elbow	Olecranon
Right/Left wrist	Ulnar styloid process
Tip of the right/left middle finger	Distal phalange
<i>LEG LANDMARKS</i>	
Right/left hip	Most lateral part of the iliac crest
Right/left knee	Patella
Right/left ankle	Anterior border of distal tibia

Only the subjective position of the navel was marked on the wall and used as visible fixed landmark throughout the task.

4.3.1.4 Data acquisition of BIT

To calculate actual and subjective sizes of body parts and to compare real and subjective participants' body measures, a software was developed in the MatLab environment. In order to produce a consistent output, the pictures (including the final photo of the participant) were cropped according to the specific four frame's reference points and scaled to a standard dimension of 1262×2668 pixels. The software automatically detected the four frame reference points and transformed pixels into actual distances expressed in centimetres. It also recorded the position of each subjective landmark that referred to specific body parts (i.e. the points indicated by the participants). This procedure was conducted for each set of pictures obtained from each of the three trials. Finally, the 'real' image of the participant was considered, and the experimenter manually marked all 17 body parts to obtain the real body map. The software computed the distances (expressed in centimetres) between different points and produced two sets of outputs for both real and subjective body maps: i) actual/subjective distance between landmarks and ii) graphic analogical representation of all landmarks. Width and length of body parts were calculated by measuring distances, expressed in centimetres, between

pairs of points as described in Table 4.2. Two width measures were considered, one for upper body (shoulders) and one for lower body (hips); two length measures were considered for each limb (arms and legs) and one length measurement was considered for the central part of the body (i.e. torso).

Two overall measures were then considered: the *Real Body Measure* (RBM) and the *Subjective Body Measure* (SBM). Similar to previous studies (i.e., Fuentes et al., 2013), real and subjective body measurements (RBM and SBM, respectively) were compared and analyzed in *percentage body part estimation error* (%BPE), which is expressed as the percentage difference between the perceived length/width and the participant's real body part length/width:

$$\%BPE = \frac{SBM - RBM}{RBM} \times 100$$

According to this formula, negative BPE values indicate underestimation, while positive values indicate overestimation; zero indicates perfect estimation.

Table 4.2. Length of body segments.

	BODY SEGMENTS	POINTS CONSIDERED
LENGTH	Right/Left Upper Arms	Right/Left Shoulder-Elbow
	Right/Left Lower Arms	Right/Left Elbow-Hand
	Right/Left Torso	Right/Left Shoulder-Hip
	Right/Left Upper Legs	Right/Left Hip-Knee
	Right/Left Lower Legs	Right/Left Knee-Ankle
WIDTH	Shoulder	Right-Left Shoulders
	Hip width	Right-Left Hips

4.3.2 Results

4.3.2.1 BIT

Body parts - Lengths

The most evident result was that participants tended to underestimate the lower part of the arms (overall BPE mean -19.07%) but overestimated the lower parts of the legs (+34.24%) (see Figure 4.2a and b). This pattern of results was similar for both views (Frontal and Dorsal) and sides (Right and Left).

In order to assess whether there was a significant distortion of individual body parts, a series of two-tailed t-tests, one for each body part, was carried out to compare BPE with zero (i.e., no distortion). Bonferroni correction for multiple comparisons was applied (i.e., 12 comparisons; significant p values < .004). Results showed that the length of 6 out of 10 body parts were significantly distorted from real size in the *Frontal* and 7 out of 10 in the *Dorsal* view (see Table 4.3 – Lengths). In detail, the forearms and the torso were

Table 4.3. Results of two-tailed t-tests comparing percentage of distortion (bpE) with 0 (no distortion).

Body parts	Frontal view (n = 28)			Dorsal view (n = 28)			
	t-critical	p	d	t-critical	p	d	
L E N G T H S							
Upper Arm	right	-1.67	.101	.31	-1.64	.113	.31
	left	-1.44	.162	.27	-1.69	.105	.32
Lower Arm	right	-11.35	<.004*	2.15	-12.36	<.004*	2.34
	left	-8.63	<.004*	1.63	-9.23	<.004*	1.74
Torso	right	-5.73	<.004*	1.08	-4.47	<.004*	.84
	left	-6.49	<.004*	1.22	-5.24	<.004*	.99
Upper Leg	right	-2.28	.031	.43	-2.32	.028	.44
	left	-2.72	.011	.51	-3.10	<.004*	.59
Lower Leg	right	9.10	<.004*	1.71	-7.04	<.004*	1.33
	left	10.79	<.004*	2.03	-8.63	<.004*	1.63
W I D T H S							
Shoulder		-1.88	.070	.36	-3.28	<.004*	.62
Hip		-1.44	.161	.27	-1.98	.058	.37

%BPE indicates the percentage difference between the perceived length/width and the participant's real body part length/width. Negative t-values indicate underestimation. In bold significant differences following correction for multiple comparisons.

consistently underestimated in both sides (Left and Right) and views (Frontal and *Dorsal*), whereas the lower legs were consistently overestimated in both sides and views. Upper arms and upper legs tended to be underestimated in all conditions, but the distortion was significant only for the left upper leg in *Dorsal* view.

A repeated measure ANOVA 5 (Body Part) \times 2 (View) \times 2 (Side) was performed to consider possible differences among body parts, side and view. Results yielded main effect of Body Part [$F(2.6, 70.24) = 74.85, p < .001; \eta^2_{\text{partial}} = .74$] whilst there was no effect of View [$F(1,27) = .73, p = .40; \eta^2_{\text{partial}} = .026$], Side [$F(1,27) = .52, p = .27; \eta^2_{\text{partial}} = .010$] nor interactions. Post-hoc analysis of the single body parts (corrected for 12 multiple comparisons, $p < .004$) showed that the BPE for forearms and lower legs significantly differed from BPE of all the other body parts ($p < .001$).

Finally, to evaluate whether participants' mental representation of their own body (i.e., SBM) reflected their real measures (i.e., RBM), a bivariate Pearson correlation was performed to assess whether there was a correlation between the SBM and the RBM of each body parts (i.e. total length of the arms, legs, and torso expressed in centimetres).

Since previous analyses showed no differences between the two views (Frontal and *Dorsal*) and the body sides (Left and Right), these factors were collapsed.

Results showed a positive correlation for all the body parts considered (arms: $r = .59, p = .001$; legs: $r = .51, p = .005$; torso: $r = .51, p = .006$), suggesting that, even if participants hold a distorted representation of some of their own body parts, this representation is still reflecting participants' real sizes. In addition, the SBM of the torso correlated positively with the SBM of the arms ($r = .68, p < .001$) but not with legs ($r = .28, p = .14$).

Body parts - Widths

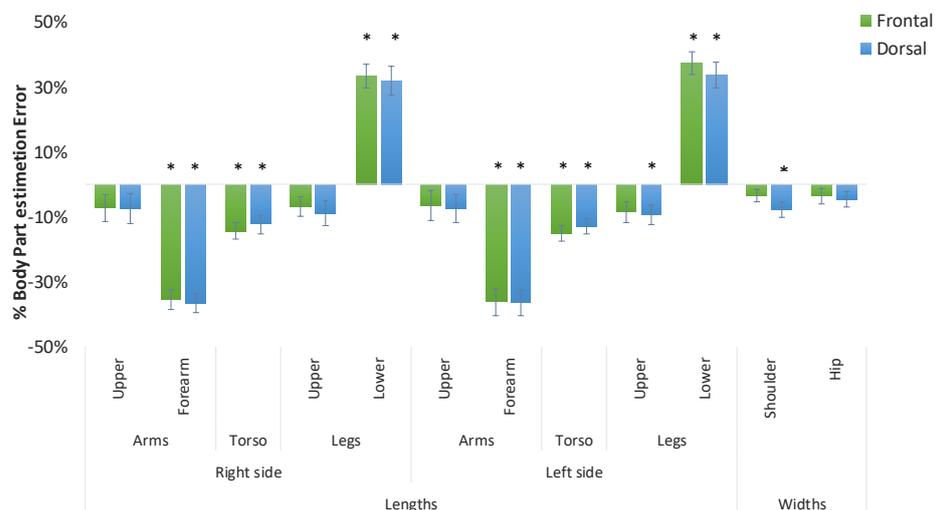
Overall, participants showed a trend in underestimating the width of shoulders and hips (i.e., -13.67% and -4.86%, respectively; See Figure 4.2a & b). Analyses on

distortions by means of t-test comparisons between BPE and zero (i.e., no distortion) showed that only shoulder width was significantly underestimated but only in the Dorsal view (See Table 4.3 – Widths).

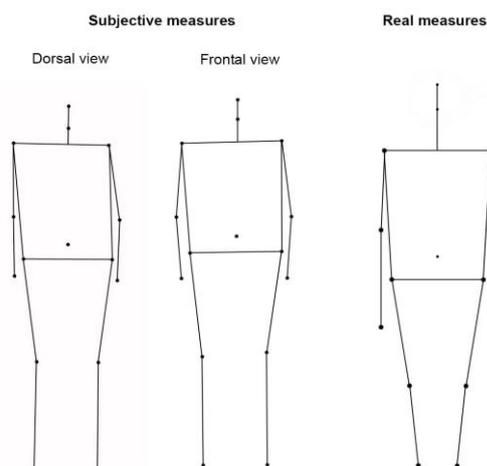
A repeated ANOVA 2 (Body Part) \times 2 (View) to consider possible difference between different body parts and views, showed no significant main effect of Body Part [$F(1,27) = .87, p = .36; \eta^2_{partial} = .031$], View [$F(1,27) = 3.15, p = .087; \eta^2_{partial} = .11$] nor Body Part \times View [$F(1,27) = 1.43, p = .24; \eta^2_{partial} = .05$].

Figure 4.2. Under/overestimation in perceived body parts' length.

a)



b)



a) %BPE averaged across 28 individuals. **b)** Graphic output of averaged subjective responses and real body dimensions for 28 participants. Note that in both Frontal and Real images, the egocentric right side is on the left of the drawing and viceversa.

As for the lengths, a Pearson correlation between the SBM and the RBM widths for shoulders and hips (width expressed in centimetres) was carried out. Results showed a positive correlation for shoulder width ($r = .67$, $p < .001$) but not for hip width ($r = 0.34$, $p = .07$).

Visuo-spatial estimation task

To investigate whether the distortion observed on the body parts' length could be related, at least in part, to participants' general visuo-spatial estimation skills, individual estimation accuracy for 1 meter vertical segment and the size (height and width) of A4 sheet in landscape view was considered. The percentage of the estimation measurement error (%ME) for the Subjective Mean (SM) and Real Mean (RM) of both measures was calculated using a formula similar to the one adopted for %BPE, that is:

$$\%ME = \frac{SM - RM}{RM} \times 100$$

On average, for the 1 meter segment, participants ME was -10.57% (SD = 9.5); whereas for the A4 sheet size was -15.01% (SD = 14.01) for height and -6.61% (SD = 7.53) for width. We ran Pearson correlations between individual averaged BPE values and averaged ME values for each of the visuo-spatial tasks. Results showed no significant correlation for any BPE and ME (highest value: $r = 0.35$, $p = 0.07$), suggesting that estimation errors for body parts' measures was not easily tracked back to a more general visuo-spatial bias.

4.3.3 Preliminary discussion

Unlike recent studies showing dissociation between different view representations, such as dorsal and palmar views of the hand (e.g., Mancini, Longo, Iannetti & Haggard, 2011; Longo & Haggard, 2011), participants showed a systematic pattern of distortion of their body representation regardless the prospective (*Frontal* or *Dorsal* views) and a symmetrical representation with no difference between sides (left or right). Results allowed to exclude that participants have maintained a preferred viewpoint (e.g., frontal

view) during both conditions otherwise they would have incorrectly reported landmarks referring to the right or left side. It seems more likely that, in this task, participants managed to maintain a reliable perspective of their silhouette under different conditions. Under these circumstances, participants showed a similar and systematic distortion of body parts in all conditions. In detail, the upper body parts, in particular forearms, were considerably underestimated (almost 20%) whereas the lower parts, in particular lower legs, were overestimated by more than one third. Therefore, the upper and lower parts of the body appear to be asymmetrically represented with the first being shrunk and the second being more elongated than real lengths. Despite the emergence of such stereotyped pattern of distortion, the represented measures positively correlated with the true body size. Nonetheless, it is possible that the seated position may have been, at least in part, responsible for the distorted representation. In fact, to avoid that participants' responses reflected a mere 'translation' on the wall of the current body landmark positions, they were asked to perform the task while seated in order to induce a mismatched between the landmarks of the actual position and those of the imagined silhouette on the wall. If the seated position had any significant effect on the representation of the silhouette on the wall, we would have observed a considerable underestimation of the upper legs, and a very accurate estimation of the lower legs since the position of knees and ankles were those matching their position on the wall. On the contrary, results showed a greater systematic distortion, in terms of overestimation, of the lower legs and only a marginal underestimation of the upper legs, the latter only significant for the left leg under dorsal view. Therefore, it seems unlikely that the seated position can explain the specific different distortion between representation of upper and lower parts of the body.

A further possible reason for the subjective overestimation of the legs may be due to participants' expectation induced by the instructions. Since participants were asked to imagine themselves standing, the instructions implied that their feet should have touched

the floor. As showed in Figure 4.2b, the perceived position of the navel, indicated at the beginning of the task, was slightly higher than the real one. As such, it is possible that this initial ‘misjudgement’ may have determined an “artefact” stretch of the lower legs ‘to touch’ the floor. To address this potential alternative explanation for leg overestimation, a follow-up experiment was conducted (Experiment 1b) in which participants were asked to imagine their silhouette in an inverted position.

4.4 Experiment 1b - Localization of body landmark in inverted position

4.4.1 Methods and procedures

4.4.1.1 Participants

Based on the results of Experiments 1a, sixteen participants (9 females and 7 males) took part to a second experiment. None of them entered in the previous experiment. Age ranged from 18 to 33 years, with a mean of 23.8 years ($SD = 4.2$). All participants gave informed consent. All participants were right-handed (Edinburgh Inventory mean score = mean = 0.93; $SD = 0.09$). The study was approved by the Goldsmiths Ethics Committee and it was carried out in accordance with the Declaration of Helsinki (BMJ 1991; 302: 1194). All participants gave informed written consent.

4.4.1.2 BIT – Inverted position

The main procedure and data acquisition were similar to the Experiment 1a. Because in the previous experiment no differences were observed for the variable View, participants were asked to perform the task only in the Frontal view (i.e. imagining themselves standing with their back against the wall).

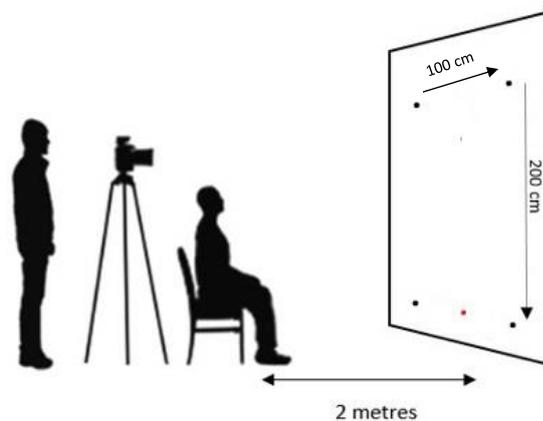
The experiment consisted of two conditions. In the first condition (*Upright Condition*) participants were asked to imagine themselves standing with the back against the wall (as **if** they are looking into a mirror). In the second condition (*Inverted Condition*) participants were asked to imagine their silhouette upside down (head touching the floor). Each participant performed both conditions which were counterbalanced across participants.

Participants sat on a chair and, following the initial instructions about the anchor point, they were asked to indicate using the laser pointer, each of the remaining 16 landmarks (See Table 4.1). As in Experiment 1.a, the first location requested was always the navel. To avoid possible ‘shift’ of the imagined silhouette during testing, the perceived position of the navel was marked (with a small dot) on the wall and was used as visible landmark.

The examiner recorded each response by taking a picture with a Nikon Reflex D3100 as in the previous experiment.

Before leaving the experimental setting, a picture of each participant standing against the wall was taken for the analysis.

Figure 4.3. Schematic sketch of the experimental setting.



The camera is positioned on a tripod behind the participant and it is aligned with the center of the wall frame. The red dot indicates the location of the head in this task (note that the head landmark was not given).

Body parts - Lengths

As in the previous experiment, when participants were asked to imagine they own silhouette in a canonical position (i.e. *Upright* condition), they showed an underestimation of the length of their upper body parts (BPE -23.85%) and overestimate the lower legs (BPE +35.81%). However, a different pattern of distortions was observed

in the *Inverted* condition with a general tendency to overestimate upper body parts (BPE +6.68%) and underestimate the lower legs (-4.99%) (see Figure 4.4a and b).

A series of t-tests, corrected for multiple comparisons (significant p values < 0.004) showed that the length of 6 out of 12 body parts were significantly distorted in the *Upright* condition, and 4 out of 12 in the *Inverted* condition (see Table 4.4). The pattern of distortion in the *Upright* condition closely resembled the one observed in Experiment 1a with forearms, torso significantly underestimated and lower legs overestimated. In the *Inverted* condition, participants seemed to be more accurate with less body parts significantly distorted. Crucially, they maintained a perceived underestimation of the forearms but significantly overestimated the torso length. Also, although not significant, an inverted trend can be noted for the upper arms which, compared to the *Upright* condition were overestimated.

Table 4.4. Two-tailed t-tests results comparing %BPE with 0.

Body parts	Upright view (n = 16)			Inverted view (n = 16)			
	t-critical	p	d	t-critical	p	d	
L E N G T H S							
Upper Arm	right	-2.39	.03	.59	2.73	.015	.68
	left	-1.77	.097	.44	2.57	.021	.64
Lower Arm	right	-8.35	<.004*	2.08	-4.78	<.004*	1.19
	left	-8.13	<.004*	2.03	-7.76	<.004*	1.94
Torso	right	-5.44	<.004*	1.36	3.41	.004*	.85
	left	-5.56	<.004*	1.39	3.46	.003*	.87
Upper Leg	right	-1.13	.276	.28	-1.05	.308	.26
	left	-2.17	.046	.54	-.587	.566	.15
Lower Leg	right	6.06	<.004	1.51	-.439	.667	.11
	left	8.71	<.004	2.17	-.867	.399	.22
W I D T H S							
Shoulder		-2.04	.070	.51	-.419	.681	.10
Hip		.239	.814	.06	.073	.943	.02

%BPE indicates the percentage difference between the perceived length/width and the participant's real body part length/width. Negative t-values indicate underestimation. In bold significant differences following correction for multiple comparisons.

Results from a three-way factor ANOVA 5 (Body Part) \times 2 (Condition) \times 2 (Side) yielded a significant main effect of Body Part [$F(2.11, 31.71) = 17.58, p < .001; \eta^2_{\text{partial}} = .54$] and Condition [$F(1, 15) = 8.63, p = .01; \eta^2_{\text{partial}} = .37$] as well as a significant interaction effect of Body part \times Condition [$F(2.52, 37.91) = 22.91, p < .001; \eta^2_{\text{partial}} = .61$].

Pairwise comparisons on Body Part highlighted that the forearms were significantly underestimated compared to all other body parts ($p = .001$) and that the lower legs were larger than the upper legs ($p = .05$).

Post hoc analyses on the interaction showed that upper arms, torso and lower legs were differentially distorted between the *Upright* and the *Inverted* conditions. Specifically, while the upper arms and torso were perceived longer in the *Inverted* condition (+30.5% and +21.8% respectively), the lower legs were underestimated (-5.1%).

The Pearson correlation between the SBM and RBM of body parts (arms, legs, torso) showed a positive correlation for the arms ($r = .55, p = .03$) and legs ($r = 0.51, p = 0.04$) whilst torso did not show a significant correlation ($r = .19, p = .47$) in the *Upright* condition. None of the SBM lengths in the *Inverted* condition correlated with the RBM lengths. Interestingly, in both conditions the SBM length of the torso showed a significant correlation with the SBM length of the arms (Upright: $r = 0.63, p = .008$; Inverted: $r = 0.81, p < .001$) but not with the legs (Upright: $r = 0.25, p = .35$; Inverted: $r = 0.07, p = .79$).

Body parts - Width

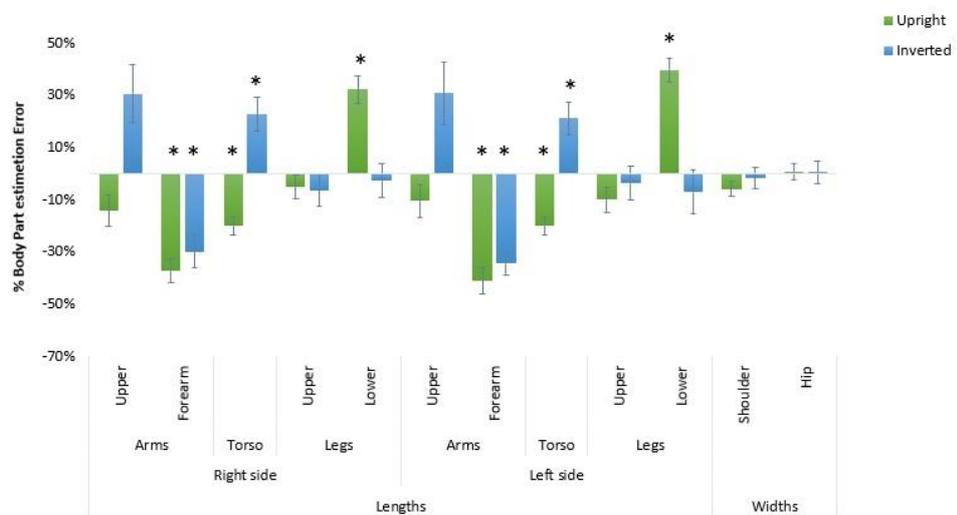
Participants showed a trend in underestimating the width of shoulders (-3.88%) and minimally overestimating then hips (+0.5%; see Figure 4.4a and b) yet, t-test comparisons between BPE and zero (no distortion) did not show significant distortions in both conditions.

A 2 (Body Part) \times 2 (Condition) ANOVA showed no significant effects of Body Part [$F(1, 15) = 2.97, p = .11; \eta^2_{partial} = .17$] nor Condition [$F(1, 15) = .561, p = .47; \eta^2_{partial} = .036$]. Interaction was also not significant.

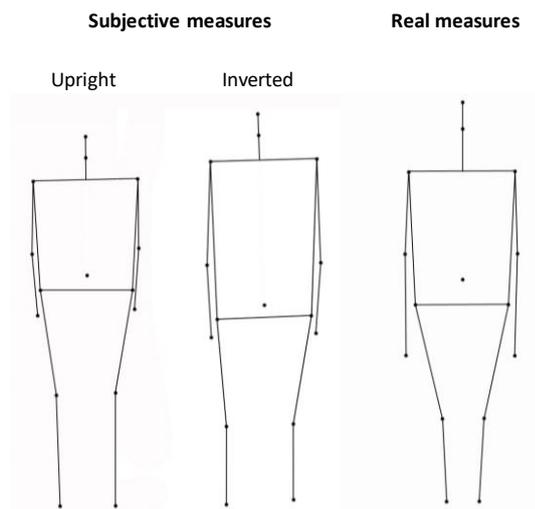
The Pearson correlation between the SBM and RBM of shoulder and hip width was not significant for both body parts in both conditions.

Figure 4.4. Under/overestimation in perceived body parts' length.

a)



b)



a) %BPE averaged across 16 individuals. **b)** Graphic output of averaged subjective responses and real body dimensions for 16 participants. Note that in both Upright and Inverted images, the egocentric right side is on the left of the drawing and viceversa.

4.4.2.2 Visuospatial performance

It was evaluated whether participants' BPE correlated with estimation accuracy of 1 metre (mean = -9.59%, SD = 8.51) and A4 sheet size (length: mean = -5.34, SD = 6.86; width: mean = 12.4, SD = 11.66). For the *Upright* condition, Results showed a significant positive correlation between the BPE of the upper arm and estimation errors of A4 sheet height ($r = 0.7$, $p = .003$). In the *Inverted* condition a significant positive correlation was present between the BPE of the hip width and estimation errors of 1 metre segment ($r = 0.62$, $p = .009$). No other significant correlations were observed.

4.4.3 Preliminary Discussion

Results from the Experiment 1b replicated the same pattern of findings observed in the previous experiment, when participants were asked to perform the task in the *Upright* condition. Interestingly, a different pattern of distortions manifested when participants imagined their own silhouette in the *Inverted* condition. In particular, the forearms were again considerably underestimated but the torso was significantly overestimated.

Recent studies have demonstrated that human bodies, like faces, are susceptible to the *inversion effect*. It has been shown that discriminating two inverted body postures is more difficult than discriminating two upright body postures. In other words, the recognition performance of inverted bodies is poorer than recognition of upright bodies (Reed, Stone, Bozova, & Tanaka, 2003; Reed, Stone, Grubb & McGoldrick, 2006; Minnebusch & Daum, 2009; Yovel, Pelc, & Lubetzky, 2010). It has been argued that, at the perceptual level, body recognition relies on a configurational processing due to visual expertise associated with the frequent observation of other bodies. This means that, as a result of perceiving bodies frequently, individuals tend to extrapolate specific configural relations typical of a human body. It has been suggested that configural processing involves four main mechanisms: *first-order* relational information, *structural information*, *second-order* relational information and *holistic processing* (Reed, et al., 2006). *First-order* relational information refers to the absolute spatial coordinates of

individual bodily features (e.g. the arms above the legs). On the other hand, *structural information*, refers to the spatial relationship of each body part within the overall structural hierarchy of the body. In fact, legs and arms may vary in how far above or below each other they are in space, but they are always attached to the same parts of the torso. *Second-order* relations refer to metric distances between bodily features (e.g., the distance between the hand and elbow). Lastly, *holistic processing* refers to the perception of the body as an integrated representation.

It has been suggested that both *first-order* relational information and *structural information* are involved in the *body inversion effect*. Specifically, the *inversion effect* has been interpreted as a mismatch between the internal spatial representation, and the perceptual input (i.e. the inverted body) which leads to a decrease in discrimination performance for inverted bodies (Pavlova & Sokolow, 2000; Sumi, 1984).

The data from Experiment 1b are of particular interest as they may provide further insight into the *body inversion effect*. The performance on the *Inverted* condition was qualitatively and quantitatively different from the *Upright* one, suggesting that not only the inversion effect might manifest at the visuo- perceptual level, but also at a more internally generated representation of the body. Imagining the body upside-down significantly modulated the metric representation and disrupted the correspondence between the participants' real measures and the represented ones, as shown by the absence of correlation between the RBM and SBM. Nonetheless, even in this circumstance, the relationship between arms and torso was maintained.

In light of this, it could be argued that the *Inverted* condition, due to the unusual and “unrealistic” body posture, cannot fully provide an effective control for the original ambiguity of legs overestimation identified in Experiment 1a and in the *Upright* condition of Experiment 1b. Furthermore, it cannot be excluded that the distortions measured in the *Inverted* condition are not genuinely reflecting distortions in the body representation but

a spatial bias due to the unrealistic posture. Therefore, the results observed do not allow to exclude a potential conceptual bias associated with lower legs overestimation in the original upright posture. To clearly address this aspect, a third experiment was conducted (Experiment 1c) in which participants were asked to imagine their silhouette in ‘canonical’ but elevated positions.

4.5 Experiment 1c - Localization of body landmark on elevated positions

4.5.1 Methods and procedures

4.5.1.1 Participants

Based on the results of Experiments 1a and 1b, ten participants (5 females and 5 males) took part in the third experiment. None of them entered in the two previous experiments. Age ranged from 19 to 26 years, with a mean of 23 years (SD = 2.1). All participants were right-handed (Edinburgh Inventory mean score = 0.95; SD = 0.07). The study was approved by the Goldsmiths Ethics Committee and it was carried out in accordance with the Declaration of Helsinki (BMJ 1991; 302: 1194). All participants gave informed written consent.

4.5.1.2 BIT – Elevated position

The main procedure and data acquisition were similar to the previous two experiments. Participants were asked to perform the task only in the *Frontal* view, that is imagining themselves standing with their back against the wall. There were two conditions: in one condition, the top of the forehead was given before initiating the task as fixed anchor point (*Head* condition) and in the second condition the navel (*Navel* condition) was given as fixed anchor point by the examiner. In both conditions, the anchor points were located in an elevated (i.e. higher than normal) position to control for the possible implicit bias of participants locating the ankles close to the floor. In the *Head* condition the anchor point was located at the top edge of the frame at 198 cm from the floor; whereas in the *Navel* condition the anchor point was located at 115cm from the

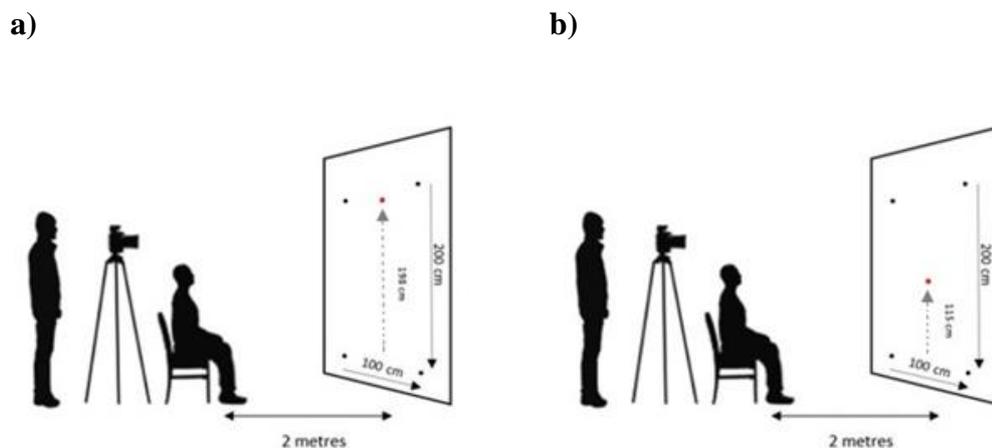
floor (See Figure 4.5). Each participant performed both conditions which were counterbalanced across participants. The procedure adopted was similar to Experiment 1a; however, the participants were asked to imagine themselves as if their forehead or navel, depending on the condition, were actually located at the fixed and visible anchor point. They were also told that, their feet may not touch the floor. Participants sat on a chair and, following the initial instructions about the anchor point, they were asked to indicate using the laser pointer, each of the remaining 16 landmarks (See Table 4.1). As in Experiment 1a and 1b, landmarks were read aloud one at the time in pseudorandom order and each of the 16 landmarks was asked 6 times (3 for the Head and 3 for the Navel conditions) for a total of 96 trials across both conditions. The examiner recorded each response by taking a picture with a Nikon Reflex D3100 as in the previous experiment.

Before leaving the experimental setting, a picture of each participant standing against the wall was taken and actual location of the navel was noted for later analyses.

4.5.1.3 Visuo-spatial estimation task

The participants' ability to estimate the length and size of a vertical line of 1 meter and a A4 sheet on landscape view was assessed. Participants were asked to make their

Figure 4.5. Schematic sketch of the experimental setting.



a) *Head* condition: the landmark was located at the top edge of the frame (198 cm from the lower edge); **b)** *Navel* condition: the landmark was located 15 cm above the middle of the frame (115 cm from the lower edge of the frame).

judgment by pointing on the wall the extremities of the 1 metre line and the four corners of the A4 sheet by means of the laser pointer.

4.5.2 Results

4.5.2.1 BIT – Elevated position

Body parts - Lengths

As in Experiment 1a and 1b (*Upright* condition), participants showed a general tendency to underestimate the length of their upper body parts (BPE -15.52%) and overestimate the lower legs (BPE +22.54%) (see Figure 4.6a and b).

A series of t-tests, corrected for multiple comparisons (significant p values < 0.004) showed that the length of 4 out of 12 body parts were significantly distorted in the Head condition, and 3 out of 12 in the Navel condition (see Table 4.5). Overall, participants displayed a similar trend to the one observed in Experiment 1a, that is the left and right

Table 4.5. Two-tailed t-tests results comparing %BPE with 0.

Body parts	Head (n = 10)			Navel (n = 10)			
	t-critical	p	<i>d</i>	t-critical	p	<i>d</i>	
LENGTHS							
Upper Arm	right	-1.41	.119	.45	-1.83	.100	.57
	left	-.772	.035	.24	-.69	.505	.21
Lower Arm	right	-7.56	<.004*	2.39	-4.41	.002*	1.39
	left	-7.62	<.004*	2.41	-5.41	<.004*	1.71
Torso	right	-3.08	.013	.97	-2.92	<.017	.92
	left	-2.47	.035	.78	-5.07	<.004*	1.60
Upper Leg	right	-2.84	.019	.89	-1.72	.119	.54
	left	-3.25	.010	1.02	-1.34	<.212	.42
Lower Leg	right	4.61	.001*	1.45	2.92	<.017	.92
	left	3.87	.004*	1.22	3.25	<.010	1.02
WIDTHS							
Shoulder		2.13	.061	.67	-1.47	.175	.46
Hip		.771	.461	.24	-.81	.435	.25

%BPE indicates the percentage difference between the perceived length/width and the participant's real body part length/width. Negative t-values indicate underestimation. In bold significant differences following correction for multiple comparisons.

forearms were significantly underestimated for both *Head* and *Navel* conditions, whereas the upper legs showed an overestimation only in the *Head* condition. The left side of the torso was significantly distorted in the *Navel* condition, only.

Results from a three-way factor ANOVA 5 (Body Part) \times 2 (Condition) \times 2 (Side) confirmed the original finding of a significant main effect of Body Part [$F(2.66, 23.95) = 23.81, p < .001; \eta^2_{\text{partial}} = .72$]; whilst no main effect of Condition [$F(1,9) = 1.51, p = .25; \eta^2_{\text{partial}} = .14$] nor Side [$F(1,9) = .18, p = .68; \eta^2_{\text{partial}} = .020$] was found. None of the interactions were significant.

The Pearson correlation between the SBM and RBM of body parts (arms, legs, torso) showed a positive correlation for the arms ($r = .65, p = .04$) and legs ($r = 0.79, p = 0.006$) whilst torso did not show a significant correlation ($r = .42, p = .22$). Yet, as in the previous experiment, the SBM length of torso showed a significant correlation with SBM length of the arms ($r = 0.69, p = .03$) but not with legs ($r = 0.59, p = .73$).

Body parts - Width

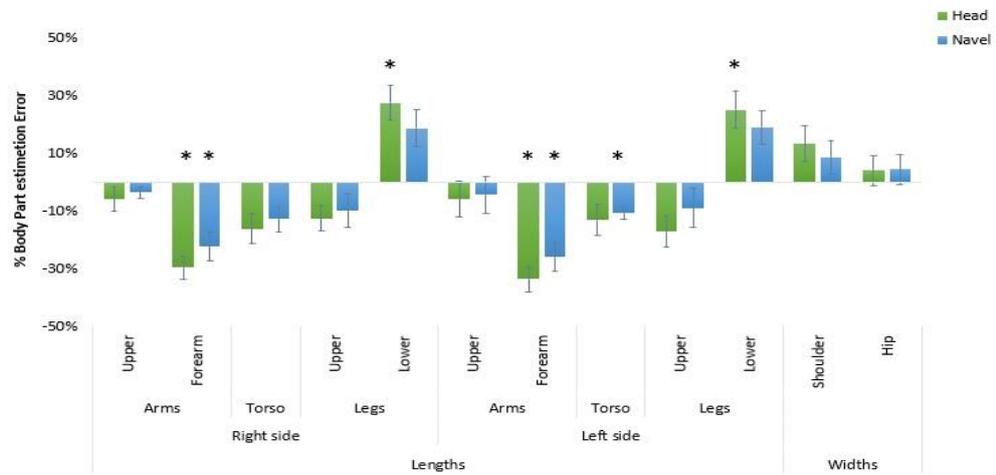
Participants showed a trend in overestimating the width of shoulders and hips (i.e., +10.79% and +4.12%, respectively; See Figure 4a and b) yet, t-test comparisons between BPE and zero (no distortion) did not show significant distortions in both conditions.

A 2 (Body Part) \times 2 (Condition) ANOVA showed no significant effects of Body Part [$F(1, 89) = 1.34, p = .28; \eta^2_{\text{partial}} = .129$] nor Condition [$F(1, 9) = .561, p = .47; \eta^2_{\text{partial}} = .059$]. Interaction was also not significant.

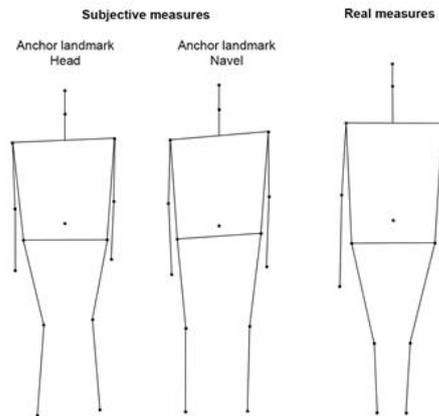
The Pearson correlation between the SBM and RBM of shoulder and hip width was not significant for both body parts ($r = .47, p = .16; r = .49, p = .15$ respectively).

Figure 4.6. Under/overestimation in perceived body parts' length.

a)



b)



a) %BPE averaged across 28 individuals. **b)** Graphic output of averaged subjective responses and real body dimensions for 10 participants in both conditions. Note that in all the three images, the egocentric right side is on the left of the drawing

4.5.2.2 Visuospatial performance

It was evaluated whether participants' BPE correlated with estimation accuracy of 1 metre (mean = -7.54%, SD = 8.99) and A4 sheet size (length: mean = -5.07, SD = 6.53; width: mean = 10.6, SD = 12.96). Results showed a significant positive correlation between the BPE of the upper arm and estimation errors of 1 metre segment ($r = 0.67$, $p = 0.034$). No other significant correlations were reported.

4.5.3 Preliminary Discussion

Results from the Experiment 1c, with elevated positions, replicated the same pattern of findings observed in the previous experiments, whereby a systematic distortion of specific body parts occurred. In particular, the forearms were again considerably underestimated and the lower legs were significantly overestimated. Changing the location of the anchor points had little impact on the metric representation of the lower legs.

It should be noted that the systematic pattern of results of short arms and long legs is not, at first glance, in line with findings by Fuentes and collaborators (2013). Their participants were asked to indicate body landmarks on a PC screen and they tended to delineate silhouettes with overall longer arms and shorter legs. Inspecting Fuentes and collaborators' figure (Fig. 2, p. 346) the tip of the hands were aligned with the waist line, which represents the semantic lower landmark of the upper half of the body (Reed et al., 2004; de Vignemont, Majid, Jola, & Haggard, 2009). In other words, it seems that also in Fuentes and coll.'s study, arms tend to be represented within the upper section of the body delimited by the hips. Interestingly, the closer relationship between arms and torso is confirmed in the present study as the length of torso was positively correlated with arms but not with legs. Therefore, the represented length of body parts seems to be defined by the relationship with other body parts rather than an intrinsic distortion of each part. Recent studies (Romano et al., 2018; Ferretti, 2016; D'Angelo, di Pellegrino, Seriani, Gallina, & Frassinetti, 2018) showed a close relationship between function (i.e. motor training) and perceived length of the arms and fingers. In line with these findings, the observed asymmetrical representation for upper and lower parts of the body, could be better interpreted considering the functional link between specific body parts and the actions we perform with them. In this respect the arms (and hands) are mainly used to bring objects toward the upper side of the body whilst the legs are mainly used to walk "away" or hit objects (e.g. kicking a ball; Ferretti, 2016). This may result in an implicit

modulation of the represented upper limbs as shorter, or above the waist line (as in Fuentes et al., 2013), and lower limbs as longer.

The fact that arms and torso were highly correlated in all the three experiments in all conditions seems to support the idea of a close relationship between these two body areas. It would then be interesting to explore the extent of this relationship by keeping the size of the torso ‘fixed’ while the size of the limbs is manipulated. Furthermore, since the general motor functions of upper and lower limbs are common to all human beings, similar findings, regardless the method (metric or depictive) adopted and ownership of the silhouette considered, should be observed. In other words, it is predicted to find a qualitatively similar pattern of results for *body image* and for own or other people’s body. To this aim, a last experiment was conducted where the metrics of the body image were explicitly assessed by means of a depictive task where the limbs of own or an avatar’s silhouette were distorted while the torso’s size remained unchanged.

4.6 Experiment 2 - Depictive task for own and prototypical body

In this experiment two types of stimuli were used: a “prototypical” body (Avatar) and a participants’ image (Own) taken before the start of the study.

4.6.1 Methods and procedures

4.6.1.1 Participants

Experiments 1a, 1b and 1c showed quite large effect sizes for both differences between real and represented body measures as well as among represented body parts. Therefore, we carried out two a priori power analysis assuming large effect sizes. For one sample t-test we set the parameters of $d = 1$, $\alpha = .05$, and power = .95 and the calculation indicated a sample size of 16. For a repeated measures ANOVA with 2 conditions and 2 body parts estimations, we calculated the sample size for $\eta^2_{partial} = .2$, $\alpha = .05$, and power = .95. The analysis showed that a sample of 16 participants would be appropriate to find an effect.

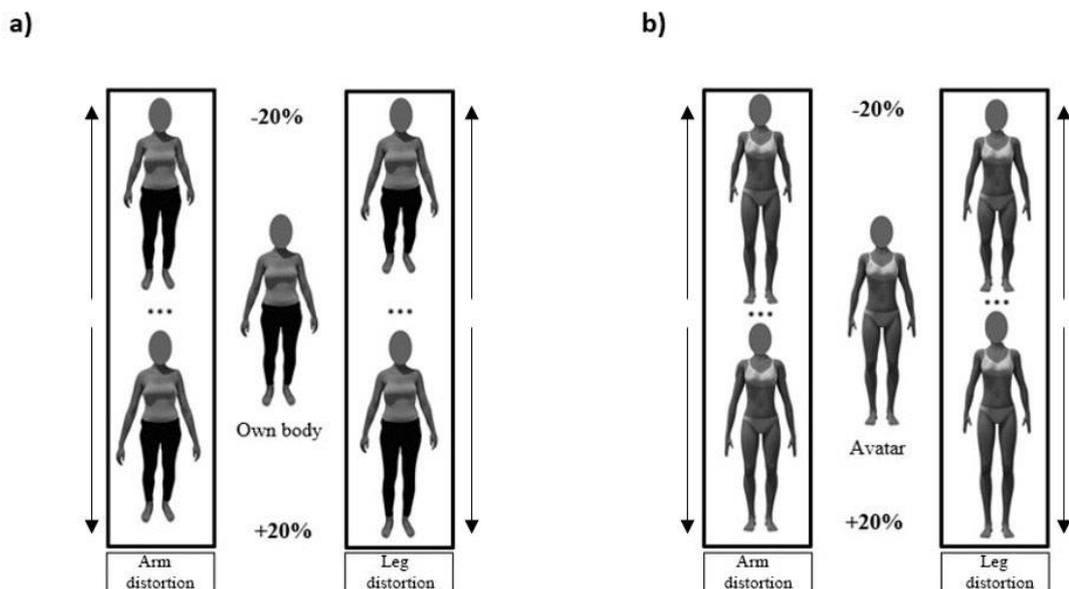
Twenty participants (10 females) took part the Experiment 2. None of them participated in the previous experiments. Age ranged 20 to 28 years, mean 23.9 years (SD = 2.9). All participants were right handed (Edinburgh Inventory mean score = 0.96; SD= 0.06; range: 1 - 0.89).

The study was approved by the Goldsmiths Ethics Committee and it was carried out in accordance with the Declaration of Helsinki (BMJ 1991; 302: 1194). All participants gave informed written consent.

4.6.1.2 Stimuli

Two types of stimuli were used: i) *Own* - a digital photograph of each participant taken in advance; and ii) *Avatar* - a standard avatar of a prototypical male or female body. Both types of stimuli were in black and white on a monotonous, white-coloured background in a frontal standardized pose (i.e. standing with arms aligned with the body

Figure 4.7. Types of stimuli adopted in the Experiment 2.



For both conditions, two sets of images were created (arms and legs). Each set ranged from maximum overestimation of +20% to a maximum underestimation of -20% from the original picture. Consecutive distorted images differed of +/-2% and each set consisted of 21 pictures (10 stretched, 10 shortened and 1 non-distorted). An example of 'female' avatar is reported here. Avatar gender was matched with the participant one.

From Caggiano and Cocchini (2020).

and the feet aligned approximately to the shoulder width). The pictures showed the participants' and avatar's whole body; however, following a pilot study, it was decided to blur the face area to reduce attentional drift toward the face. A customized computer program was used to stretch or shrink the arms or the legs of the pictures (the rest of the body was not modified). Based on previous pilot studies, the distortion ranged from +20% to -20% of the body part increasing or decreasing by 2% (See Figure 4.7). Therefore, we obtained 20 images with distorted arms (10 shorter and 10 longer), 20 images for legs (10 shorter and 10 longer) and 2 images with non-distorted arms and legs for *Own* and for *Avatar* conditions. To maintain a realistic appearance of the body part's shape, hands and feet were not distorted. While stimuli for the *Own* condition changed with every participant, the stimuli for the *Avatar* condition remained the same for all participants and only changed to match the participant's gender.

4.6.1.3 Depictive body parts estimation task

Images were displayed on a computer screen (resolution 1280×1024 pixels) using E-prime 2.0. Participants were seated on a chair in front of the computer screen at approximately 60 cm distance. They were instructed to fixate on the central cross that was displayed 300 msec before each stimulus was presented. Stimuli remained visible until response or for 1000 msec, then a blank screen followed. Participants provided a response by pressing two buttons on a standard keyboard. Feedback was not provided. Each *Own* and *Avatar* condition consisted of two blocks: Arms (where only arms were distorted) and Legs (where only legs were distorted). The stimuli were presented according to the method of limits, from shortest to longest length and reverse. Each block consisted of seven ascending and seven descending trials. Participants were informed that the pictures were distorted and that specific body parts (i.e. arms or legs) were longer or shorter than the original picture. After each stimulus, participants were asked to decide whether the target body part (arms or legs, depending on the series of stimuli presented) was veridical (for own images) or proportionate to the rest of the body (for avatar stimuli).

The pilot study indicated that a distortion of 20% was well above the subjective threshold of distortion detection and easily identified, therefore each block of stimuli started from +/- 20% distortion it was expected that participants had no difficulty to correctly identify the first images as distorted (i.e. too short or too long, depending if ascending or descending order, respectively). Presentation series continued until participants' responses changed (e.g., switched from 'not veridical' to 'veridical'). Then the next series in the opposite direction began. To avoid adaptation effect and participants switching response after a set number of trials, four series out of seven had different starting points; two series started at +/-18% distortion level and two started at +/-16%. The presentation order of the series was random. Also, presentation order of conditions (own or avatar), ascending/descending series and body part distorted (arm and leg) were counterbalanced across participants.

4.6.1.4 Data analysis

For each series (both ascending and descending) the *Transition point*, which corresponds to the average point where the participants' response changed (i.e., the last "not veridical" response and the first "veridical" response) was calculated. For example, on a descending series, if the last "not veridical" was at a distortion level of +6%, and the "veridical" response at +4%, the transition point was +5%. Transition points for each trial were then averaged across ascending and descending conditions. These values represented the discrepancy between the actual midpoint of the ascending and descending series (the non-distorted image at 0% distortion level) and the "perceived" midpoint of the series (point of subjective equality).

4.6.2 Results

Figure 4.8a shows a general tendency to underestimate the arms (*Own*: -3.3%, *Avatar*: -3.7%) and overestimate the legs (*Own*: +1.8%, *Avatar*: +0.7%). Two-tailed t-test, comparing transition points with zero, showed that the under- and over-estimation of the body parts in both conditions were statistically significant (see Table 4.6).

Table 4.6. Results of two-tailed t-tests comparing transition points with 0 for Own body and Avatar.

	Own body			Avatar		
	t-critical	p-value	<i>d</i>	t-critical	p-value	Cohen's <i>d</i>
Arms	-30.13	<.001*	6.74	-17.24	<.001*	3.85
Legs	4.08	.001*	0.91	10.34	<.001*	2.31

Transition points indicates the percentage difference between the perceived length/width and the avatar or the participant's real body part length/width. Negative t-values indicate underestimations. In bold significant differences following correction for multiple comparisons.

A two-way factor ANOVA 2 (Condition) \times 2 (Body part) showed significant main effects of Body Part [$F(1,19) = 515.39, p < .001; \eta^2_{partial} = .96$] and Condition [$F(1,19) = 11.19, p = .003; \eta^2_{partial} = .37$] as well as a two-way interaction [$F(1,19) = 7.26, p = .014; \eta^2_{partial} = .27$]. Post-hoc analyses with Bonferroni correction ($p < .025$) were conducted comparing the same body part between conditions. Results revealed that leg length was perceived as significantly different between the *Avatar* and *Own* conditions ($p < .002$), while the difference between the two conditions for the arms was not significant ($p = .24$).

Further analyses were conducted to assess if the presentation order of the stimuli affected participants' responses between conditions (See Figure 4.8 b and c). Two separate ANOVAs were carried out, one for each body part. A two-way factor ANOVA 2 (Order) \times 2 (Condition) for the Arm blocks showed significant main effects of Order [$F(1,19) = 163.91, p < .001; \eta^2_{partial} = .89$] and a trend for the interaction Order \times Condition [$F(1,19) = 4.31, p < .052; \eta^2_{partial} = .19$] while Condition did not show any significant effect [$F(1,19) = 1.47, p = .24; \eta^2_{partial} = .07$]. Regardless of the condition, arms were significantly underestimated in the ascending series more (-6.2%) than the descending series (-1.04%). For the leg blocks, a two-way factor ANOVA 2 (Order) \times 2 (Condition) showed significant main effects of Condition [$F(1,19) = 175.56, p < .001; \eta^2_{partial} = .91$] and Order [$F(1,19) = 15.61, p < .001; \eta^2_{partial} = .45$] but no interaction [$F(1,19) = 1.98, p = .18; \eta^2_{partial} = .07$].

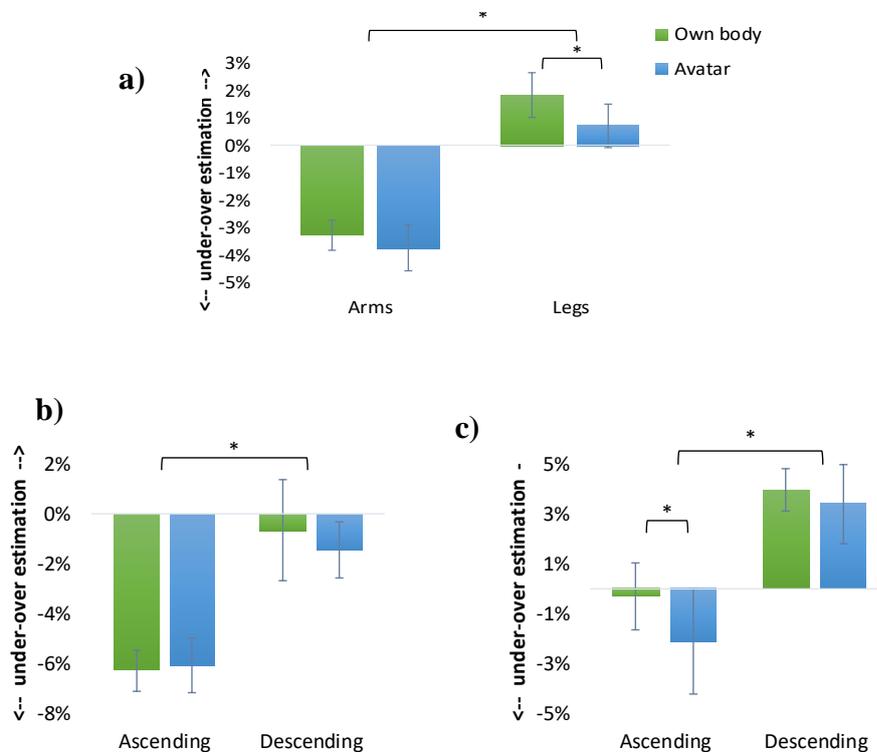
.09]. Participants underestimated the legs in the ascending series (-1.21%) and overestimated them in the descending series (+3.71%). As previously reported, the overestimation was more marked in the *Own* condition compared to the *Avatar* one.

Findings indicate that participants considered images with arms shorter and legs longer than the original own picture and standard avatar as proportional.

4.7 Discussion and Conclusion

Overall, the pattern of distortions found in this experiment was qualitatively similar to the previous findings with the metric task. In detail, the legs were overestimated and the arms were underestimated. In line with previous studies (e.g., Longo & Haggard, 2010) participants were more accurate when performing the depictive than the localization task. This is not surprising as in the depictive task the torso size remained constant across the trials, allowing less margin of errors for the other body parts.

Figure 4.8. Under/overestimation in perceived body parts' length.



a) Point of subjective equality averaged across participants for both arms and legs. *indicates significant difference between conditions and series direction. **b)** Percentage of distortion of arms perceived as “veridical” or “proportional” according to presentation order. **c)** Percentage of distortion of legs perceived as “veridical” or “proportional” according to presentation order.

The pattern of findings reported in the present study may be linked to the particular structural components of the body representation (i.e. *body image*) modulated by the function that specific body parts fulfill when performing actions (*body schema*; Ferretti, 2016; Brozzoli, Makin, Cardinali, Holmes, & Farnè, 2012; Costantini, Ambrosini, Scorolli, & Borghi, 2011; Cardinali, Brozzoli, & Farnè, 2009; Holmes & Spence, 2004; Mora et al., 2018; Cocchini et al., 2018).

Crucially, to fully understand the nature of these distortions, not only the usual action linked to each body part but also ‘where’ this action usually occurs should be taken into account. In fact, in everyday life we use our arms (and hands) mainly in the upper personal and peri-personal space (for example, using objects, writing, eating, gesturing when we talk); therefore, the movements that we perform on a daily basis may affect the content of the *body image* in relation to the function and the feeling of these body parts operating mainly in the upper personal space.

Bearing in mind the operational cogency of the triadic taxonomy of body representation (Schwoebel & Coslett, 2005; Sirigu et al., 1991), it is argued that the coherence of the body representation is the result of a dynamic interaction between sub-components of the *body image* and the *body schema*. Despite the structural representation of the body being mainly based on visual information, it also feeds on semantic information that describes and conceptually identifies the functional purpose of body parts. Ultimately, the type of actions and where these occur in space may modulate the represented physical features of body parts (e.g. limbs; D’Angelo et al., 2018).

The positive correlation between represented arms and torso lengths seems in line with this interpretation and strongly supports the involvement of configural processing in body representation (Reed et al., 2006). From visual inspection of the analogic illustrations in Figures 2 and 4, the perceived location of the tips of the hands does not go much below the hip, suggesting a close relationship between arms/hands and the waist,

which may represent the lower border of the upper body. A similar pattern of distortion was observed for own and avatar's silhouettes in Experiment 2. This point is crucial as it may reconcile findings from recent studies investigating whole body representation in healthy adults. Indeed, also in Fuentes et al. (2013) the arms terminated just above the hip. In other words, the nature of the distortion depends on the relationship between body parts rather than merely its intrinsic size properties. Arms and torso were showing a similar profile as, they are functionally part of the upper body.

The overestimation of the lower legs also appears to be a consistent finding within the study. In Experiment 1c a possible methodological bias was dismissed by providing the participants with a fixed and elevated landmark to be used as anchor points to build the representation of their own body. The amplitude of the error was slightly reduced compared to Experiment 1a; nonetheless, the distortion was still significant. The overestimation of the lower leg seems to fit within the hypothesis mentioned above. The actions we actively perform with legs on a daily basis mainly involve extension movements of the lower section of the leg (e.g., walking, running, kicking; Ferretti, 2016). This interpretation is in line with the data reported and may also explain the different trend of distortions between upper and lower legs.

Data reported in previous studies (i.e. Linkenauger et al., 2015; Sadibolova et al., 2019) showed that individuals tend to generally overestimate their body size. According to these authors, the perceived size of their own body parts depends on tactile sensitivity and physical size (*reversed distortion hypothesis*), so that bodily areas with lower numbers of tactile receptive fields are overrepresented in a cortical body map in order to compensate for this lack of resolution (Linkenauger et al., 2015). According to the authors, this implies that arms and legs, which have similar degree of tactile sensitivity, tend to be more distorted compared to other more sensitive body parts. However, because legs are physically larger than arms, they should be overestimated less. This explanation

accounts for Sadibolova et al.'s (2019) study but does not fully explain the present findings and why Fuentes et al. (2013) reported overestimation of arms and underestimation of legs. It can be argued that the subjective over- or under-estimation of a body part, is not just an intrinsic feature of that segment, but that various factors can interact and modulate the subjective map. Following this line of thought, differences between previous research and the present results are not necessarily in contrast and can be considered within the frame of the *co-construction model* (Pitron et al., 2018; Pitron & de Vignemont, 2017). Task demand characteristics may modulate and influence the direction of the outcome. According to this model, *body schema* and *body image* interact and, the direction of such interaction is modulated by whether or not the body is considered (and represented) as an object in space. By definition, *body schema* consists in sensorimotor representations of the body that guide actions, these actions necessarily occur in space therefore the spatial component is pivotal in the building up of a coherent representation. In this circumstance, *body schema* information may be predominant regardless to whether the task is depictive or metric because body parts need to be represented in space and in relation to one another and this has a direct effect in the representation of body parts size and their spatial relationships. Instead, when the task requires to imagine a body segment length relative to another metric standard, as in Linkenauger et al.'s (2015) and Sadibolova et al.'s (2019) studies, such body parts are represented in more "abstract" terms, where the spatial context is less relevant. In these cases, more "weight" is given to somatosensory information in the construction of a body representation and, as a consequence, a different pattern can be observed. Therefore, according to the *co-construction model*, different body representations result from different interactions between *body schema* and *body image* and the weight that each component has in a specific context and task. However, this model has only been recently

developed and, as such, more systematic investigation is needed to support it with empirical evidence.

The primary aim of the present study was to establish how *body image* and *body schema* can normally interact with each other in a “steady state”. In line with previous studies, it was reported a pattern of distortions that could be explained as the result of a possible influence of typical motor functions even when action is absent. Critically, information concerning the physical aspects of one’s own body is integrated with the peripersonal space and the motor perspective as well as to the motor capabilities of the individual performing an action (Ferretti, 2016; Brozzoli et al., 2012; Costantini et al., 2011). Therefore, the representation of our body and the surrounding space may be influenced by actions that can be potentially/usually performed within such space with specific body parts, even in the absence of a concomitant motor performance. Such a remark is also supported by Cocchini et al. (2018) who showed that motor expertise can modulate and have profound and long-lasting effect on body metric representation.

In conclusion, as for other parts of the body, such as hands (e.g., Longo & Haggard, 2012a, 2012b) and face (Mora et al., 2018), the representation of the body as a whole is distorted and representation of its parts seem to be modulated, at least in part, by their motor functions. These findings imply that the *body image* is not necessarily based on “pictorial” information only, but there is a crucial influence of the *body schema* information that, indirectly, shapes the mental image of our body.

STUDY 2

4.8 Overview

In Study 1 it was shown that distortions associated with specific body parts may be explained in terms of their functional role to operate *on* and interact *with* the environment. Recent accounts also suggest that the functional information of an object, defined as the action that can be performed with it, is embedded in the actual object’s mental

representation. This implies that the object representation encompasses how objects relate to the body. In Study 2, the relationship between body and objects is directly investigated by assessing whether recognition of specific body parts can be facilitated by a brief exposure of objects functionally related. Both behavioural and electrophysiological approaches are used to obtain a deeper understanding of the extent of this possible relationship. The findings confirmed the existence of a link between objects and body parts and provide further support of a functional representation of specific body parts.

4.9 Introduction

Throughout our lives we get in contact and have experience with a number of objects that have different shapes dimensions, weights, colours etc. Some of these characteristics determine whether and how objects can be used for a specific action. Therefore, objects can be characterized not only by their physical characteristics but also by their intrinsic functional properties which can be defined as the ‘actions performed with/on’ an object (Bonfiglioli, 2010). Such dynamic property implies that the mental representation of an object is not only based on perceptual characteristics (what it is) but also on how it can be used (Barsalou, 1999; 2008). A number of studies have shown that tools observation activates motor-related and somatosensory cortical areas (Grafton, Fadiga, Arbib, & Rizzolatti, 1997; Chao & Martin, 2000; Creem-Regehr & Lee, 2005; Proverbio, 2012), highlighting that, even in the absence of actual movement, these areas process objects that have a motor valence. These data suggest that our cognitive system includes a representation of the motor component associated with a given object (e.g., Bub, Masson, & Cree, 2008; Buxbaum & Saffran, 2001). Crucially, this information (the perceptual configuration of the object and motor traces) must be integrated with the representation of our own body (de Vignemont, 2010; Gallagher, 2005; Head & Holmes, 1911; Longo & Haggard 2010) as ultimately, we perform the actions through our body.

Performing an action, it has been shown, can modulate our representation of the spatial extension of the body with respect to the external world (Bassolino et al., 2015; Gallese & Sinigaglia, 2010). Similarly, it has been reported that tool-use modulates the representation of the *body schema* by inducing subjective changes on the metric representation of the own body (Bolognini Casanova, Maravita, & Vallar, 2012; Sposito, Bolognini, Vallar, Posteraro, & Maravita, 2010; Tosi, Romano, & Maravita, 2018; Garbarini et al., 2015; Sposito et al., 2012; Romano et al., 2019).

As discussed at the end of Study 1 (current chapter), the *body image* and the *body schema* are not independent components but they can interact and re-shape each other (Pitron et al., 2018; Pitron & de Vignemont, 2017) therefore, motor information may not only modulate *body schema* (as reported in the studies aforementioned) but also the *body image* (Caggiano & Cocchini, 2020). In line with this hypothesis, Bonfiglioli (2010) reported evidence of implicit association between objects and the body parts involved in the accomplishment of their use, showing that the mental representation of objects includes conceptual links to body parts. Similarly, Borghi and colleagues (2007) reported that the visual presentation of objects activates information regarding how to manipulate and use them. In their study, the authors asked participants to categorize objects that could be manipulated with different hands' grip. Results indicated faster reaction times when the objects were preceded by pictures of hands showing a posture congruent with the type of grip required by the object. These studies suggest that visual stimuli automatically activate motor information; however, the extent of this relationship and its pliancy remain under investigated. Critically, the focus has mainly been on the representation of objects and how it may relate to the body.

In order to shed some light on the role of possible factors that may modulate the representation of the body and its parts, the current study addresses the issue from a different angle: how the body (and body parts) representation relates to objects. The aim

is to explore the role of objects 'function' in body representation by investigating the existing association between body parts and objects.

In a first experiment, participants had to press a different key to decide whether body parts presented on the screen were hands or feet. Both body parts were preceded by a prime image of an object that afforded a hand-based interaction (drum), a foot-based interaction (foot-pump), or a neutral interaction (meaningless object with no obvious hand or foot match). Following the predictions of classic priming paradigms, better performances should be expected when the prime is congruent with the body part required to manipulate the object. The task was then replicated in a second experiment, where the analysis of evoked-related potentials was used to further explore and expand on the behavioural results of Experiment 1. This was done to determine whether the N200 and P300 components were sensitive to the potential interplay of object processing and object-effector knowledge.

4.10 Experiment 3 – Functional priming task

4.10.1 Methods and procedures

4.10.1.1 Participants

Sample size was determined by an a priori power analysis run with G* Power (Faul, et al., 2009), which considered the type of analyses required to assess differences between represented body measures among different conditions by means of analysis of variance. The power analysis for a repeated measures design with three conditions with a $\eta^2_{partial} = .2$, $\alpha = .05$ and power of .95. The analysis suggested a sample of 12 participants to obtain an appropriate effect.

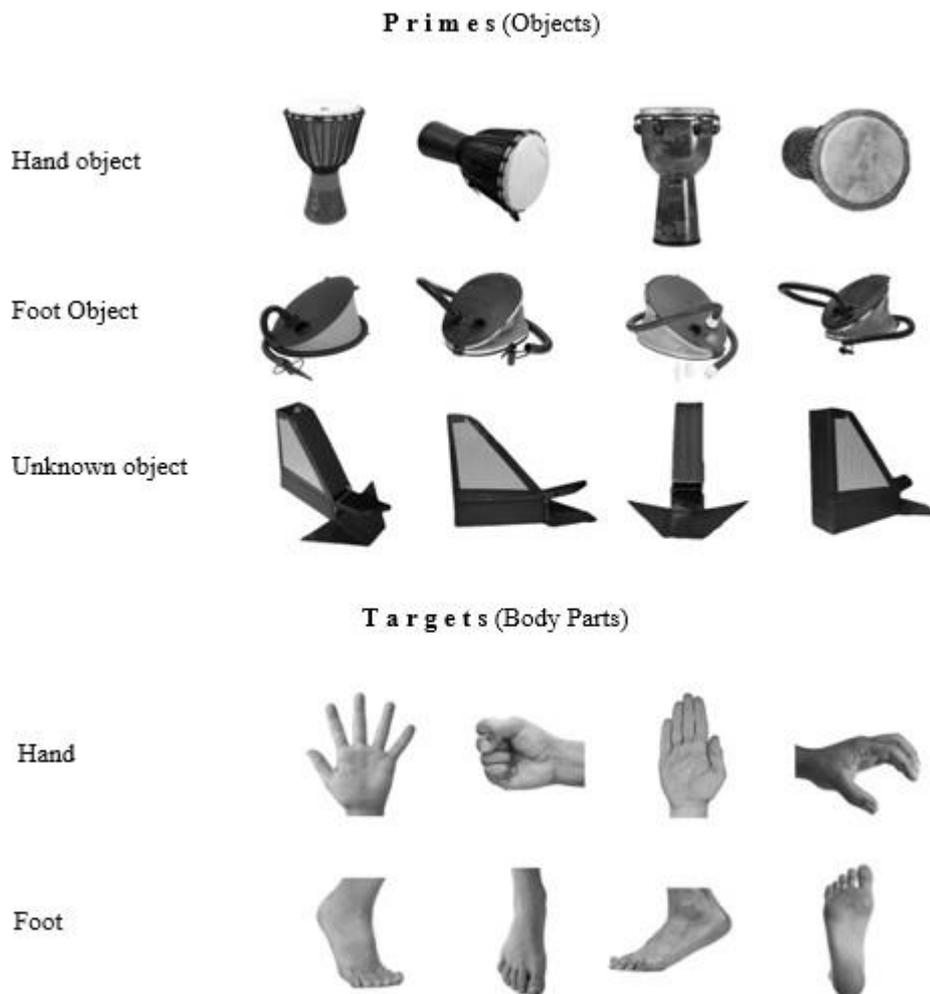
A sample of 15 participants (8 females) took part in the experiment. The Edinburgh Handedness Inventory showed that the participants were right-handed (mean = .95; SD = .07). Their average age was 26.13 (SD = 2.53; range: 22-31). All participants had normal or corrected to normal vision, with no history of neurological or psychiatric illness. They

were naïve to the hypothesis and purpose of the study. The study was approved by the Goldsmiths Ethical Committee and all participants provided written consent.

4.10.1.2 Stimuli and materials

Stimuli consisted of a set of 20 digital greyscale photos. A subset of stimuli illustrated three types of prime objects: a drum, a foot-operated pump (pump) and an unknown object. The unknown object was a custom-built object defined as unfamiliar by an initial pilot study with participants not included in the current experiment. Each prime object was presented in four different perspectives (see Figure 4.9). A second set of stimuli illustrated two target body parts (i.e., hand and foot). Each stimulus (8 x 8 cm)

Figure 4.9. Stimuli (objects and body parts) presented during the task.



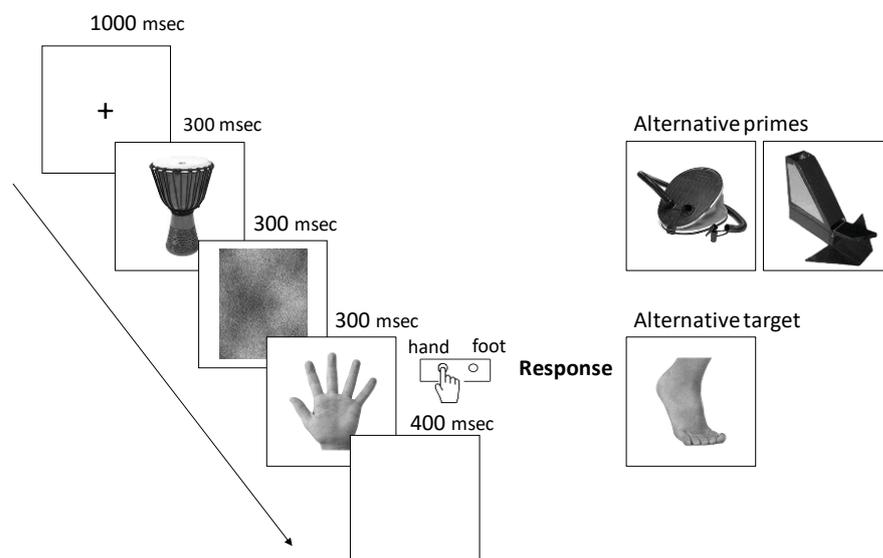
was presented in 4 different perspectives and displayed centrally against a white background on a 19 inches CRT screen (42.06 cm x 23,66 cm). Stimulus presentation and data acquisition were controlled by a custom-made E-Prime 1.1 program (Schneider, Eschman, & Zuccolotto, 2002).

4.10.13 Procedure

Participants sat at approximately 60cm from the screen in an attenuated sound room, performing a priming task. The illustrations of the objects acted as prime stimuli for the target stimuli (i.e. body parts). Each trial started with the presentation of a fixation cross in the centre of the screen. After 1000 msec, one of the primes was displayed for 300 msec followed by a mask (300 msec) and then by one of the targets (see Figure 4.10).

Participants were instructed to decide as quickly as possible, by pressing two keys with their index fingers, whether the target was a ‘hand’ or a ‘foot’. Accuracy and response latencies were recorded. Key-responses were counterbalanced across participants. Depending on the type of the prime preceding the target, the following conditions were considered: i) Related: the prime object preceding the target was coherent

Figure 4.10. Example of *Related* condition. Response buttons were counterbalanced across subjects.



with the body part that is usually used to carry out the action (i.e., drum followed by a hand or pump followed by a foot); ii) Unrelated: the prime object was not coherent with the body part that is usually used to carry out the action (i.e., drum followed by a foot or pump followed by a hand); iii) Neutral: the prime object was not related to the target (i.e., unknown object followed by either a hand or a foot). To ensure that the participants attended the event corresponding to the prime object, they were instructed to withhold their responses (no-go trials) if a ‘star’ was superimposed to the prime object. The experiment comprised a total of 300 trials (i.e. 100 for each condition) of which 60 were no-go trials equally distributed across conditions. Trials were presented in pseudo-randomised order and administered in a single session lasting approximately 15 minutes.

4.10.1.4 Data Analysis

Accuracy (ACC) and response latencies (RL) were obtained from each participant’s performance.

Accuracy and response latencies of experimental trials were first analysed separately and then combined adopting the speed accuracy trade-off formula (Soria Bauser, Suchan & Daum, 2011; Kiss, Driver & Eimer, 2009; Townsend & Ashby, 1983) in order to obtain an integrated performance. Speed-accuracy trade-offs were calculated by dividing the mean RL for the proportion of correct responses, as in the following formula:

$$\text{Speed – accuracy trade off} = \frac{RL (ms)}{\left(\frac{ACC}{100}\right)}$$

According to the formula, low speed-accuracy indicates good performance whereas high speed-accuracy indicates poor performance.

4.10.2 Results

Results of ACC, RLs and speed accuracy trade-offs are reported in Figure 4.11.

4.10.2.1 Accuracy

Participants did not show false alarms when responding to no-go trials. Trials where RLs were more than two standard deviations from the mean of correct trials were removed. Overall, participants correctly responded on 88.4 % of the trials, with better performance for related condition (mean = 91%; SD = 6.9) than unrelated (mean = 87.5%; SD = 9.3) and neutral (mean = 86.6%; SD = 8.5). A 3 (Condition) × 2 (Body parts) ANOVA yielded main effect of Condition [$F(2,28) = 5.44, p = .01; \eta^2_{\text{partial}} = .28$] but not of Body Parts [$F(1,14) = .037, p = .85; \eta^2_{\text{partial}} = .003$] The interaction Condition × Body Part was also not significant [$F(2,28) = 1.63, p = .21; \eta^2_{\text{partial}} = .104$]. Pairwise comparisons corrected for multiple comparisons ($p \leq .016$) on Condition, showed that participants were significantly more accurate in the *Related* compared to the *Unrelated* condition [$t(14) = 2.83, p = .014, d = .72$]. A trend was observed between *Related* and *Neutral* conditions [$t(14) = 2.51, p = .023, d = .65$] while no significant differences were reported between *Unrelated* and *Neutral* conditions [$t(14) = .636, p = .49, d = .16$].

4.10.2.2 Response latencies

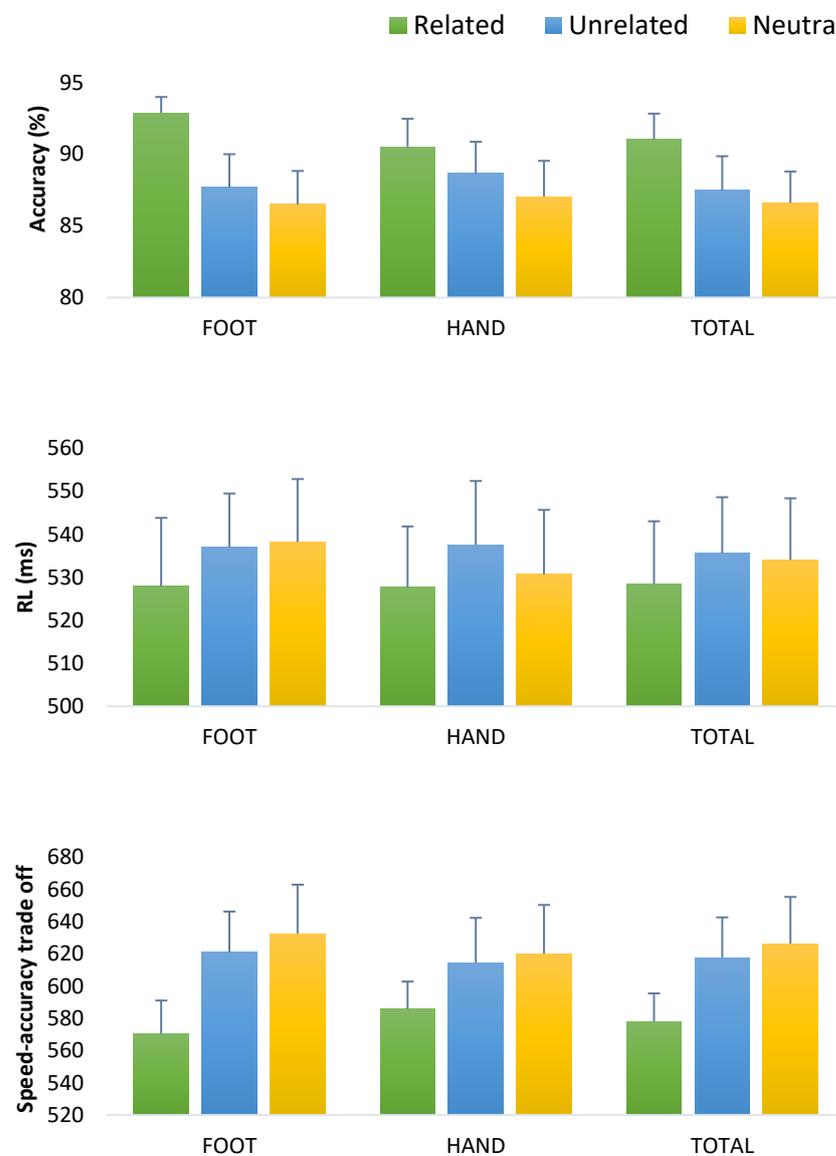
Participants showed similar RLs in the three different conditions (*Related*: 528.5 msec; *Unrelated*: 535.5; *Neutral*: 534.1 msec). Repeated measures ANOVA 3 (Condition) × 2 (Body Part) did not show any significant main effects for Condition [$F(2,28) = 2.05, p = .14; \eta^2_{\text{partial}} = .12$] nor for Body Parts [$F(2,14) = .202, p = .66; \eta^2_{\text{partial}} = .014$]. The interaction Condition × Body Parts was also not significant ($F(2,28) = .503, p = .61; \eta^2_{\text{partial}} = .035$).

4.10.2.3 Speed-accuracy trade off

Similar ANOVA was conducted for speed-accuracy trade off data. A significant main effect of Condition [$F(2,28) = 5.67, p = .009; \eta^2_{\text{partial}} = .28$] was observed, whereas

Body Parts [$F(1,14) = .008, p = .92; \eta^2_{\text{partial}} = .001$] and interaction Condition \times Body Parts [$F(2,28) = 1.19, p = .32; \eta^2_{\text{partial}} = .078$] were not significant. Pairwise comparisons corrected for multiple comparisons ($p \leq .016$) on Condition, showed that participants' performance was significantly better in the *Related* compared to the *Unrelated* condition [$t(14) = 2.92, p = .011, d = .75$]. A trend was observed between the *Related* and *Neutral*

Figure 4.11. Participants' performance (average and error standard) on the Priming task in terms of ACC, RLs and speed-accuracy trade off.



Low speed-accuracy indicates good performance whereas high speed-accuracy indicates poor performance.

conditions [$t(14) = 2.54, p = .023, d = .66$]. Differences between *Unrelated* and *Neural* conditions were not significant [$t(14) = .692, p = .49, d = .18$].

4.10.3 Preliminary discussion

The Experiment 3 investigated the existence of functional links between objects and body parts and whether this is mediated by the type of action. Results showed that motor aspects of an object can modulate recognition of its body effectors. Specifically, participants showed a better performance on trials in the *Related* compared to the *Unrelated* conditions, suggesting a specific link between object-action-effector. Since performance on the *Neutral* condition was not significantly different from the *Unrelated* condition and there was only a trend between *Related* and *Neutral* conditions, it is difficult to establish whether the findings should be interpreted as a benefit for object-effector congruency or a detrimental effect for object-effector incongruence. It could be also possible that both interpretations are correct, where performance in the unrelated trials has been ‘penalised’ whilst performance in related trials has been advantaged. In either case, all these possible interpretations imply a pre-existing link between an object and its common body effector. In line with Bonfiglioli’s (2010) study, it seems that mental representations of objects comprise functional links with the body parts normally used to perform the related action. Similar body-action networks have been observed in language, where different areas of the motor homunculus were activated when participants passively read related action words (e.g., foot area while reading the word ‘walking’; Pulvermüller, 2005).

Furthermore, studies on tool embodiments have shown that a relatively short training requiring action can lead to changes in body representation and in particular in *body schema* (e.g. Iriki, Tanaka, & Iwamura, 1996; Maravita & Iriki, 2004). Moreover, a recent study has underlined how this modulation is crucially linked to the specific type of action required (Romano et al., 2019). Therefore, while there is growing evidence of

functional networks between actions and body parts, it remains unclear the extent and flexibility of this modulation.

During the last decade, a number of studies have shown that the extrastriate cortex contains regions that are sensitive to the perception of human bodies and body parts: the extrastriate body area (EBA) (Downing et al., 2001) and the fusiform body area (FBA) (Peelen & Downing, 2005; Schwarzlose et al., 2005). Further studies have also suggested that the organizational principle of body parts selectivity may reflect body parts functional properties coded as ‘motor effectors’ (Bracci et al., 2012; Bracci et al., 2015; Bracci & Peelen 2013; Lingnau & Downing, 2015). In line with this hypothesis, a recent study on functional and structural connectivity profiles of EBA, indicated strong connection between EBA and parietal cortex (Zimmerman, Mars, de Lange, Toni, & Vernhagen 2018). Such anatomical evidence seems to further support the involvement of EBA in action planning and goal-oriented behaviour (Zimmermann, Meulenbroek, & de Lange, 2012, Zimmermann, Verhagen, de Lange, & Toni, 2016).

The functional specialisation of EBA has been also documented in electrophysiological literature. Recent studies have identified a body-specific cortical negative evoked response that peaks around 200 ms after stimulus onset (N190). This component has been observed bilaterally over the occipito-temporal electrodes (PO7, PO8, P7, P8, P9, P10) (Sadeh, Pitcher, Brandman, Eisen, Thaler, & Yovel, 2011; Rossion & Jacques, 2008) and source localization has identified EBA to be the neural generator of such component (Thierry et al., 2006; Giabbiconi et al., 2016).

In Experiment 4 the *functional hypothesis* is further explored by means of the analysis of evoked-related potentials adopting of same paradigm aforementioned. It is predicted to observe a modulation of the N200-P300 complex during the visual presentation of a body parts, according to whether they are preceded by a functional-related or functional-unrelated object. A second set of analysis was also conducted on

the ERPs related to the primes. However, specific expectations were not set since the visual presentation of objects with and without motor valence has not been previously investigated in EBA by means of evoked-related potentials technique.

4.11 Experiment 4 – Functional priming task (ERP analysis)

4.11.1 Methods and procedures

4.11.1.1 Participants

Twenty-one participants were recruited for the experiment. Of these, data from two participant were irredeemably corrupted and could not be used for analysis. Therefore, a final sample of 19 right-handed participants (10 females) was considered. Sample size was in accordance with power analysis conducted for the Experiment 4 and in line with previous studies on EBA event-related potential components (Thierry et al. 2006; Moreau et al. 2018).

The Edinburgh Handedness Inventory has been used to assess the participants' handedness showing that they were all right-handed (mean = .98; SD = .05). Their average age was 26.71 (SD = 2.76; range: 22-32). All participants had normal or corrected to normal vision, with no history of neurological or psychiatric illness. They were naïve to the hypothesis and purpose of the study. The study was approved by the Goldsmiths Ethical Committee and all participants provided written consent.

4.11.1.2 Materials and methods

The set of stimuli and experimental procedure were the same as in the previous Experiment 3. Because the focus of the investigation was electroencephalogram recording during passive observation, to ensure that the participants paid attention to the task and in particular attended the event corresponding to the prime object, they were instructed to respond only if a 'star' was superimposed to the prime object. The experiment comprised a total of 360 trials of which 60 (17%) required participants to

respond. Trials were presented in pseudo-randomised order and administered in a single session divided in two blocks lasting approximately 15 minutes.

4.11.1.3 EEG recording and analysis

EEG was continuously recorded using a BioSemi ActiveTwo amplifier from 64 Ag–AgCl electrodes placed according to the extended 10–20 system. Two electrodes were placed on the ear lobes and were used for off-line re-referencing of the EEG signal. Four electrodes, placed at the left and right lateral canthi and above and below the left eye, were used to monitor vertical (i.e. blinks) and horizontal (i.e. saccades) eye movements, respectively. Offline pre-processing and analysis of the EEG data was conducted using EEGLAB and ERPLAB.

It has been reported that the executing movements activate EBA (Astafiev et al., 2004). Therefore, to minimize the effect of a potential motor interference on EBA, analyses were conducted only on trials where participants did not provide a response. Data were filtered with a 0.1–40 Hz band-pass filter. Computerized artefact rejection was performed to discard epochs in which eye movements, excessive muscle potentials or amplifier blocking occurred. Across all participants, the rejection rate was on average of about 10%.

Two sets of epochs were extracted to perform independent analysis on ERPs prime-related and target-related. Both sets of epochs ranged from -100 msec to 500 msec and baseline correction, between -100 to 0 from stimulus onset, was conducted prior data extraction.

4.11.2 Results

In previous studies, the face-selective N1 has been termed the N170, whereas the N1 for bodies has been labelled the N170 or the N190 (Minnebusch et al., 2009; Peelen & Downing, 2007; Righart & de Gelder, 2007; Thierry et al., 2006; Stekelenburg & de Gelder, 2004). Faces, bodies and body parts usually elicit a strong N1 component at

occipito-temporal sites P8, PO8, and P10 (Rossion & Jacques, 2008). In the present work, general term N200 is used to refer to the fact that the negative component of interest peaked at around 200 msec post target.

4.11.2.1 ERPs related to target

Posterior N200

Analysis were conducted after baseline correction -100 to 0 msec before target presentation. The mean amplitude of the N200 component was measured bilaterally at posterior sites (P7, P8, P9, P10, PO7 and PO8) between 150 and 300 msec (150 msec time window) post target. Peak latency averaged across the electrodes considered was 236 msec post target.

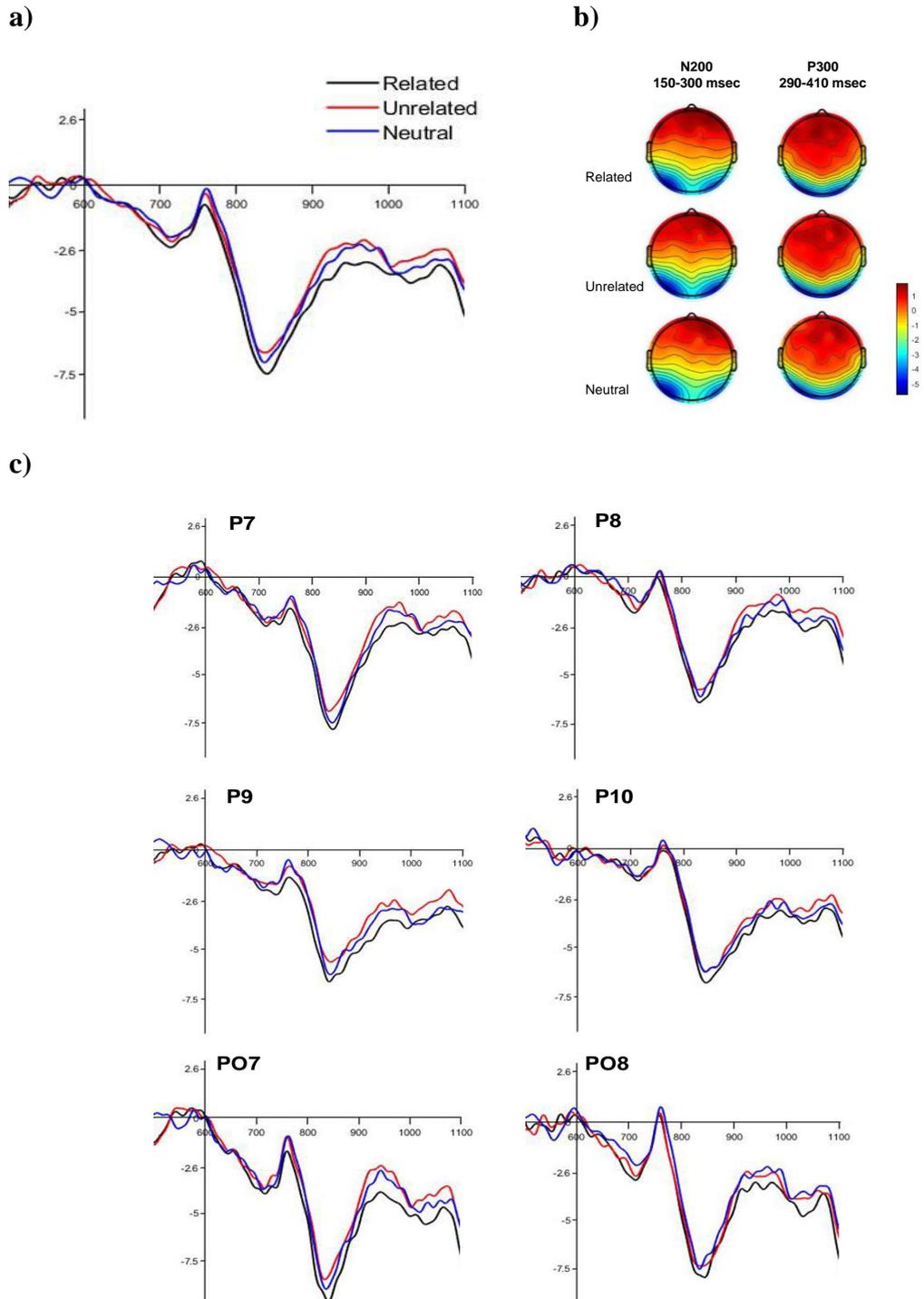
ERP data were subjected to repeated-measures ANOVA. The factors considered were “Condition” (*Related*, *Unrelated* and *Neutral*), “Electrode” (P7/P8, P9/P10 and PO7/PO8), and “Hemisphere” (left and right). Multiple comparisons of means were corrected with Bonferroni adjustment. Figure 4.12 shows the grand-average waveforms (N= 19) recorded in response to whether the targets were related, unrelated, or “neutral” to the prime over posterior scalp sites.

A 3 (Condition) \times 3 (Electrode) \times 2 (Hemisphere) ANOVA yielded main effect of Condition [F(2,36) = 3.69, p = .035; $\eta^2 = .17$] and Electrode [F(2,36) = 14.26, p < .0001; $\eta^2_{partial} = .35$] but not Hemisphere F(1,18) = 2.36, p = .14; $\eta^2_{partial} = .12$]. Two-way interactions Electrode \times Hemisphere [F(4,36) = 7.23, p = .002; $\eta^2_{partial} = .27$] and Hemisphere \times Condition [F(2,36) = 3.93, p = .029; $\eta^2 = .18$] were significant.

Pairwise comparisons on Condition, showed more negative ERP responses to *Related* (-4.71 μ V) than *Unrelated* (-4.14 μ V) [t(18) = 3.43, p = .009, d = .79] and *Neutral* (-4.13 μ V) [t(18) = 2.26, p = .036, d = .52]. The difference between *Unrelated* and *Neutral* was not significant [t(18) = .017, p = .98, d = .003]. Post hoc analysis on Electrode showed that recorded ERPs on the electrodes PO7 and PO8 were significantly larger (-5.09 μ V)

than those recorded on P7 and P8 ($-4.08\mu\text{V}$) [$t(18) = 4.69, p < .0001, d = 1.07$] and P9 and P10 ($-3.79\mu\text{V}$) [$t(18) = 4.02, p = .003, d = .92$]. P7/P8 and P9/P10 did not show significant differences in voltage recording [$t(18) = 1.32, p = .21, d = .31$].

Figure 4.12. Grand average waveforms for 19 participants.



a) Grand average waveforms collapsed across the six channels considered. **b)** Scalp topographies for each condition **c)** Grand average waveforms for each channel.

Electrode \times Hemisphere showed that on the left hemisphere, recorded ERPs on the electrode PO7 were significantly larger ($-5.66\mu\text{V}$) than those recorded on P7 ($-4.54\mu\text{V}$) [$t(18) = 5.15, p < .0001, d = 1.18$] and P9 ($-3.85\mu\text{V}$) [$t(18) = 6.83, p < .0001, d = 1.57$]. Differences were observed also between P7 and P9 [$t(18) = 3.39, p = .009, d = .78$]. On the right hemisphere, recorded ERPs were significantly different between PO8 ($-4.53\mu\text{V}$) and P8 ($-3.62\mu\text{V}$) only [$t(18) = 3.41, p = .009, d = .72$]. Hemisphere \times Condition showed that on the left hemisphere ERPs recorded for the *Related* condition ($-5.15\mu\text{V}$) were significantly different from *Unrelated* ($-4.37\mu\text{V}$) [$t(18) = 4.08, p = .003, d = .94$] and *Neutral* ($-4.53\mu\text{V}$) ones [$t(18) = 2.91, p = .042, d = 1.04$] while on the right hemisphere a significant difference was observed between *Related* ($-4.25\mu\text{V}$) and *Neutral* ($-3.73\mu\text{V}$) only [$t(18) = 2.16, p = .045, d = .66$]. *Related* and *Unrelated* ($-3.91\mu\text{V}$) showed a trend [$t(18) = 2.08, p = .052, d = .48$].

Posterior P300

P300 component was measured at posterior sites (P7, P8, P9, P10, PO7 and PO8) between 290 and 410 msec post target (120 msec time window). Peak latency averaged across the electrodes considered was 356 msec post target.

ERP data were subjected to repeated-measures ANOVA. The factors were “Condition” (Related, Unrelated and Neutral), “Electrode” (dependent on ERP component of interest), and “Hemisphere” (left and right).

A 3 (Condition) \times 3 (Electrode) \times 2 (Hemisphere) ANOVA yielded main effect of Condition [$F(2,36) = 4.87, p = .013; \eta^2_{\text{partial}} = .21$] and Electrode [$F(2,36) = 11.89, p < .0001; \eta^2_{\text{partial}} = .39$] but not Hemisphere [$F(1,18) = .646, p = .43; \eta^2_{\text{partial}} = .035$]. None of the interactions were significant.

Pairwise comparisons on Condition, showed more positive ERP responses to *Unrelated* ($-2.75\mu\text{V}$) than *Related* ($-3.54\mu\text{V}$) [$t(18) = -3.81, p = .003, d = .87$]. Post hoc analysis on Electrode showed that recorded ERPs on the electrodes P7 and P8 were

significantly larger ($-2.17\mu\text{V}$) than those recorded on P9 and P10 ($-3.54\mu\text{V}$) [$t(18) = 5.31$, $p < .0001$, $d = 1.22$] and those recorded on PO7 and PO8 ($-3.56\mu\text{V}$) [$t(18) = 5.07$, $p < .0001$, $d = 1.17$].

4.11.2.2 ERPs related to primes

In this second set of analysis, the terms N100 and P200 are used to refer to the fact that the negative and positive components of interest peaked at around 175 msec and post 268 msec post prime, respectively.

Posterior N100

The mean amplitude of the N100 component was measured bilaterally at posterior sites (P7, P8, P9, P10, PO7 and PO8) between 140 and 200 msec from stimulus onset. ERP data were subjected to repeated-measures ANOVA. Peak latency averaged across the electrodes and primes was 175 msec post target.

The factors considered were “Object” (Drum, Foot-pump and unknow), “Electrode” (P7/P8, P9/P10 and PO7/PO8), and “Hemisphere” (left and right). Multiple comparisons of means were corrected with Bonferroni adjustment. Figure 4.13 shows the grand-average waveforms ($N = 19$) recorded in response to whether the primes were drums, foot pumps or “unknown” object over posterior scalp sites.

A 3 (Object) \times 3 (Electrode) \times 2 (Hemisphere) ANOVA yielded main effect of Object [$F(2,36) = 8.36$, $p = .001$; $\eta^2_{\text{partial}} = .33$] and Electrode [$F(1.42, 25.59) = 18.42$, $p < .0001$; $\eta^2 = .51$] but not Hemisphere [$F(1,18) = .791$, $p = .39$; $\eta^2_{\text{partial}} = .04$]. Two-way interactions Electrode \times Object was significant [$F(2.05, 36.99) = 9.56$, $p < .0001$; $\eta^2_{\text{partial}} = .35$].

Pairwise comparisons, showed smaller ERP responses for the Unknown object ($.71\mu\text{V}$) compared to both the Drum ($2.063\mu\text{V}$) [$t(18) = 3.31$, $p = .012$, $d = .76$] and the Foot-pump ($2.13\mu\text{V}$) [$t(18) = 4.19$, $p = .003$, $d = .96$]. Post hoc analysis on Electrode showed that recorded amplitudes on the electrodes PO7 and PO8 were significantly larger

(2.87 μ V) than those recorded on P7 and P8 (.84 μ V) [t (18) = 6.57, $p < .0001$, $d = 1.51$] and P9 and P10 (1.21 μ V) [t (18) = 3.65, $p = .006$, $d = .84$]. P7/P8 and P9/P10 did not show significant difference in voltage recording.

The interaction Electrode \times Object showed that on the electrodes P7/P8, recorded ERPs for the Unknown object were significantly smaller (-.05 μ V) than both Drum (1.22 μ V) [t (18) = 3.25, $p = .004$, $d = .75$] and Foot pump (1.33 μ V) [t (18) = 4.13, $p = .003$, $d = .95$]. A similar pattern was observed on the electrodes PO7/PO8 Unknown object were significantly smaller (1.61 μ V) than both Drum (3.73 μ V) [t (18) = 3.87, $p = .003$, $d = .89$] and Foot pump (3.25 μ V) [t (18) = 4.01, $p = .003$, $d = .92$] while on P9/P10 recorded ERPs were significantly different between the Unknown object (.56 μ V) and the Foot pump only (1.83 μ V) [t (18) = 3.82, $p = .003$, $d = .88$].

Posterior P200

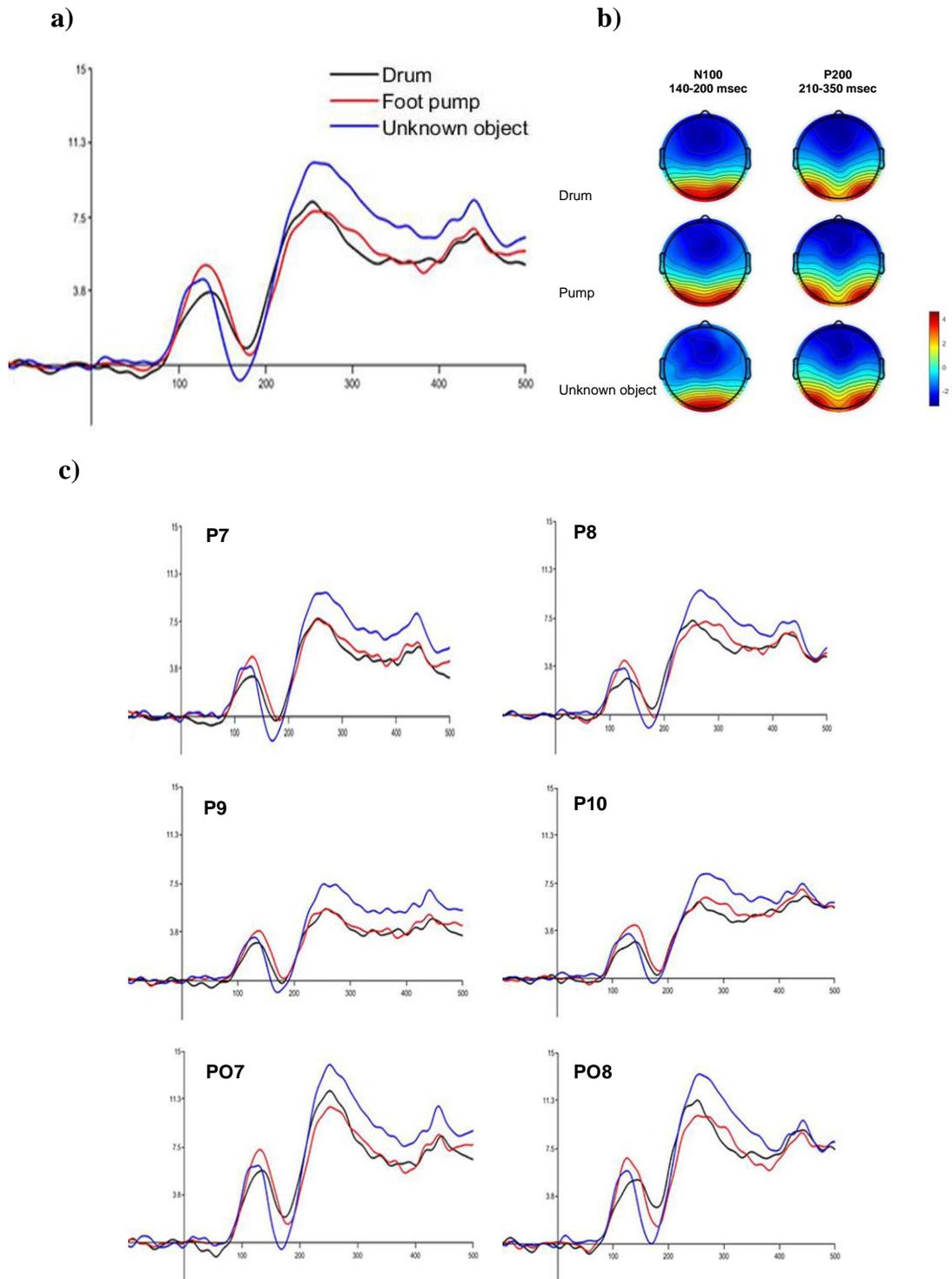
Again, the mean amplitude of the P200 component was measured at posterior sites (P7, P8, P9, P10, PO7 and PO8) between 210 and 350 msec from prime onset. Peak latency averaged across the electrodes considered was 268 msec post target.

ERP data were subjected to repeated-measures ANOVA. The factors were “Object” (Drum, Foot-pump and Unknown object), “electrode” (dependent on ERP component of interest), and “hemisphere” (left and right). Multiple comparisons of means were with Bonferroni adjustment. Figures 3 and 4 shows the grand-average waveforms (N= 19).

A 3 (Object) \times 3 (Electrode) \times 2 (Hemisphere) ANOVA yielded main effect of Object [F(2,36) = 17.24, $p < .0001$; $\eta^2_{partial} = .49$] and Electrode [F(2,36) = 36.82, $p < .0001$; $\eta^2 = .67$] but not Hemisphere F(1,18) = .371, $p = .55$; $\eta^2_{partial} = .02$]. Two-way

interactions Object \times Electrode was significant [$F(2.14, 38.52) = 6.36, p = .003; \eta^2_{\text{partial}} = .26$].

Figure 4.13. Grand average waveforms for 19 participants.



a) Grand average waveforms collapse across the six channels considered. **b)** Scalp topographies for each condition **c)** Grand average waveforms for each channel.

Pairwise comparisons corrected for multiple comparisons on Object, showed larger ERPs responses for the Unknown object (8.51 μ V) compared to both Drum (6.52 μ V) [t(18) = 5.14, $p < .0001$, $d = 1.18$] and Foot pump (6.59 μ V) [t(18) = 4.28, $p < .0001$, $d = .98$]. Post hoc analysis on Electrode showed that recorded RPs on the electrodes PO7 and PO8 were significantly larger (9.59 μ V) than those recorded on P7 and P8 (6.67 μ V) [t(18) = 6.67, $p < .0001$, $d = 1.53$] and P9 and P10 (5.35 μ V) [t(18) = 6.57, $p < .0001$, $d = 1.51$]. P7/P8 and P9/P10 did also show a significant difference [t(18) = 3.31, $p = .012$, $d = .76$]. The interaction Object \times Electrode showed that on all electrodes, recorded ERPs for the Unknown object were significantly larger than both Drum and Foot pump.

4.12 Discussion and Conclusions

By means of ERPs analysis, Experiment 4 provided a deeper insight into the functional link between objects and effectors. Behavioural results from Experiment 3 showed a significant difference in participants' performance when they had to discriminate hands or feet between *Related* and *Unrelated* conditions. The findings corroborated the "functional" hypothesis according to which such difference can be the results of an implicit link between objects and body parts. However, it was unclear whether the findings were the result of a facilitation in the *Related* condition or a detrimental effect of the *Unrelated* condition.

In Experiment 4, electrophysiological data highlighted a systematic modulation of the N200 component during body part visual presentation. The results showed similar amplitudes for the *Unrelated* and *Neutral* conditions, which both significantly differed from the *Related* one. These results are in line with previous studies on the relations between objects and function (Bonfiglioli, 2016; Chao & Martin, 2000; Creem-Regehr & Lee, 2005). Furthermore, the finding agrees with previous ERP literature describing a posterior negative deflection peaking around 200–250ms after stimulus onset observed when subjects view recognizable and familiar images such as words, pictures, faces and

bodies (Martín- Loeches, 2007; Peelen & Downing, 2005; Downing et al., 2001). It has been proposed that such posterior component reflects early semantic processing and is sensitive to semantic expectancy (Dien, Frishkoff, Cerbone, & Tucker, 2003). The experimental paradigm was developed so that targets were always body parts therefore, differences between conditions can only be explained considering the priming associated with the target. In this context, results seem to suggest that when objects are congruent with the effector, they facilitate the recognition of the body part involved in their use: body parts are perceived as ‘functionally’ appropriate relatively to the primes. The difference between the *Related* and both *Unrelated* and *Neutral* conditions might be the result of implicit participants’ expectation associated with the objects presented that is matched in the *Related* condition. In this view, it could be argued that the data obtained may be the result of a pre-existing association of the objects and the body parts based on experience and familiarity.

In a later time-window, a second marker was observed in the form of a larger P3 in response to body parts for the *Unrelated* and *Neutral* conditions. However, only the *Unrelated* condition significantly differed from the *Related* one. This activity can be interpreted as a sign of increased attention allocation toward the body part that is ‘incongruent’ to the prime. Indeed, the P300 component is thought to reflect neural activity related to attentional and working memory processes (Polich & Kok, 1995) and increased excitability of the posterior attention system due to orienting of visual attention (Soltani & Knight, 2000). Classically, P300 amplitude gets larger as target probability gets smaller (Donchin, 1981, Luck, 2005). In this view, if it is true that a functional link exists between specific objects and body parts, then the association in the *Unrelated* condition could have been - subjectively speaking – perceived as less probable resulting in a larger P300. Crucially, probability in this particular circumstance was not based on the number of trials or targets presented (as in a classic oddball paradigm) as they were

all the same number across conditions. Therefore, data may suggest that participants interpreted targets in the *Related* condition “more probable” due to the congruent association between the object and the body part. This interpretation may also explain why P300 amplitudes were not significantly different between the *Neutral* and *Related* conditions. In the *Neutral* condition, due to the novelty of the object and therefore, lack of familiarity, such incongruence might not have been perceived as strong as in the *Unrelated* due to the ambiguity of the object.

The analysis of ERPs related to primes seem to suggest that the ERPs responses for the body parts in the *Unrelated* and *Neutral* condition, despite similar, may be the result of two different mechanisms: one underpinning a pre-existing association (*Unrelated*) and one based on the lack of familiarity (*Neutral*). In support of this claim, a larger N100-P200 complex for the ‘unknown object’ compared to the drums and foot-pumps was observed. It is reasonable to assume that the ‘unknown object’, being different and therefore more salient among the prime sets, might have attracted attention more than the other two objects. Indeed, participants did not have any experience of the object and the shape was custom made to avoid familiarity in terms of physical characteristics with other geometrical figures. The difference between the familiar objects and the unfamiliar one might index an attentional process that was stronger for the unknown object (more salient) (Rugg & Curran, 2007). Because, both drum and foot pump elicited similar ERPs it is reasonable to exclude that the differences observed are only due to the visual characteristic of the objects (both drums and foot pumps have different shapes). This observation provides additional support to the original assumption of participants’ lack of familiarity with the ‘unknown object’. These data can also explain why behaviourally (Experiment 3) *Related* and *Neutral* conditions did not differed significantly. The object-body part congruency seems to facilitate early visual recognition; however, this effect is

quickly modulated by a second process that weights incongruence strongly based on the previous knowledge of the objects.

Overall, these findings provide new electrophysiological evidence that perceptual contents and action plans are coded as single units in a common representational map (Hommel, 2015; Hommel, Müsseler, Aschersleben, & Prinz, 2001).

In the literature on *embodied cognition*, it has been suggested that our interactions with the environment may play a fundamental role in the development of our perceptual and cognitive abilities (Shapiro, 2019; Fossataro, Bruno, Giurgola, Bolognini, & Garbarini, 2018; Garbarini & Adenzato, 2004; Martinaud, Besharati, Jenkinson, & Fotopoulou, 2017; Wilson, 2002). Therefore, it would not be surprising that the way we interact and navigate in the environment may affect the way we represent our body, which is, beyond any doubt, the only means by which we can perform such activities. The primary aim of this chapter was to critically evaluate the extent of such possibility.

With a set of four experiments, Study 1 highlighted that the represented metrics of specific body parts seem to be linked to the function that body parts fulfil when performing actions. Experiment 2 showed that this configuration is also maintained at more explicit visuo-perceptual level.

The perceptual component was further assessed in Study 2. The behavioural results from Experiment 3, suggested that the representational content of some body parts (i.e. hands and feet) may carry information about motor functions. This interpretation seems to find further confirmation following the analysis of specific ERPs classically associated with body perception (Experiment 4).

In light of the results from Study 1 and 2, a critical interaction between *body image* and *body schema* seems to emerge: the representation of specific body parts seems to be strongly influenced by their functional role. In this view, arms, legs, hands and feet are not merely parts of *a* body but they are defined and represented, as effectors. The

information related to actual (and potential) actions is intrinsically carried in the representation of these body parts.

At this point, it can be argued that in both studies the motor component has not been controlled, making the arguments susceptible to critics. It should be noted though the importance of setting a 'baseline' to understand body representation in a 'steady' state. Therefore, in the next chapter the role of action is systematically explored.

Chapter 5

Modulation: do actions shape body representation?

STUDY 3

5.1 Overview

In Chapter 4 it was described how, even ‘at rest’, the link with potential motor information may play a crucial role in shaping the conscious representation of our own body. The evidence provided, point to a *functional* view of the body representation which arises from a plausible interaction between the *body schema* and the *body image*. The present chapter reports three experiments designed to test the effect of motor training in modulating body representation. The results provide evidence for a critical effect of action onto the conscious representation of the body.

5.2 Introduction

There is no doubt that, as living organisms, we constantly move and perform actions to interact with the external environment. There is a growing consensus that body representation shares similarities with the representation of the surrounding space with respect to its being action-oriented (Maravita & Iriki, 2004). As clearly pointed out by Gallese & Sinigaglia (2010), the nature of the *body schema* does not consist only of sensory attributes, but also of motor action-oriented qualities which intrinsically define such body representation component. In this sense, it is precisely because of these

qualities, that actions may modulate the perceived localization and length of body segments and therefore, shape how the body is represented (Gallese & Sinigaglia, 2010). This observation highlights the potential interaction between *body image* and *body schema*. As showed in Study 1 (Chapter 4), the represented body metrics and configuration (i.e. relationship between specific body parts) are systematically distorted. The direction of distortion, it was argued, seems to reflect the functional characteristics of specific body parts defined as the type of motor actions that can be potentially performed in space. In support of this claim, recent findings on the analysis of the effect of tool use strongly suggest that tools can shape one's own *body schema*, extending the reaching space. Studies on non-human primates have shown that five minutes of tool use are enough to modify the visual receptive fields of bimodal visuo-tactile neurons in parietal regions, as if the tool used was incorporated into the paw. Crucially, when the macaques stopped using the tool, the visual receptive fields returned to their previous extension indicating that tools can shape one's own *body schema* by extending the reaching space (Iriki et al., 1996; Ishibashi, Hihara, & Iriki, 2000). Similar results have been reported also in humans. Consistent with the hypothesis of a 'malleable' *body schema*, Maravita and colleagues (2002) showed that prolonged active tool-use modulates visuo-tactile spatial integration, so that visual stimuli located at the end of a 75 cm long tool interacted with tactile stimuli delivered on the tool's handle (Maravita, Spence, Kennet, & Driver, 2002). More recently, it has been shown that tool-use not only alters the kinematic profile of arm movements in a reach-to-grasp task but, more importantly to the scope of the present study, also the subjective perception of the arms' length (Cardinali, Frassinetti, et al., 2009). Similarly, Sposito et al. (2010) showed that after a training with a 60 cm long tool, participants showed an increase of the represented length of the arm handling the tool. Notably, the majority of studies on tool-use have investigated the effect of tools in modulating body representation without explicitly addressing the

motor component required to operate the tool and perform the appropriate action. A recent study by Bruno et al. (2019) addressed this point by evaluating the effect of active and passive use of tools on body metrics. To do so, the authors developed a paradigm in which participants carried out two different training sessions. In one session, participants had to actively use a tool; in a second one, participants were asked to maintain a relaxed posture during the tool-use while, by means of robotic assistance, the action was passively performed. Interestingly, compared to the baseline, participants exhibited a significant increase in the perceived arm length after the active training session, while no modulation was observed after the passive one. These results clearly suggest that the simple and passive reproduction of tool action is not enough to impact on subjective body metrics; the effect occurs insofar as the action is actively enforced by the agent (Bruno et al., 2019).

In light of the studies discussed above, there seems to be strong evidence that the active use of tools critically impacts on body representation. This effect fits well into the view of plasticity of *body schema* and - according to Study 1 - interaction with *body image*. Was this the case, it should be argued that the modulation of body representation is not, strictly speaking, due to the use of tools *per se*, rather is the action performed to use such tools. Crucially, as demonstrated by Bruno et al. (2019), motor programs must be actively represented and performed in order to modulate body representation. Other evidence supporting this view comes from a study conducted by Bassolino et al. (2015), which investigated the effect of over-use and immobilization of the upper limb on the perceived arm dimension. The authors found that limb overuse resulted in participants representing their arm longer compared to the baseline, while a prolonged immobilization did not have any effect on the represented length, suggesting a link between body size perception, space and the possibilities of action (Bassolino et al., 2015; D'Angelo et al., 2019). Indeed, two studies from Longo and Lourenco (2009, 2007) have shown that the

perceived length of the arms and its motor action-oriented qualities can systematically modulate the ‘extent’ of peripersonal space. These findings provide interesting insight on the role of action in shaping body representation and, because actions occur *in* space, set the ground to address the representation of body parts in different portions of space. As suggested in the previous chapter (Study 1), if the metric representation is associated with where actions usually occur, then changing the location of where an action is performed can potentially modulate the represented size of body part involved in the action execution. Therefore, to better understand the relevance of the acting space in the context of body representation, in a first experiment (Experiment 5) the subjective size of the body was compared before and after two similar motor trainings that took place in two different sectors of space. In one condition participants were asked to carry out a sorting task in the upper sector of space (i.e. on a table) while in a second condition the task was carried out on the floor (lower sector of space). By means of a modified version of the BIT (Caggiano & Cocchini, 2020; Fuentes et al. 2013), the analyses of the absolute differences across the representations before and after trainings provided evidence of a systematic modulation of the dimension of the arms when the action was performed in a ‘less canonical’ position (i.e. lower sector of the space). Furthermore, and perhaps more interestingly, such modulation was not restricted only to the arms but impacted on the overall proportions of body configuration.

Critically, when looking at the role of action in shaping the body, besides to *where* an action occurs, a further consideration concerns *how* it is performed. Indeed, actions require the integration of motor information with the representation of our own body (de Vignemont 2010; Gallagher 2005; Head & Holmes 1911; Longo & Haggard 2010). Therefore, it is reasonable to assume that different motor patterns, performed with the same body part, can differentially modulate the body metric representation. In a second experiment (Experiment 6), it was tested whether actions, that engage different segments

the upper limb, differentially affect body metrics and whether, in line with the studies mentioned above, the use of tools may further mediate the modulation of body metrics. To do so, the arm bisection task (Garbarini et al. 2015; Sposito et al. 2012, 2010; Tosi et al. 2018; D'Angelo et al., 2019) was adopted to measure the subjective forearm length before and after two training sessions that required more proximal or more distal motor control of the arm. The results showed a crucial role of motor programming in the dynamic modulation of body representation and that the use of tool further enhance such modulation.

Lastly, to further expand on findings of Study 2, Experiment 7 explored whether the use of a previously unknown object can selectively facilitate the visual recognition of the body part used to operate the object. Specifically, participants were asked to use an unfamiliar object with a hand or a foot and then were tested on the same priming task described in Study 2 (Chapter 4). As originally argued by Gibson (1979), objects elicit certain action possibilities that serve to ground functionally adequate behaviour. It follows that by systematically manipulating the behaviour towards an entirely new object, it should be possible to trigger a selective link between the body part involved in the use of the object and the object itself as a result of the motor experience. The results clearly showed that participants categorized the visually presented hands and feet more effectively when these were congruent with the type of training carried out.

Altogether, the findings reported in the present study, provide interesting insight on the role of action in shaping body representation

5.3 Experiment 5 – Localization task following motor training in different spatial locations

5.3.1 Methods and procedures

5.3.1.1 Participants

Sample size was determined by an a priori power analysis run with G* Power (Faul et al., 2009), for a repeated measures, within-between interaction design with two groups

and 10 body parts to estimate with medium size $\eta_{partial}^2 = .04$, $\alpha = .05$ and power of .95.

The analysis suggested a sample of 32 participants to obtain an appropriate effect.

Thirty participants (20 females) took part in the experiment; their age ranged from 20 to 30 years, with a mean of 24.2 years (SD = 2.8). All participants were right-handed (Edinburgh Inventory mean score = 0.95; SD= 0.11). The study was approved by the Goldsmiths Ethics Committee and it was carried out in accordance with the Declaration of Helsinki (BMJ 1991; 302: 1194). All participants gave informed written consent.

5.3.1.2 Procedure

The experiment consisted of a modified version of the Body Image Task (BIT; Fuentes et al., 2013; Caggiano & Cocchini, 2020). Participants were asked to imagine their silhouette with their arm aligned with the body, as if they were standing.

Participants were seated on a chair located 2 meters away from a white wall. Participants were informed that during the task they would see a gray oval (14×7.8 cm) with a black dot at the center resembling the outline of a head projected at the top of the illuminated area on the wall. The projecting area was 140×192 cm at 150cm from the floor. Participants, who were not aware of the projecting area size, were instructed to imagine their silhouette with their arm aligned with the body, as if they were standing in front of a mirror. Participants were asked to scale the imagined picture of themselves such that the size of their head (i.e. face outline) matched the size of the displayed oval on the wall. In the previous experiments (Chapter 4) dots were used as references (i.e. navel, tip of the nose or tip of the forehead). In the current experiment, because the pointing was not in real scale, the head was used as landmark to provide a reference to scale the body. The name of the body part to be located during the task was displayed, in random order, at the bottom left of the projecting area. Participants used a laser pointer to indicate where they thought the body parts would be and were asked to hold the position until the

experimenter recorded the response with a cursor by clicking the corresponding location on a computer connected to the projector. To avoid possible ‘shift’ of the imagined silhouette during testing, the gray oval was used as landmark and remained visible throughout the task. A total of 13 body parts: 1 midline point (navel), 6 landmarks for the arms and 6 landmarks for legs.

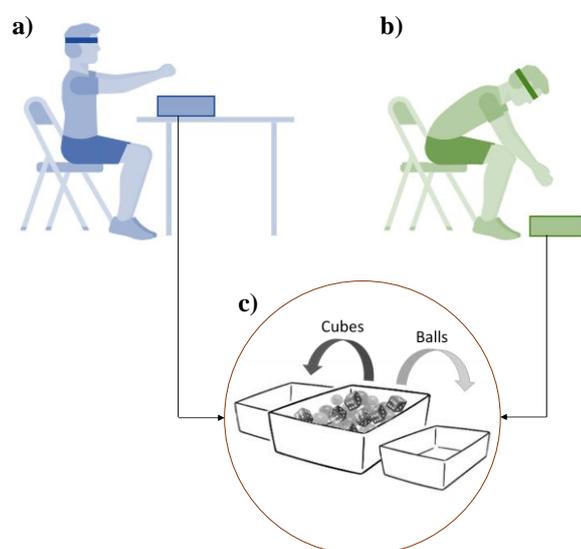
Before leaving the experimental setting, a picture of each participant standing against a white wall was taken and actual location of the navel was noted for later analyses.

The task was repeated two times: before and after a motor training.

5.3.1.3 Training sessions

After locating the body parts on the wall, participants were asked to run a 10-minute training and then they were re-tested on the BIT. During the training, participants were engaged in a sorting task in which they had to sort cubes and balls from a container into separate containers: cubes in the container to the left, balls in the container to the right. Half of the participants had to sort cubes and balls from a container located on the floor (*Down-training*), the other half from a container located on a table (*Top-training*). In both conditions, participants were blindfolded and asked to execute the task with their arms outstretched (Figure 5.1). To ensure that participants were able to correctly reach the

Figure 5.1. Schematic representation of training sessions.



a) ‘Top’ training, b) ‘Down’ training, c) sorting task.

boxes after being blindfolded, the experimenter guided participants hand onto the correct location. The aim was to maximize the use of afferent somatosensory information to carry out the sorting and, maintain an outstretched position of the arms across the two conditions. Therefore, in both trainings the task's goal and procedure as well as the arms configuration, remained outstretched while the location of the action execution changed (*Top vs Down*). To encourage participants to perform the task as best they could, the experimenter took a live count of how many cubes and balls were divided correctly until the end of the training.

5.3.1.4 Data acquisition of BIT

Two measures were considered: the *Real Body Measure* (RBM) and the *Subjective Body Measure* (SBM). Similar to previous studies (i.e., Fuentes et al., 2013; Caggiano & Cocchini, 2020), real and subjective body measurements (RBM and SBM, respectively) were compared and analyzed in *percentage body part estimation error* (%BPE). Negative BPE values indicate underestimation, while positive values indicate overestimation; zero indicates perfect estimation. For the purpose of the present experiment, subjective body widths (shoulder and hip) were not considered for statistical analysis.

In a second set analysis, we compared body part ratios to test whether the motor training would modulate the overall represented body proportions. We calculated the following three ratios for each participant: leg/torso, arm/torso and arm/leg.

5.3.2 Results

5.3.2.1 Body parts - Length

Overall, participants from both groups showed a tendency to underestimate most of their body parts, in particular the forearms (-44%) and overestimate the torso (+10%) and lower legs (+7%).

In order to assess whether the distortion of individual body parts was significant, a series of two-tailed t-tests were performed, one for each body part, to compare %BPEs with zero (i.e., no distortion). Bonferroni correction for multiple comparisons was applied

(i.e., 10 comparisons; significant p values < .005). Results showed that the length of 3 out of 10 body parts was significantly distorted from real size in the *Down-training* and 4 out of 10 in the *Top-training* groups (see Table 5.1). In detail, the forearms were consistently underestimated in both sides (left and right) and training groups, whereas the upper right arm was significantly underestimated only in the *Down-training* group. The upper right leg and left torso were underestimated and overestimated respectively in the *Top-training* group only (see Figure 5.2).

Table 5.1. Two-tailed t-tests results comparing %BPE with 0.

Body parts		<i>Down-Training</i> group (n = 15)			<i>Top-Training</i> group (n = 15)		
		t-critical	p	<i>d</i>	t-critical	p	<i>d</i>
Upper Arm	right	-3.82	.002*	2.04	-1.76	.101	.94
	left	-2.11	.054	1.13	-1.75	.103	.93
Forearm	right	-17.43	<.005*	9.31	-11.41	<.005*	6.10
	left	-12.56	<.005*	6.71	-8.26	<.005*	4.42
Torso	right	.937	.364	.50	2.57	.022	1.37
	left	.927	.371	.50	3.27	.006	1.75
Upper Leg	right	-2.51	.025	1.34	-3.29	.005*	1.76
	left	-1.91	.078	1.02	-2.29	.038	1.22
Lower Leg	right	.862	.403	.46	1.92	.076	1.03
	left	.621	.545	.33	1.51	.153	.81

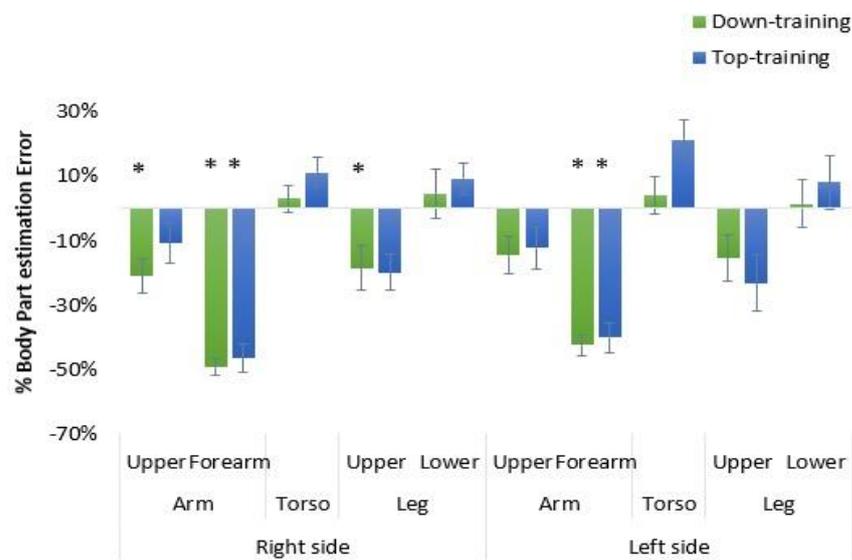
%BPE indicates the percentage difference between the perceived length/width and the participant's real body part length/width. Negative t-values indicate underestimation. In bold significant differences following correction for multiple comparisons.

Three main factors were considered: Body Part (upper and lower arm, upper and lower leg and torso), Side (left and right) and Group (Top-training and Down-training).

A mixed factor ANOVA 5 (Body Part) × 2 (Side) × 2 (Group) was performed to consider possible differences among body parts, side and groups. Results yielded main effect of Body Part [$F(2.5, 70.02) = 37.15, p < .0001; \eta^2_{partial} = .57$] while Side [$F(1,28)$

= 3.07, $p = .09$; $\eta^2_{partial} = .09$], Group [$F(1,28) = 1.01$, $p = .33$; $\eta^2_{partial} = .04$] and interactions were not significant. Post-hoc analysis of the single body parts (corrected for 10 multiple comparisons, $p < .005$) showed that the BPE for lower arms significantly differed from BPE of all the other body parts ($p < .001$), torso differed from all body parts ($p < .001$) excepted lower legs and similarly, lower legs significantly different from all body parts ($p < .001$) excepted torso.

Figure 5.2. Under/overestimation in perceived body parts' length.



Positive values indicate overestimation. Negative values indicate underestimation. * indicates significant ($p \leq .005$) difference from 0 (no distortion). Error bars indicate standard error.

Three main factors were considered: Body Part, Side and Time (pre-training and post training). An ANOVA 5 (Body Part) \times 2 (Side) \times 2 (Time) was performed to assess possible differences among body parts, after training for the *Down-training* group. Results showed a significant main effect for Body Part [$F(2.1, 29.59) = 27.07$, $p < .0001$; $\eta^2_{partial} = .66$] and Time [$F(1,14) = 12.82$, $p = .003$; $\eta^2_{partial} = .48$] but not for Side [$F(1,14) = 4.26$, $p = .058$; $\eta^2_{partial} = .23$]. Also, the interaction Body Part \times Time resulted significant [$F(2.3, 33.61) = 5.58$, $p = .006$; $\eta^2_{partial} = .29$]. Post-hoc analysis showed that in the post-

training task, participants significantly overestimated the upper arms (pre: -16.5%; post: +4.5%) [$t(14) = 6.19, p < .001, d = 3.31$] and torso (pre: +4.8%; post: +18.3%) [$t(14) = 3.72, p = .01, d = 2.01$] compared to the baseline.

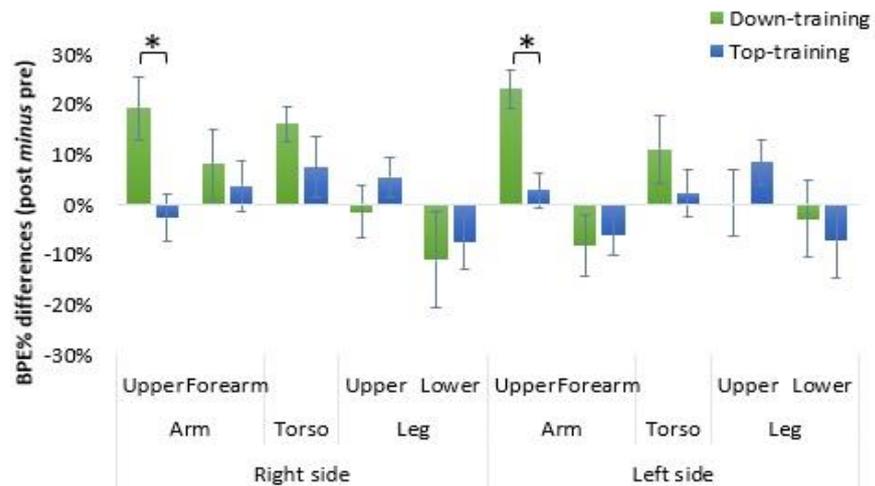
A second ANOVA 5 (Body Part) \times 2 (Side) \times 2 (Time) for the *Top-training* group was performed. Results showed significant effects for Body Part [$F(2.4, 33.95) = 18.13, p < .0001; \eta^2_{\text{partial}} = .56$] and Body Part \times Time interaction [$F(2.9, 39.91) = 3.12, p = .039; \eta^2_{\text{partial}} = .18$], while main factors Side [$F(1,14) = 1.74, p = .21; \eta^2_{\text{partial}} = .11$] and Time [$F(1,14) = .135, p = .72; \eta^2_{\text{partial}} = .01$] were not significant. Post-hoc analysis highlighted a significant difference between the BPEs of the upper legs which showed a reduced underestimation in the post training compared to baseline (pre: -19.4%; post: -12.5%) [$t(14) = 2.48, p = .026, d = 1.32$].

Since both groups did not differ significantly on the pre-training session, to have a clearer measure of the amplitude of a potential training effect, *delta* BPEs (i.e., post-*minus* pre-training) were calculated for each participant (see Figure 5.3). A mixed factor ANOVA 5 (Body Part) \times 2 (Side) \times 2 (Group) was then carried out to test significant discrepancies for body parts between the two groups. A significant main effect for Body Part [$F(2.6, 72.98) = 6.26, p = .001; \eta^2_{\text{partial}} = .18$] was observed as well as Body Part \times Group interaction effect [$F(2.6, 72.98) = 3.39, p = .028; \eta^2_{\text{partial}} = .11$]. Side [$F(1,28) = .325, p = .57; \eta^2_{\text{partial}} = .01$] and Group [$F(1,28) = 4.32, p = .047; \eta^2_{\text{partial}} = .13$] were not significant. Post-hoc analysis revealed that in the *Down-Training* group, the differences (*delta* BPEs) for the upper arms were significantly larger than forearms [$t(14) = 3.57, p = .003, d = 1.91$], upper [$t(14) = 4.08, p = .001, d = 2.18$] and lower legs [$t(14) = 3.04, p = .009, d = 1.62$] torso larger than upper legs [$t(14) = 3.21, p = .006, d = .86$]. No differences were found in the *Top-training* group. Furthermore, the *Down-Training* group showed larger *delta* BPEs for the upper arms compared to the *Top-Training* group [$t(28)$

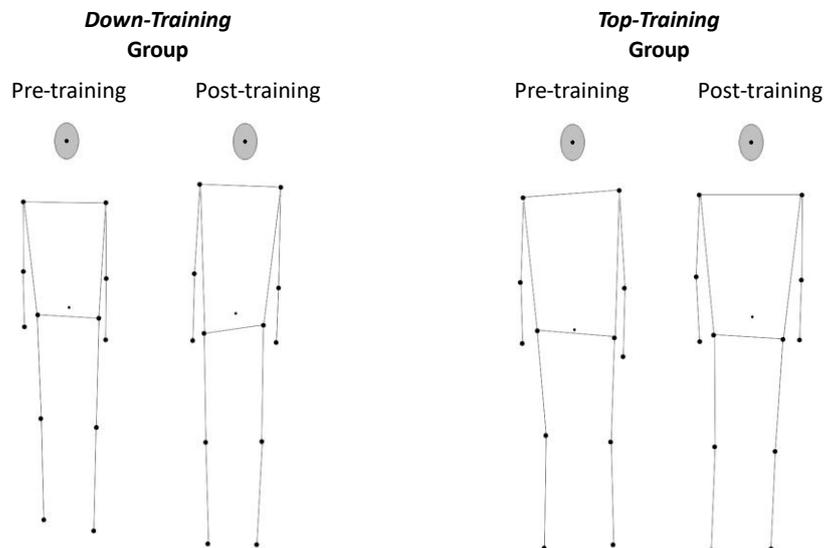
= 5.08, $p < .001$, $d = 1.91$]. No significant differences were observed for any other body part.

Figure 5.3. Differences between post-training and pre-training %BPEs.

a)



b)



a) Positive values indicate an increase in perceived length in the post-training phase compared to baseline. Negative values indicate a decrease in perceived length in the post-training phase compared to baseline. * Highlight the significant difference between delta BPEs for the *Down* and *Top-training* groups. Error bars indicate standard error. **b)** Graphic output of averaged subjective responses (pre- and post-training). Note that the egocentric right side is on the left of the drawing and viceversa.

5.3.2.2 Body parts - Ratios

A further investigation of distortions in body metrics across groups was conducted by comparing body aspect ratios. Specifically, three body part ratios were calculated for each participant: leg/torso, arm/torso and leg/arm. As for to BPEs, ratios were then expressed as the difference between the perceived ratio and the participant's true ratio, as a proportion of the true ratio. As for the body parts lengths, a similar set of analyses was carried out.

To evaluate whether participants' mental representation of their specific body parts ratios reflected their real ones, two-tailed t-tests was conducted for each ratio compared with zero. Bonferroni correction for multiple comparisons was applied (i.e., 3 comparisons; significant p values < 0.016). Results showed that, with the exception of leg/torso in the *Down-training* group, participants perceived body ratios were significantly different from the real ones (see Table 5.2). A 3 (Ratio) × 2 (Group) ANOVA to assess possible differences among ratios and groups showed a significant effect of Ratio [$F(1.11, 30.87) = 83.99, p < .001; \eta^2_{\text{partial}} = .75$] but not of Group [$F(1, 28) = .694, p = .41; \eta^2_{\text{partial}} = .02$] nor interaction [$F(1.11, 30.87) = .149, p = .72; \eta^2_{\text{partial}} = .005$]. Pairwise comparisons on Ratio showed that all three body aspect ratios significantly differed from each other ($p < .001$).

Table 5.2. Two-tailed t-tests results comparing % ratio aspects with 0.

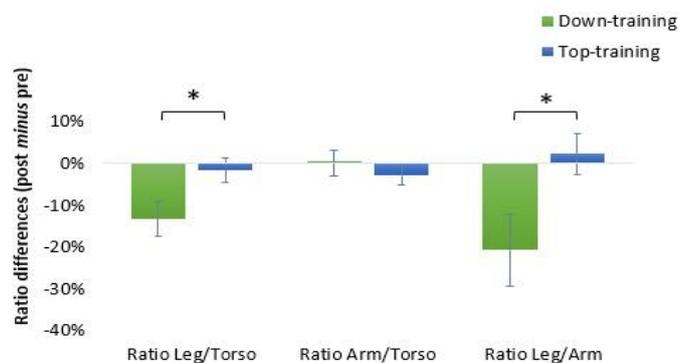
Ratios	<i>Down-Training</i> group (n = 15)			<i>Top-Training</i> group (n = 15)		
	t-critical	p	<i>d</i>	t-critical	p	<i>d</i>
Leg/Torso	-1.64	.122	.43	-3.26	.006*	.84
Arm/Torso	-12.83	<.001*	3.31	-15.31	<.001*	3.85
Leg/Arm	3.88	.002*	1	3.19	.006*	.82

Negative t-values indicate underestimation. In bold significant differences following correction for multiple comparisons.

Two separate 3 (Ratio) \times 2 (Time) ANOVAs were carried out to assess possible differences among body parts, before and after training for each group. For the *Down-training* group, results yielded main effect of Ratio [$F(1.3, 15.77) = 52.26, p < .0001; \eta^2_{\text{partial}} = .79$] and Time [$F(1,14) = 9.46, p = .008; \eta^2_{\text{partial}} = .41$]. The interaction Ratio \times Time showed a trend [$F(1.1, 14.98) = 3.84, p = .067; \eta^2_{\text{partial}} = .22$]. Paired wise comparisons showed that all body aspect ratios differed from each other. For the *Top-training* group results showed a main effect of Ratio [$F(1.1, 15.27) = 56.15, p < .0001; \eta^2_{\text{partial}} = .80$]. Both Time [$F(1,14) = .135, p = .72; \eta^2_{\text{partial}} = .01$] and interaction Ratio \times Time [$F(1.2, 16.45) = .589, p = .48; \eta^2_{\text{partial}} = .04$] were not significant.

Finally, a third 3 (Ratio) \times 2 (Time) ANOVA was carried out on the ratios' differences (post- *minus* pre-training) between groups. Whilst Ratio was not significant [$F(1.1, 31.08) = 1.62, p = .22; \eta^2_{\text{partial}} = .05$], both Group [$F(1,28) = 6.13, p = .02; \eta^2_{\text{partial}} = .18$] and the interaction Ratio \times Group [$F(1.1, 31.08) = 4.14, p = .047; \eta^2_{\text{partial}} = .13$] yielded significant results. Post-hoc tests showed a significant difference between the two

Figure 5.4. Differences between post- and pre-training body part ratios.



Positive values indicate that ratios considered were larger in the pre-training compared to the post-training condition. Negative values indicate that ratios were smaller in the pre-training compared to the post-training condition. Error bars indicate standard deviation.

groups for leg/torso [$t(28) = 2.31, p = .029, d = .87$] and arm/leg [$t(28) = 2.31, p = .027, d = .88$] but not for arm/torso [$t(28) = .858, p = .39, d = .32$].

5.3.3 Preliminary discussion

Results from Experiment 5 were in line with findings observed in Study 1, whereby a systematic distortion of specific body parts occurred. At baseline, among the two training groups, bodily distortions were statistically significant for 4 out of 10 body parts. The most striking effect was the consistent underestimation of the forearms for both groups, while the right upper arm was significantly distorted in the *Down-training* group and right upper leg in the *Top-training* one, only.

The main purpose of Experiment 5 was to assess whether, after a motor training, participants experience a modulation of the body part involved in the action. In Chapter 4, it was argued that the particular representation of body observed in the first study could be explained by the function of the body parts and the location in which actions usually occur. For this reason, Experiment 5 controlled for a motor component asking two separate groups of participants to perform an identical sorting task in two different spatial locations (*Down* vs *Top*). Results showed that a significant modulation occurred only for the group that performed the sorting task on the floor (*Down-training*) while no significant effect was observed for the *Top-training* group for any of the body segments. Specifically, the training had an effect on the upper arms and torso, with both of them being significantly less underestimated in the post-training phase compared to the pre-training phase.

These findings are particularly interesting as they seem to suggest that, although the motor training is relevant to modify the perceived length of body segments, the location in which the action occurs also plays a pivotal role in re-modulating the body parts representations and their relationship. But why should spatial location be important?

In literature, the peripersonal space is described as a particular region surrounding the body that acts as an interface between the body and the environment, functionally defined according to the distance at which an object can be reached (Cardinali, Brozzoli, & Farne, 2009). This definition crucially involves the ‘action’ as an important component in the definition of what the peripersonal space is. The *body schema*, as discussed in Chapter 2, also plays a role in action execution and for this reason both the peripersonal space and *body schema* are tightly linked.

On the other hand, the personal space is the space occupied by the body itself. The body, by nature, is spatially organized with clear anatomical landmarks that define its structure. Inevitably, body representation must be constrained by the physical reality of the body, at least in healthy individuals. In fact, when asked to locate body parts, participants maintain a reasonable configuration of the body, without committing gross errors, in regards to the overall relationship between body parts (Caggiano & Cocchini, 2020; Fuentes et al., 2013). Notably, the emergent body configuration manifests a similarity in the way left and right sides are represented, while on the other hand, upper and lower limb distortions are not fully symmetrical and appear to follow different trends suggesting that the upper and lower body space are represented differently (Fuentes et al., 2013). Ultimately the body is a means *for* action. Therefore, performing an action in a spatial location with body segments that are not naturally (or frequently) represented in that portion of space may extend the subjective action range and impact on represented body parts *for* action. In this sense, the type of actions and where these occur in space may modulate both spatial and bodily representations.

Crucially, action requires a more integrated representation of body parts. This consideration leads to the second point of the current discussion. Results showed that the modulation of arms’ length is coupled with a modulation of torso’s length. One would expect that, because to perform the *Down training* the torso needs to be slightly tilted in

order to reach the floor, this should have resulted in an underestimation in the post-training testing phase. However, the arm/torso ratios remained constant in the post-training compared to the pre-training phase. It seems therefore that the torso's length was implicitly adjusted to reflect arms elongation, reflecting an integrated representation of these to body parts during action. Thus, although the represented body is indeed distorted, a coherence between body parts must be maintained. This reasoning is in line with findings coming from studies on the sense of ownership. For example, Tsakiris, Prabhu and Haggard (2006) showed that in a RHI paradigm the illusory ownership was confined to the stimulated finger. However, when the stimulated finger was actively moved, the illusion included other fingers because, arguably, the movement triggered a re-modulation of the relationship between the finger and the hand as a whole. In other words, it seems that action requires a unified and integrated representation of the body that puts individual body parts back together (de Vignemont et al., 2009).

Interestingly, in the experiment reported, the training did not significantly modulate the forearms' length. Possibly, this was due to task demands that consisted in participants being asked to imagine the configuration of the whole body. For this reason, a second experiment (Experiment 6) was developed to isolate the perceived length of the arm by means of the arm bisection task (Garbarini et al., 2015; Sposito et al., 2012, 2010; Tosi et al., 2018; D'Angelo et al., 2018) with a series of trainings that involved the use of one arm only. Two experimental questions were considered: first, whether the engagement of different sections of the arm leads to a differential modulation of the perceived arm length; second if the tool-use can further enhance the effect of actions on body representation.

In regard to the latter point, the trainings were specifically designed for participants to achieve the same goal. This aspect is particularly important in tool-use as it has been previously reported that the same tool, used for different tasks, differently affects arm

length representation, depending on how it is used (i.e., to grasp object or to perform a perceptual task) (Cardinali, Jacobs, Brozzoli, Frassinetti, Roy, & Farnè, 2012). This indicates that the potential relationship between *body schema* and actions is not exclusively confined to the kinematical constraints that enable action execution, but also to the level of motor goal-relatedness (Gallese & Sinigaglia, 2010). Therefore, the perceived body metrics could be differently modulated, according to the way in which specific goals and motor programs of a tool action are represented as also indicated by the results from Study 2 (Chapter 4). To this aim, in Experiment 6 the arm bisection task (Garbarini et al. 2015; Sposito et al. 2012, 2010; Tosi et al. 2018; D'Angelo et al., 2019) was adopted to test whether training sessions requiring more proximal or more distal motor control of the arm can differently modulate body metrics.

5.4 Experiment 6 – Arm bisection task following motor training with different arm segments⁵

5.4.1 Methods and procedures

5.4.1.1 Participants

Based on the results of previous experiments and taking into account studies adopting an experimental paradigm similar to the one of the present experiment (e.g. D'Angelo et al. 2018), a priori power analysis was conducted assuming a large effect size. Parameters were considered for a repeated measures ANOVA and set with sample size for $\eta^2_{partial} = .1$, $\alpha = .05$, and power = .95. The analysis showed that a sample of 22 participants would be appropriate to find an effect.

Twenty participants were recruited for the experiment however, one had to be removed as he dropped out and did not complete all the tasks required by the experiment. Nineteen participants (11 females) were considered; their age ranged from 19 to 35 years,

⁵ The data collected for the present study have been incorporated in a larger co-authored study (Romano et al., 2018).

with a mean of 29.4 years (SD = 3.8). All participants were right-handed (Edinburgh Inventory mean score = 0.97; SD= 0.66). The study was approved by the Goldsmiths Ethics Committee and it was carried out in accordance with the Declaration of Helsinki (BMJ 1991; 302: 1194). All participants gave informed written consent.

5.4.1.2 Bisection task

To assess subjective forearms length, participants were asked to perform the forearm bisection task (Garbarini et al. 2015; Sposito et al. 2012, 2010; Tosi et al. 2018; D'Angelo et al., 2019). Participants sat on a chair in front of a table where they were asked to place both arms in an extended position with the palm of the hand down. After being blindfolded, participants were asked to point at the perceived midpoint between the elbow and the tip of the middle finger of their arms for both left and right arms, using the contralateral index finger with ballistic movements without making any correction. Each trial started with pointing index finger located at 30-cm distance from the midsagittal plane. In order to record the perceived midpoint and remove tactile feedback from the bisection task, an adjustable custom-made plastic ruler was placed just above the arm that had to be bisected. Participants were asked to carry out the task ten times for both the left and right arm (the order was counterbalanced across participants). For the recording, zero was set at the most proximal landmark (i.e. elbow) and the real arm lengths and objective arm midpoint were measured at the end of the session. The perceived midpoint was calculated by dividing each pointing position for the total length of the arm times 100 to obtain the percentage deviation scores:

$$\% \text{ deviation scores} = \frac{\textit{perceived midpoint}}{\textit{real arm length}} \times 100$$

According to this formula, values below 50% indicate a proximal deviation (i.e. a perceived midline shift towards the elbow), values above 50% indicate a distal deviation

(i.e. a perceived midline shift towards the wrist) and a value equal to 50% indicates perfect estimation.

5.4.1.3 Trainings

Participants were asked to carry out four training sessions (Figure 5.5) of the duration of 15 min each. The trainings were sub-divided according to whether the use of a tool was involved or not and designed to engage different sections of the arm. For each sub-set of training, one was designed to engage the wrist (distal tasks) and one to engage the shoulder (proximal tasks). The training order was balanced across participants and a break of 20 min was given between each training. Participants had to carry out the forearm bisection task before and after each training session.

Proximal tasks without tool

A rubber ball of 7 cm diameter was hung up at 155 cm from the ceiling by a rope and located at 1 m distance in front of the participants. The aim of the training was for the participants to strike a set of targets displayed on the wall with different size, colour and shape and reach the highest possible score by targeting the most difficult ones. In order to do so, participants were asked to hit the ball with the palm of their dominant hand, by performing a movement that involved the entire arm and engaged mainly the shoulder. To avoid as much as possible movements of the wrist, participants were provided with a wristband reinforced with two small wood splints positioned on the ventral and dorsal sides of the wrist–forearm section. The distance from the ball was adjusted according to the participants' arm length to allow an easy reach of the ball

Distal task without tool

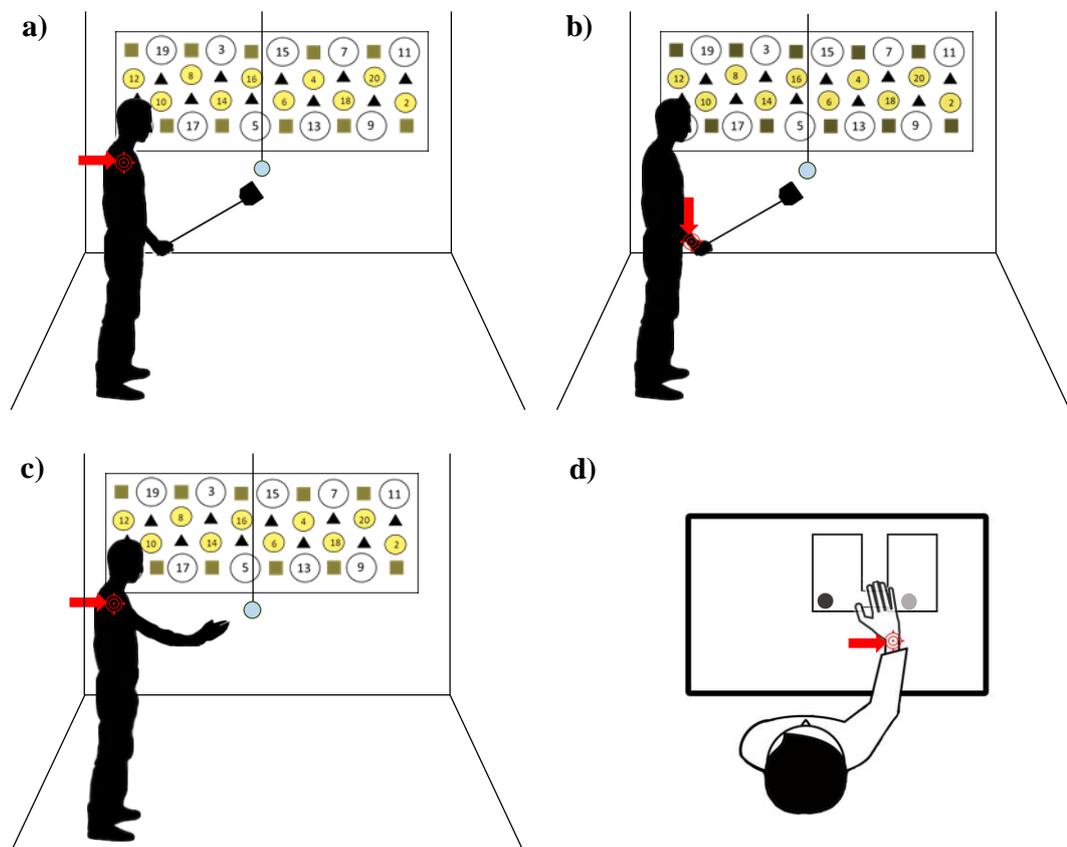
Two boxes were located in front of the participants on a 110 cm height table. The boxes were slightly inclined (about 35°) towards the participants so that the balls rolled towards the lower side of the boxes and be always at hand's reach distance. The boxes were attached with a communication passage that allowed the balls to be easily moved from one box to another. Participants were asked to grab and move the highest number

of balls from one box to another according to their colour. The participant's position and distance from the target balls was adjusted to make it reachable by wrist movements. To reduce possible movements of the upper part of the arm, two Velcro bands were used to surround participants' chest, (from underneath the non-dominant armpit and covered the dominant arm section just below the deltoid muscle) and the waist and covered the arm section just above the elbow blocking the upper part of the arm to participants' torso.

Proximal task with tool

The training setting and goal were the same as in the proximal task without tool. However, in this version of the task, participants were provided with a stick 70-cm-long stick with an ergonomic handle at one extremity and a squared flat surface at the other and instructed to hit the ball by using the tool "like a tennis player" to engage the shoulder.

Figure 5.5. Schematic representation of the trainings involving distal and proximal movements.



a) Proximal task with tool, **b)** distal task with tool, **c)** proximal task without tool and **d)** distal task without tool.

Again, to limit wrist movements, participants had to wear a wristband reinforced with two small wood splints.

Distal task with tool

Participants to hit the ball and strike the targets displayed on the wall with the 70-cm-long stick. In this circumstance, participants were instructed to operate the tool by using the wrist only. As for the grasping task, to reduce possible movements of the upper part of the arm, two Velcro bands were used to surround the dominant arm section just below the deltoid muscle and the section just above the elbow. The experimenter ensured that the forearm was maintained almost parallel to the floor and the angle formed by the upper arm and forearm was approximately 90°.

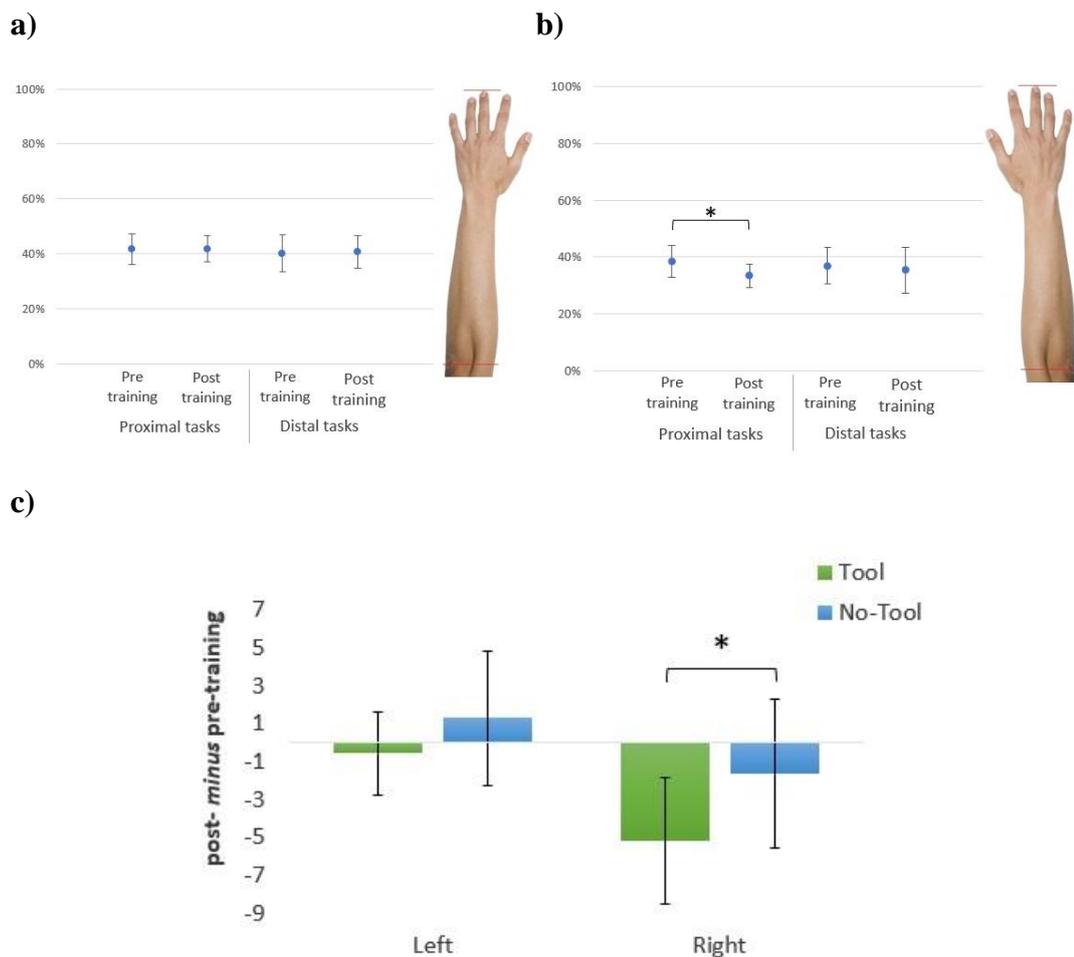
5.4.2 Results

Descriptive statistics showed that, at baseline, participant tended to commit a mislocalization error of -10.66% (SD = 4.23) from the real midpoint. Four main factors were considered: Time (pre-training and post training), Side (left and right arm), Training (distal and proximal), Tool (with and without tool-use). An ANOVA 2 (Time) × 2 (Side) × 2 (Training) × 2 (Tool) was carried out. Results yielded a significant main effect of Time [F(1,18) = 12.39, $p = .002$; $\eta^2_{partial} = .41$] and Side [F(1,18) = 44.39, $p < 0.001$; $\eta^2_{partial} = .71$], while the main factors Training [F(1,18) = .421, $p = .52$; $\eta^2_{partial} = .02$]; and Tool were not significant [F(1,18) = .001, $p = .97$; $\eta^2_{partial} = .001$]. The interactions Time × Side [F(1,18) = 30.97, $p < .0001$; $\eta^2_{partial} = .63$], Time × Tool [F(1,18) = 10.79, $p = .004$; $\eta^2_{partial} = .38$] and Training × Tool [F(1,18) = 5.43, $p = .032$; $\eta^2_{partial} = .22$] were also significant. More importantly, the three-way interaction Time × Side × Training [F(1,18) = 7.11, $p = .016$; $\eta^2_{partial} = .28$] was statistically significant. Post-hoc analysis revealed that a significant effect on the bisection task was present only for the right arm (37,78% - 34,39%, $p < .0001$) but not for the left (40.88% - 41.26%). Furthermore, the differences

between pre- and post-training were significant after the use of tool (pre: 40.01%, post: 37.17%; $p < .0001$) but not when the tool-use was not required (38.65% - 38.49%, $p = .82$).

To solve the three-way interaction, two separate ANOVAs 2 (Time) \times 2 (Training), one for each arm, were performed. Analysis for the right arm showed a significant effect of Time [$F(1,18) = 27.56$, $p < .001$; $\eta^2_{partial} = .61$] and interaction between Training \times Time [$F(1,18) = 5.43$, $p = .032$; $\eta^2_{partial} = .23$]. Conversely, the analysis on the left hand showed absence of any significant effect. More in detail, the dominant hand showed a

Figure 5.6. Perceived position of the middle point between the tip of the middle finger and the elbow.



a) Percentage deviation scores of proximal and distal tasks averaged between tool and no-tool trainings for the left arm. **b)** Percentage deviation scores of proximal and distal tasks averaged between tool and no-tool trainings for the right arm. **c)** Differences between post- and pre-training percentage deviation scores. Error bars indicate standard deviation.

significant shift of the perceived midpoint after the proximal training (pre: 38.6%; post: 33.5%) [$t(18) = 5.67, p < .001, d = 2.67$] but not after the distal training (pre: 36.9%; post: 35.3%) [$t(18) = 1.58, p = .13, d = .74$] (see Figure 5.5 a and b).

Lastly, *delta* deviation scores were calculated. Analysis on differences between performances post- and pre-training (post- *minus* pre-training) showed a significant effect of both Tool [$F(1,18) = 10.79, p = .004; \eta^2_{\text{partial}} = .38$] and Side [$F(1,18) = 30.97, p < .001; \eta^2_{\text{partial}} = .63$] but no interaction, suggesting that even if the effect in the same direction was present on the right hand after both trainings with and without tool, it was significantly stronger after tool use (Figure 5.5 c)

5.4.3 Preliminary discussion

Experiment 6 explored whether different actions performed with the same body part can have different impact on subjective metric representation of the body and if tool-use has a different weight in the potential modulation. Participants were asked to indicate the perceived midpoint of their forearm before and after four different types of training that selectively maximized either the engagement of the wrist or shoulder with and without tool-use. In line with the results of previous experiments, participants tended to perceive the forearms shorter than real length, as indicated by the proximal shift at baseline. Specifically, it was observed an averaged percentage deviation score of about -10% in the bisection task at baseline. Furthermore, these findings suggest that actions can drive a potential modification of body metric representation. A modulation of the perceived midline occurred only for the arm used to carry out the tasks while no effect was observed for the left (still) arm. However, the effect was found only after the training involving the shoulder, while the training that involved the wrist did not have a significant effect. It is noteworthy that, despite these findings build upon the role of motor practice in changing the subjective body metrics (Cardinali, Frassinetti, et al. 2009; Sposito et al. 2012; Garbarini et al. 2015), they are in contrast with the direction of the effect. Studies on tool-

use have reported a distal shift after the use of a tool (Garbarini et al. 2015; Sposito et al. 2012). This effect has been generally interpreted as result of the physical embodiment of the tool and consequent change of the subjective peripersonal reaching space (Canzoneri et al. 2013; Farné, Serino, & Ladavas, 2007; Iriki et al. 1996). There is no doubt that tool-use impacts on the perceived action space, likewise there is no doubt that using a tool requires specific motor programs that are appropriate for its correct use. In Experiment 6, the motor components (proximal *versus* distal), task demands (hit *versus* grasp) and tool-use (same goal *versus* different action) were controlled to assess their individual weight in modulating participants' performance on the forearm bisection task.

In the proximal tasks, a shift in the perceived midpoint occurred regardless the presence of tool suggesting that is motor pattern that drives the direction of the perceived arm length. In other words, the presence of the tool appeared to not be necessary to induce a bisection shift related to body part movements nonetheless, the tool significantly enhanced the bisection modification effects, as suggested by the analysis on the differences. The absence of effect in the distal trainings could be possibly due to the actions required in the trainings. Indeed, compared to the proximal tasks, the distal tasks involve a minor group of muscles. In this sense, the weight of sensorimotor information might not have been enough to induce a subjective change in the forearm length. However, this strengthen even more the hypothesis of the role motor programs. In fact, if it was the mere use of tool enough to trigger a change, then both proximal and distal trainings with tool should have induced the same effect. It appears evident that, in the context of tool-use, the key factors that come into play are not only the tool-use *per se* but also, *how* it is used. Also, it has been recently shown by D'Angelo and collaborators (2018), that agency is involved in both body representation and peripersonal space modulation. In their study, the authors asked participants to virtually grasp objects and make precision grip by controlling a 3D virtual hand located far or near to the participants'

real hand. In a synchronous condition, the virtual hand movements corresponded, in real time, to participants' own right-hand movements, while in an asynchronous condition, the virtual hand moved three seconds after the participants' real hand movements. The results showed that significant changes, in the extent of arm length's representation and peripersonal space, occurred only in the synchronous condition. Critically, the congruency between the intention to perform the action, the motor output and the corresponding virtual hand movement, increased participants' sense of agency over the 3D hand and ultimately induced a modulation of body metrics and peripersonal space (D'Angelo et al., 2018).

Generally speaking, the *sense of agency* refers to the feeling of control over actions and their consequences and it depends on the mental association between an intentional action and its sensory outcome (Haggard, 2017; Haggard & Chambon, 2012). However, a crucial distinction has been made in the literature between the *Feeling of agency* and the *Judgment of agency* (Moore, 2016; Synofzik, Vosgerau, & Newen, 2008a). As the word suggests, the former refers to a pre-reflexive feeling of being an agent. This means, that we do not necessarily need to think about the fact that we, as agents, perform actions. The latter, on the other hand, requires active reflection on our actions that enable us to judge the "level" of agency and control over actions. While the *feeling of agency* requires simple low-level sensorimotor information to occur, the *judgment of agency* involves higher-level cognitive processes (Moore, 2016).

Therefore, it is reasonable to argue that, the difference in the findings between the present experiment and the studies on tool-use aforementioned (i.e. Garbarini et al. 2015; Sposito et al. 2012), lies in controlling the type of movement required to perform the task. Explicitly asking to perform a specific movement, might have enhanced participants' agency (i.e. explicit attribution of agency over the type of action) in regard to the effector used to accomplish the action. The focus put on the action, might have had an effect at a

more personal – egocentric - level (proximal shift) rather than extending the perceived reaching – peripersonal - space (distal shift, as reported in the studies aforementioned).

These data suggest that the observed changes of body representation are influenced by the actions involved in using the tool. In other words, this means that body representation is not only sensory but also motor in nature (Gallese & Sinigaglia, 2010). To further explore this aspect, a further experiment has been conducted. The Experiment 7 looks at the more visuo-perceptive components of body representation and whether the effect of motor actions impacts on the body part that are selectively used during training.

Specifically, with the crucial addition of an active motor component, the following experiment also expands on the findings from Experiment 3 reported in Chapter 4. The underlying assumption is that if an object representation includes information about its related actions, it may also include information of its effector. Therefore, if a new object is selectively used with a specific body part, the functional relation between the object and the effector should be univocal. The Experiment 6 showed that the way an object is used, modulated the perceived metrics of the effector. The Experiment 7 aims at evaluating if the way an object is used modulates the perceptual recognition of the effector.

5.5 Experiment 7 – Functional priming task following motor training with different body parts

5.5.1 Methods and procedures

5.5.1.1 Participants

Following a pilot study, showing practice effect, it was decided to consider a group of 20 participants (female = 12). Participants were all right-handed according to the Edinburgh Handedness Inventory (mean = .96; SD = .03). Their average age was 26.66 (SD = 2.5; range: 24-32). All participants had normal or corrected to normal vision, with no history of neurological or psychiatric illness. They were naïve to the hypothesis and

purpose of the study. The study was approved by the Goldsmiths Ethical Committee and all participants provided written consent.

5.5.1.2 Stimuli and procedure

Stimuli and experimental procedure was identical to those adopted in Experiment 3 (Study 2). A training phase was introduced before the priming task.

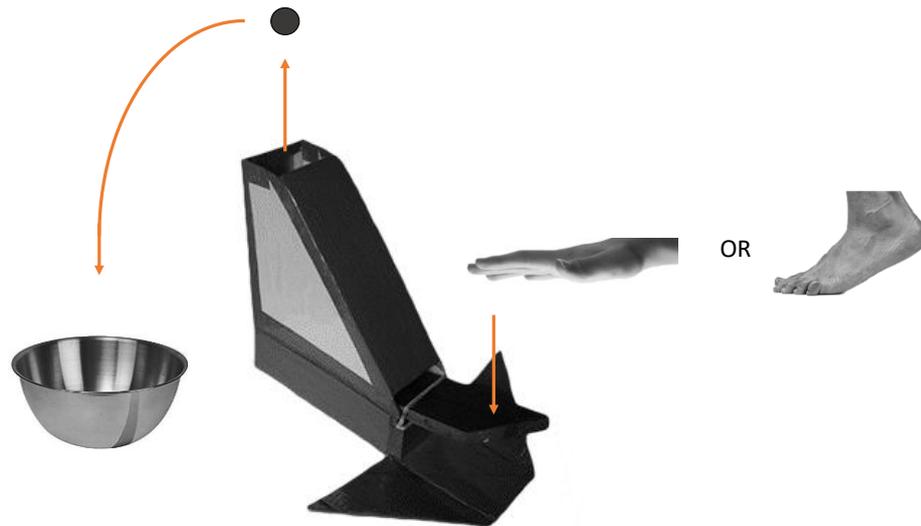
5.5.1.3 Training

Participants were asked to run a 10-minute training followed by the same test used during the Experiment 3. During the training, participants were engaged in a game using the ‘unknown object’. A series of table tennis balls were placed, one after the other, by the examiner inside the unknown object and the participants were instructed to press the lever of the object to eject the ball and enter it into a basket located at 20 cm from the object. Half of the participants pressed the level with the hand (Hand training), the other half with the foot (Foot training). The game consisted in launching in the basket as many balls as possible in the 10-minute training (Figure 5.7). The aim was to strengthen the association between the unknown object and the part of the body used to conduct the training. Therefore the ‘*Neutral*’ condition (i.e. unknown object followed by hand or foot) was now ‘*Training-Related*’ for trials where the target body part was congruent with the type of training (i.e. Hand trials following Hand training or Foot trials following Foot training) and it was ‘*Training-Unrelated*’ if the target was incongruent with the type of training (i.e., Hand trials following Foot training and viceversa).

To monitor the effect of task practice following the training, the number of balls placed into the basket was counted over the first and the last minute of training.

Both groups remained unaware of the possibility to use the same object with the other body part. Immediately after the training, the participants were asked to perform the task described in Study 2.

Figure 5.7. Schematic depiction of the motor training session.



5.5.2 Results

Concerning participants' performance during the first and last minutes of the game presented as part of the training, they showed a significant improvement (i.e. more balls inside the basket) when they used the hand [$t(9) = 2.71, p < .02$; first minute = 1.6, last minute = 2.2] and a trend when they used the foot [$t(8) = 2.0, p = 0.08$; first minute = 1.6; last minute = 2.2]. Note that one participant in the Foot training group was removed due to poor performance (see below).

As in Experiment 3, ACC and RLs were obtained from each participant's performance. Trials where RLs were larger or smaller than two deviation standards from the mean of correct trials were removed. Results of ACC, RLs and speed-accuracy trade offs are reported in Figure 5.8.

5.5.2.1 Accuracy

One participant was removed from the Foot training group as her overall accuracy performance was very poor and close to chance level (i.e., 53.3%). On average, participants provided a response to the 93.6% of trials (SD = 4.6) for the hand training and 92.9% (SD = 5.8) for the foot training. They did not show false alarms responding to no-go trials. Descriptive statistics showed that participants who carried out the Hand

training performed better in the *Related* condition (mean = 94.8%; SD = 6.7) compared to the *Unrelated* (mean = 92.9%; SD = 6.4) and *Training-Related* (mean = 92.6%; SD = 7.5). Similarly, participants who carried out the foot training showed a better performance for the *Related* condition (mean = 93.4%; SD = 5.4) than *Unrelated* (mean = 92.8%; SD = 5.1) and *Training-Related* (mean = 94.3%; SD = 6.2).

ANOVA 3 (Condition) \times 2 (Body Part) \times 2 (Training) resulted in a significant main effect of Condition [F(2,34) = 3.87, $p = .031$; $\eta^2_{partial} = .19$]. A significant two-way Body Part \times Group interaction [F(1,17) = 4.76, $p = .043$; $\eta^2_{partial} = .22$] and three-way interaction Condition \times Body Part \times Training [F(2,34) = 4.67, $p = .016$; $\eta^2_{partial} = .22$] emerged. Two separate ANOVAs for each training group were conducted to further explore the interaction.

For the Hand training group, ANOVA showed a significant main effect of Condition [F(2,18) = 4.07, $p = .035$; $\eta^2_{partial} = .31$] while Body Part and the interaction were not significant. Pairwise comparisons (significant $p < .016$) showed that participants were significantly more accurate in the *Related* condition compared to both *Training-Related* and *Training-Unrelated* conditions [t (9) = 4.08, $p = .003$, $d = 1.36$].

The ANOVA for the foot training group, did not show any significant result: Condition [F(2,16) = .593, $p = .56$; $\eta^2_{partial} = .069$] Body Part [F(1,8) = 2.48, $p = .15$; $\eta^2_{partial} = .24$] and Condition \times Body Part [F(2,16) = 2.81, $p = .09$; $\eta^2_{partial} = .26$].

5.5.2.2 Response latencies

We did not observe any significant main effect in the mixed factor ANOVA 3 (Condition) \times 2 (Body Part) \times 2 (Training) for RLs. However, the three-way interaction was significant [F(2,34) = 3.77, $p = .033$; $\eta^2_{partial} = .018$]. Two separate ANOVAs were conducted for each training group to further explore the interaction.

For the Hand training group, ANOVA showed no significant effect of both Condition [F(2,18) = 1.63, $p = .22$; $\eta^2_{partial} = .15$] and Body Part [F(1,9) = .135, $p = .72$; $\eta^2_{partial} = .015$]. The interaction Condition \times Body Part was also not significant [F(2,18) = 1.92, $p = .17$; $\eta^2_{partial} = .18$].

Similarly, for the foot training group, ANOVA did not show significant effect of Condition [F(2,16) = .127, $p = .88$; $\eta^2_{partial} = .016$] Body Part [F(1,8) = .169, $p = .69$; $\eta^2_{partial} = .021$] as well as the interaction Condition \times Body Part was also not significant [F(2,16) = 2.72, $p = .09$; $\eta^2_{partial} = .25$].

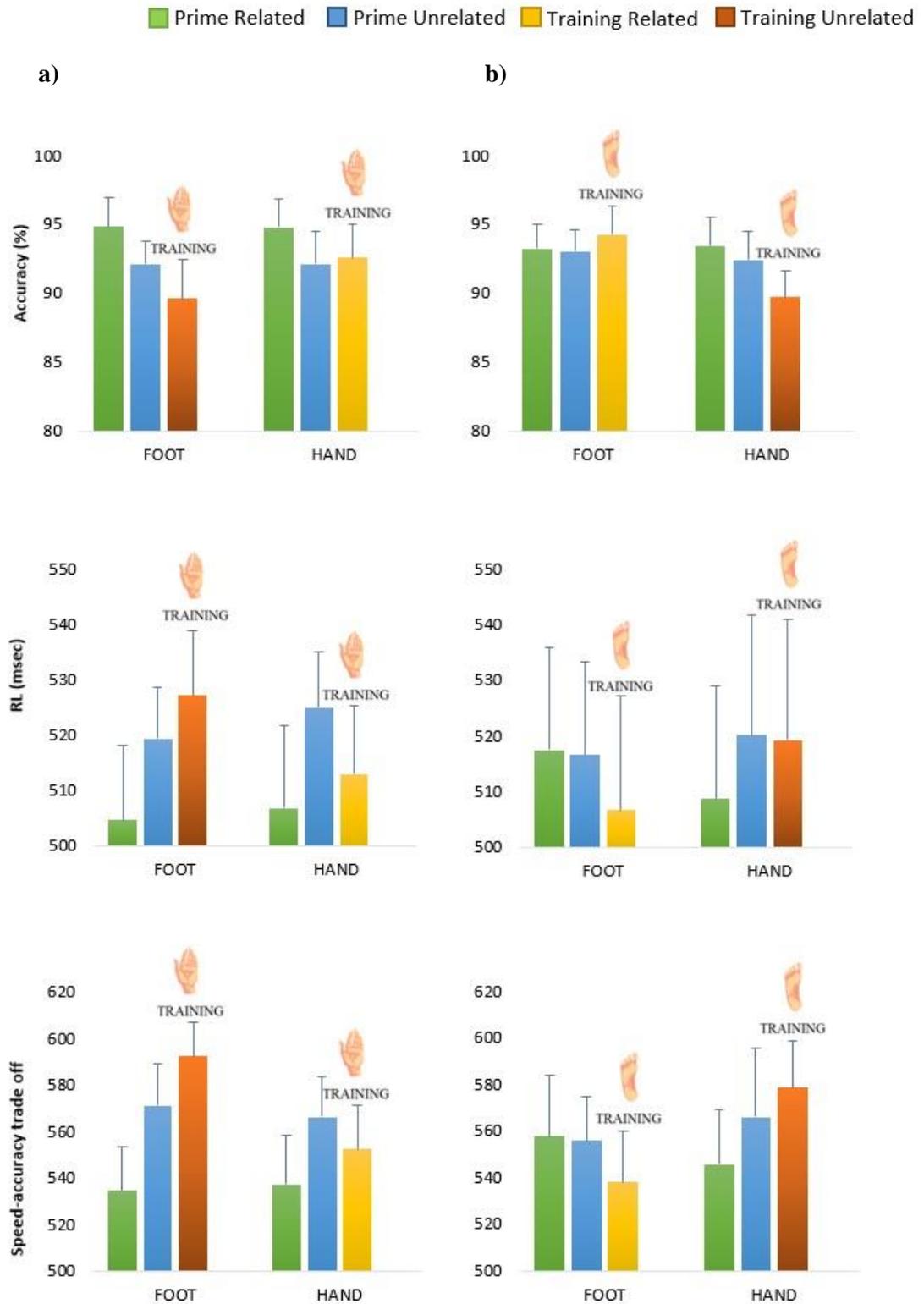
5.5.2.3 Speed-accuracy trade off

Mixed factor ANOVA for speed-accuracy trade off 3 (Condition) \times 2 (Body Part) \times 2 (Training) did not yield to significant main effect of Training [F(1,17) = .007, $p = .93$; $\eta^2_{partial} = .00$], Condition [F(2,24.9) = 2.85, $p = .09$; $\eta^2_{partial} = .14$] and Body Part F(1,17) = .012, $p = .91$; $\eta^2_{partial} = .00$]. However, a two-way interaction Body Part \times Training [F(1,17) = 6.39, $p = .033$; $\eta^2_{partial} = .024$] and three-way interaction Condition \times Body Part \times Training [F(2,32.5) = 8.65, $p = .001$; $\eta^2_{partial} = .33$] were significant. Other interactions were not significant. To resolve the three-way interaction, separate ANOVAs were performed for the two groups (Hand training and Foot training).

For the Hand training group, ANOVA yielded a main effect of Condition [F(2,18) = 4.90, $p = .02$; $\eta^2_{partial} = .35$] and an interaction between Condition and Body Part [F(2,18) = 5.25, $p = .016$; $\eta^2_{partial} = .37$]. Subsequent pairwise comparisons on Condition revealed better performance for *Related* condition compared to both *Training-Related* and *Training-Unrelated* conditions [t (9) = 3.24, $p = .01$, $d = 1.08$]. Furthermore, post-hoc analysis showed a selective improvement in the *Training-Related* condition for the body

part used during the training session (hand) compared to the other body part (foot; *Training-Unrelated* condition) [$t(9) = 3.63, p = .005, d = 1.21$].

Figure 5.8. Participants' performance (average and standard error) following: **a)** HAND training on the left column, **b)** FOOT training on the right column.



For the Foot training group, ANOVA showed a significant effect of the interaction between Condition and Body Part [$F(2,16) = 3.80$, $p = .045$; $\eta^2_{\text{partial}} = .32$] whilst both main factors Condition and Body Parts were not significant. Similarly to the previous ANOVA, post-hoc analysis showed a significant difference between body parts in the *Training-Related/Unrelated* conditions yet, this time the direction of the performance improvement was in the opposite direction with participants (who performed the training session with the foot) being more accurate in the foot trials compared to the hand trials [$t(9) = 2.98$, $p = .003$, $d = .99$].

5.6 Discussion and Conclusion

By showing a better performance in the *Related* compared to the *Unrelated* conditions in Study 2 (Chapter 4), it was highlighted that objects intrinsically carry information about the motor effector. With the introduction of a motor training, the Experiment 7 showed a slightly different profile. On one hand, the results confirmed the differences between *Related* and *Unrelated* conditions, on the other, more importantly, it highlighted a significant performance improvement for the *Training-related* condition compared to the *Training-unrelated* one. Crucially, even a relatively brief motor training led to a selective advantage in recognising the body part used with during the training, only. This suggests that the object representation for the (previously) ‘unknown’ object was likely to have been updated with this new functional/motor information.

Critically, the priming effect selectively emerged after a motor-training for the associated body part. This suggests that the visually presented object may activate motor information linked with the effector as a consequence of the pre-activation of the motor system following a training session. In other words, the training phase increased participants’ sensitivity to the congruency between prime and the body part. In fact, the training phase required participants to use a specific part of their own body to operate the object, and this might have induced motor resonance behaviour (Borghini, Bonfiglioli,

Lugli, Ricciardelli, Rubichi, & Nicoletti, 2007). Critically, previous studies have shown that the observation of a hand in motion selectively primes hand movement, rather than other body parts movement (Gillmeister, Catmur, Liepelt, Brass, & Heyes, 2008), suggesting that motor resonance is body part specific. Arguably, the priming effect observed in the present experiment could be the result of the integration of internal action signals with external visual input. As suggested by Peelen and Downing, (2008), this may occur through *corollary discharge* signals from motor areas that might dynamically update the visuospatial description of the body (*body image*).

Interestingly, these findings may deepen the understanding of the relationship between vision and motor information. According to the classic visual two-routes model (Goodale & Milner, 1992), the two streams involved in the perceptual representation of an object and the transformation of visual information into motor commands are relatively independent. In light of the data reported, it appears that visual representation and motor information are closely linked so that, in specific circumstances, action can facilitate visuo-perceptual discrimination.

According to the Theory of Event Coding (Hommel, 2015; Hommel et al., 2001), perceptual contents and action plans are cognitively represented in a shared representational map. The interaction between these representations creates associations between motor activities and representations of their perceptual consequences (Elsner & Hommel, 2001). In this view, the contents of perception and action both represent ‘events’ in the environment. Rather than being separate and sequential processes they influence each other. Indeed, as mentioned in previous chapters, the visual presentation of tools and/or objects linked to actions, activates premotor areas (Grafton et al., 1997; Chao & Martin, 2000; Creem-Regehr & Lee, 2005) as well as occipitotemporal regions dedicated to the representation of bodies and body parts (Bracci et al., 2011).

Together with these observations, the findings from the current experiment and Experiment 6 are of particular relevance for two main reasons. Firstly, they highlight the close interconnection between *body schema* and *body image*. In fact, the *body schema* is an action-oriented body representation dynamically shaped by actions (Head & Holmes, 1911; Schwoebel & Coslett, 2005; Sirigu, et al., 1991). In the training phase, participants were asked to perform a specific action with one part of the body, which results in the formation of a motor trace that, to some extent, modulated the *body schema* representation. Nonetheless, when participants were asked to recognise a body part in the experimental task, their performance improved only on the trials where the body part matched the one used during the training suggesting that *body schema* information were feeding into the *body image* for body parts recognition. Secondly, the activation of the motor traces associated with the object perception is specific and does not reflect simple object manipulability. Had this been the case, the effect on *Training-Related* foot trials would have not been observed. Imamizu and collaborators (2000) highlighted the effects on brain plasticity when learning the use of novel objects and how this is linked to the selection of appropriate internal models for object control. This observation supports the hypothesis that interaction with an object can determine a selective two-way association between object and the body parts involved in the accomplishment of the action resulting in an experience of familiarity based on the type of interaction between the object and the effector.

In conclusion, these results, together with the findings from the other two experiments discussed in this chapter, clearly suggest that specific actions actively performed by the agent have a substantial role in selectively modulating the subjective experience of one's own body and they shed new light into the complex dynamics involved in the shaping our body representation.

Chapter 6

Personal neglect: a body representation disorder

STUDY 4

6.1 Overview

In the previous chapters, the focus has been on healthy individuals. In this last study, the representation of the hand size is assessed in a particular clinical sample. Personal neglect (PN) refers to a form of hemi-inattention toward the contralesional body space and it usually occurs following a right brain lesion (Caggiano, Beschin, & Cocchini, 2014; Caggiano & Jehkonen, 2020). PN patients show difficulties in identifying differences between left and right hands (Baas et al., 2011) and have an altered visuospatial body map, which is associated with disrupted mental body representations (Committeri, Piervincenzi, & Pizzamiglio, 2018). However, it remains unclear to what extent the impact of motor and attentional components may contribute to the manifestation of PN. In the present study, the metric representation of the hands is investigated by testing the perceived hands' width of 11 hemiplegic patients with right hemisphere cerebral lesions (5 with PN) and 12 healthy controls on a *judgment of passability* task. The findings seem to confirm an underlying distorted body representation following right brain damage. Critically, for the first time, a quantitative and qualitative difference of the impact of hemiplegia and PN on body representation of the contralesional body space is reported.

6.2 Introduction

Unilateral spatial neglect is an acquired neuropsychological disorder that affects spatial cognition, resulting in a defective ability to be aware and pay attention to stimuli located on the contralesional side (Halligan, Fink, Marshall, & Vallar, 2003; Vallar, 1998). Research on this particular disorder highlighted that neglect can be manifested with different patterns of impairment according to specific spatial frames of reference that are selectively affected (Vallar, 1998). Neuropsychological literature supports the distinction of two major sectors of space: personal space (space occupied by the body) and extrapersonal space (space surrounding the body). As regards to the extrapersonal domain, a dissociation between the near-peripersonal space (within hand reach), and the far-extrapersonal space (beyond hand reach), has been reported. However, the general term of extrapersonal neglect (EN) has often been used to classify patients who show impaired performance on standard paper-and-pencil tests (occurring in near-peripersonal space) such as the line cancellation test (Albert, 1973), the star cancellation test (Wilson, Cockburn, & Halligan, 1987) or the letter cancellation test (Diller & Weinberg, 1977) due to the lack of standardized tests assessing neglect in far-extrapersonal space (Lindell, Jalas, Tenovuuo, Brunila, Voeten, & Hämäläinen, 2007). On the contrary, patients with personal neglect (PN) show a selective “deficit relative to the side of the body contralateral to the lesion” (Guariglia & Antonucci, 1992; p.1001) whereby the contralesional half of the body is less explored (Cocchini, Beschin, & Jehkonen, 2001). For example, patients showing PN may not comb the left side of their hair, or dress only the ipsilesional side of their body. Despite PN and EN being frequently co-occurring, cases of selective PN (Guariglia & Antonucci, 1992; Beschin & Robertson, 1997; Peru & Pinna, 1997; Marangolo, Piccardi, & Rinaldi, 2003; Ortigue, Mégevand, Perren, Landis, & Blanke, 2006; Di Vita, Palermo, Piccardi, Di Tella, Propato, & Guariglia, 2016; Buxbaum et al., 2004; Guariglia, Matano, & Piccardi, 2014; Rousseaux, Allart, Bernati, & Saj, 2015) and double dissociations (Bisiach, Perani, Vallar, & Berti, 1986; Zoccolotti

& Judica, 1991; Pizzamiglio et al., 1989; Vallar, Sterzi, Bottini, Cappa, & Rusconi, 1990; Beschin & Robertson, 1997; Cocchini et al., 2001; McIntosh, Brodie, Beschin, & Robertson, 2000; Bowen, Gardener, Cross, Tyrrell, & Graham, 2005; Committeri et al., 2007; Spaccavento, Cellamare, Falcone, Loverre, & Nardulli, 2017) have also been described, supporting a differentiation between PN and EN.

In the literature, there is a growing consensus regarding the fact that PN may be ultimately related to a disrupted body representation (see Caggiano & Jehkonen, 2018; Committeri et al., 2018 for recent revisions). Studies have reported an altered visuo-spatial body map by means of the Frontal body-evocation subtest, where patients are asked to name, localize and reconstruct specific body parts (e.g., Guariglia & Antonucci, 1992; Marangolo et al., 2003; Canzano, Piccardi, Bureca, & Guariglia, 2011; Palermo, Di Vita, Piccardi, Traballese, & Guariglia, 2014; Di Vita et al., 2016). Typically, PN patients are unable to place body parts' tiles in the correct position, they tend to ignore body symmetry and confuse left with right sides. This pattern of errors is not observed when PN patients are asked to reconstruct a non-body object, such as a car suggesting that in PN, rather than having a more general representational deficit, the mental representation of the body is selectively damaged with respect to that of a common object (Di Vita et al., 2016). Further disruption of body representation in PN has been shown by means of the hand laterality task (Parsons, 1987a, 1987b), in which PN patients showed an impaired performance when asked to judge laterality of left hands and of objects manipulated by left hands, such as left rear-view mirrors (Baas et al., 2011). The authors explained the results as a general dysfunction in mental representations of the contralesional limb (Baas et al., 2011; Bisiach & Berti, 1995; Bisiach & Rusconi, 1990; Bisiach & Vallar, 2000). This distortion would affect also actions performed with this limb as in the case of left rear-view mirrors.

The hypothesis of a disruption of body representation in PN is also supported by studies on functional imaging. Committeri and colleagues (2007) observed that PN tends to be associated with lesions in the right inferior parietal areas and similar findings have been confirmed in more recent studies (Rousseaux et al., 2015; Baas et al., 2011), highlighting the relevance of inferior parietal lesions, in particular the supramarginal gyrus, in PN. These studies support the hypothesis that body centred tasks, which require conscious awareness of body representation, are affected by a functional disconnection between areas involved in processing somatosensory information, such as the post central gyrus, and areas coding for egocentric spatial information, such as and supramarginal gyrus (Galati, Committeri, Sanes, & Pizzamiglio, 2001; Committeri et al., 2007). However, despite the growing body of behavioural and neuroimaging evidence showing a strong relationship between PN and body representation, it is still unclear in which way the metric (size) representation of the body would be affected.

The present study aims at investigating how PN may modulate the perceived metric of the hand which has been specifically targeted in previous studies (Baas et al., 2011; Ronchi, Heydrich, Serino, & Blanke, 2018). The perceived dimension of the hands has been assessed in patients showing PN, patients without PN and controls by means of the aperture task. This task has been used in previous studies in the context of motor decision and affordances perception (Ishak, Adolph, & Lin, 2008; Warren & Whang, 1987). These studies have shown how body size (shoulder width specifically) is in fact used to scale the size of the apertures in order to judge 'passability' (Gordon & Rosenblum, 2004; Warren & Whang, 1987), thus providing an indirect measure of the metric representation of the body width. Performance of PN patients was compared with hemiplegic patients not showing PN and healthy controls to tease apart the impact of hemiplegia and PN on representation of the contralesional hand.

6.3 Experiment 8 – Apertures task

6.3.1 Methods and procedures

6.3.1.1 Participants

Eleven right brain-damaged patients, admitted to Casa di Cura del Policlinico (Milan, Italy) and High View Care Services (London, UK), entered the study. Ten patients suffered a stroke (1 ischemic, 7 haemorrhagic, 2 ischemic with haemorrhagic infarction) and one patient was hospitalized after parietal meningioma resection. Lesion site was documented by clinical CT or MRI scans.

Patients had no history of previous neurological and psychiatric disorders and were all right-handed, as measured by a standard questionnaire (Oldfield, 1971). Demographic and neurological characteristics of the patients are summarized in Table 1.

Twelve right-handed healthy participants with no previous history of neurological or psychiatric disease were also considered for the study. Their mean age was 42.08 years ($SD = \pm 14.25$, range 29-65), and the mean education was 13 years ($SD = \pm 5.01$; range 5–18). None of them showed physical abnormalities on their upper limbs.

The project was approved by the local Ethical Committees and informed consent was obtained from all participants according with the Declaration of Helsinki (British Medical Journal, 302: 1194, 1991)

6.3.1.2 Personal and extrapersonal neglect assessments

PN was assessed by means of the Fluff test (Cocchini et al., 2001) and the Comb and Razor/Compact test (Beschin & Robertson, 1997). In the Fluff test, blindfolded patients are required to remove 24 circles attached on the patient's clothes on the contralesional arm, the torso and both legs. The cut-off score for this test is based on the stickers detached on the contralesional left side of the body (i.e. 13 stickers detached out of 15; $\geq 86.7\%$). In the Comb and Razor/Compact Test patients are required to pretend to shave or apply make-up and to pretend to comb their hair. The number of strokes on each side of their face or head was calculated and transformed into an index of PN. Patient's

performance was compared with the cut-off ≥ -0.11 (McIntosh et al., 2000). Patients were diagnosed with PN if they scored below the cut-off criteria on at least one of these two tests.

EN was assessed through a comprehensive neuropsychological battery, including letter (Weinberg et al., 1977), star (Wilson, et al., 1987) and apple cancellation tasks, line bisection, clock drawing and complex figure drawing (Gainotti, Messerli, & Tissot, 1972). Patients were diagnosed with EN if they scored below the test cut-off on at least one of these tests.

6.3.1.3 Motor and proprioception assessment

Upper limb strength was assessed by means of the Motricity Index (Demeurisse, Demol, & Robaye, 1980). Score can range from 1 (no movement) to 100 (normal motor power). Proprioception was evaluated by asking blindfolded patients: (i) to indicate whether their left finger, hand and arm were passively moved up or down by the experimenter (*movement*); and (ii) to align their healthy right finger, hand and arm to the

Table 6.1. Demographic and neurological information of 11 right brain-damaged patients.

	Gender/Age/ Education	Oldfield	Duration of disease (months)	Etiology/ Lesion site	Lesion volume (cc)	Motricity Index (upper extremity)	Neurological examination			Proprioception	
							<i>M</i>	<i>SS</i>	<i>V</i>	<i>Movement</i>	<i>Position</i>
TW	F/61/13	.89	153	I/F P T ins	53.0	65/100	+	-	-	-	-
TA	F/79/5	.89	1	IH/F T O	73.5	1/100	++	-	++	-	-
ME	F/82/8	.68	1	H/P O	45.4	77/100	-	-	++	-	-
PM	F/68/13	1	19	H/F T P	59.4	64/100	+	ext	ext	+	++
MW	M/53/13	1	13	H/P T	na	70/100	-	-	+	-	-
CMG	F/51/13	1	3	IH/F P	167.3	26/100	++	ext	ext	-	+
VE	M/39/13	.95	30	H/F T P Ins Bg	266.2	10/100	++	+	++	++	++
CA	M/57/17	1	1	H/t	8.1	48/100	+	ext	ext	+	+
GL	F/63/13	1	1	H/t ic	3.4	73/100	+	ext	-	-	-
BO	M/55/8	.95	38	H/t ic	2.4	48/100	+	-	-	+	+
MG	F/62/8	.79	1	N/P	11.4	77/100	+	-	-	-	-

M/F: male/female; Age and formal education are expressed in years.

I/H/N: ischemic/haemorrhagic/neoplastic lesion.

F: frontal; *P*: parietal; *T*: temporal; *O*: occipital; *Ins*: insula; *ic*: internal capsule; *Bg*: basal ganglia; *t*: thalamus.

Neurological examination: *M/SS/V*, motor/somatosensory/visual half-field deficit contralateral to the damaged hemisphere; *ext*: extinction to double simultaneous stimulation (for visual and somatosensory deficit). +/+, deficit; -, no deficit. *na*: not available for mapping

same position as the correspondent left one, arranged by the experimenter in three different configurations (at the top, central, at the bottom; *position*). Furthermore, as part of the routine clinical assessment, in a sub-group of patients (CMG, VE, CA, BO, TW) cortical somatosensory evoked potentials (SEPs) were also recorded.

6.3.1.4 Aperture task

Stimuli consisted of a series of 29 A4-sized white pieces of cardboard with apertures. Each cardboard was cut in the middle in order to obtain a rectangular aperture that varied in height across each stimulus. Following a preliminary pilot study, the apertures' height ranged from 3 cm to 18 cm with an increasing rate of 0.5 cm while the width remained constant (15 cm). To minimise the impact of possible associated EN in the clinical sample, the apertures were presented vertically (see Figure 1). Participants sat on a chair in front of the experimenter with their hands on their laps concealed from sight for the whole duration of the task. The stimuli were presented (by the experimenter) one at a time on the participants' right side, in respect to their midsagittal plane, at approximately a distance of 50 cm. The task consisted of three ascending (starting from 3 cm of height) and three descending (starting from 18 cm of height) series. Participants were asked to imagine their hands with the palm wide open and the thumb stretched up almost perpendicular to the palm and decide whether each of their hands (the palm only) could fit into the aperture shown (see Figure 1). The motor component was removed as we were interested in the representational component and we asked for a 'judgment of passability' (e.g., Warren & Whang, 1987) to indirectly evaluate the patients' subjective hands' width. Participants were instructed to judge, each time, whether their left or right hand could fit in the aperture. During the descending series (from the largest to the smallest aperture) participants had to decide when the aperture became too narrow for their hand to pass through; during the ascending series (from the smallest to the largest aperture) participants had to decide when the aperture became large enough for their

palm. The stimuli presentation continued until the participants' response changed. The examiner noted the aperture size corresponding to the last 'passability' response (i.e. the size corresponding to the last 'yes' for the descending series, and the first 'yes' for the ascending series). This value was considered as the '*Imagined Width*' for that particular trial and the next presentation begun, for the same hand, in the opposite direction. Each participant was asked to consider 6 series of apertures for each hand. The presentation order of the ascending and the descending series was counterbalanced across participants as well as the order of the hands (left and right). At the end of the task, the examiner measured the real size of the participant's palm ('*Real Width*'). The percentage of under/over-estimation of the perceived hand width was calculated with the following formula:

$$\frac{\text{Averaged Imagined Width} - \text{Real Width}}{\text{Real Width}} \times 100$$

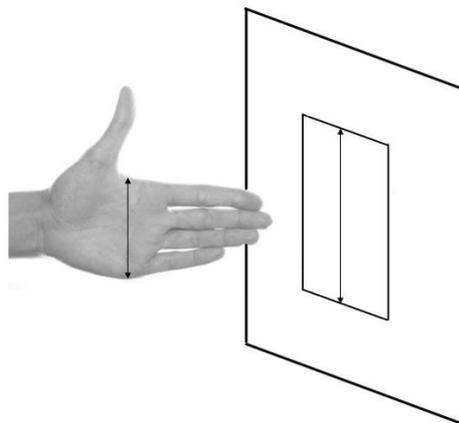
Furthermore, in order to test the body-scaled nature of the aperture judgements, a ratio between the aperture height (A) and the actual hand width (H) (A/H) has been calculated. Previous studies have used this method to confirm that passability judgements are based on body size scaling by checking the consistency in the ratio between participants (Gordon & Rosenblum, 2004; Warren & Whang, 1987). Because the A/H ratio express an intrinsic relation, the critical point should be constant across individuals of different absolute size for physically similar systems (Warren & Whang, 1987). In other words, an A/H that is consistent across individuals of different hand sizes, would suggest that participants were sensitive to the aperture in body-scaled dimensions.

6.3.2 Statistical analysis

Because of the heterogeneity and size of the sample considered, normality was not always met. Therefore, a non-parametric approach was used when necessary; Mann-

Whitney and Kruskal-Wallis tests were used when comparing two or more independent groups, respectively. Crawford and Howell's (1998) method was used for single-case analysis. Classically, methods for single case studies tend to inflate Type I error rate due to relatively small control samples (i.e. $N < 10$). The Crawford and Howell's (1998) method controls for Type I error rate regardless of the size of the control sample by treating the control sample statistics as statistics rather than as parameters and tests whether a patient's score is significantly below controls. This type of analysis has been extensively used in other studies (e.g., Della Sala, Cocchini, Beschin, & Cameron, 2009; Cocchini, Beschin, Foutopolou, & Della Sala, 2010; Cocchini, Beschin, & Della Sala, 2018; Palermo et al., 2014).

Figure 6.1. Schematic representation of the apertures task. Participants were asked to imagine whether the palm of their hand, indicated by the arrows, could fit into a series of vertical apertures.



6.3.3 Results

6.3.3.1 Personal and extrapersonal neglect assessment

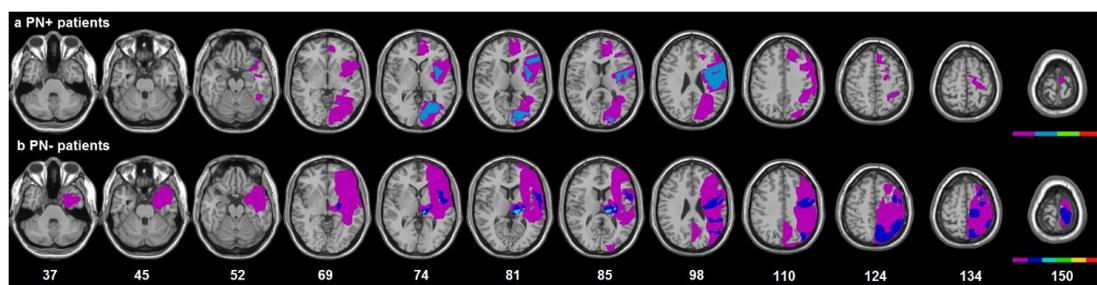
Patients were divided in two groups according to their performance on PN tests: patients showing personal neglect (PN+) and patients not showing personal neglect (PN-). Five patients were included in the PN+ group and six patients in the PN- group.

The PN+ group consisted of 4 females and 1 male with a mean age of 68.6 years ($SD = 12.14$, range 53-82), and a mean education of 10.4 years ($SD = 3.71$, range 5-13). Mean time elapsed since brain lesion of the 5 patients was 37 months ($SD = 65.14$, range

1-153); however, the group mean was skewed by one patient (TW) who was tested 153 months after the brain lesion. The PN- group included 3 females and 3 males with a mean age of 54.5 years (SD = 8.80, range 39-63) and mean education of 12.0 years (SD = 3.46, range 8-17). Mean time elapsed since brain lesion was 12 months (SD = 16.85, range 1–38). Eight patients (4 PN+ and 4 PN- patients) out of 11 showed signs of EN (see Table 2). The two groups did not show differences in terms of education [PN-: mdn = 13, PN+: mdn = 13; U = 11.5, $p = .54$, $r = .21$], onset of illness [PN-: mdn = 2, PN+: mdn = 13; U = 17, $p = .79$, $r = .12$] and age [PN-: mdn = 56, PN+: mdn = 68; U = 26, $p = .13$, $d = .52$].

The lesions' site and size were compared between the two groups. The boundaries of the lesions were drawn using the MRIcro software (Rorden & Brett, 2000) onto selected horizontal slices and mapped into a stereotactic space (Montreal Neurological Institute; Evans, Collins, Mills, Brown, Kelly, & Peters, 1993; Collins, Neelin, Peters, & Evans, 1994). The results of the lesion analyses are presented in Figure 6.2, which shows the overlapped lesion maps of 10 out of 11 right brain-damaged patients (PN+ and PN- groups). Scan images were unavailable for one PN+ (MW). The PN+ group showed the maximum overlap of lesions in the right insula, rolandic operculum, pre-central and post-central gyri and occipital lobe (2 patients); in the PN- group the maximum overlap was observed in the right thalamus (3 patients).

Figure 6.2. Superimposition of the right-hemispheric lesions for the two patient groups.



a) Four right-brain-damaged PN+ patients. **b)** Six right-brain-damaged PN- patients. Scan images were unavailable for PN+ patient MW. Montreal Neurological Institute (MNI) Z-coordinates for the shown axial slices are given. The number of overlapping lesions is indicated by different colours, coding increasing frequencies from violet to red.

6.3.3.2 Motor and proprioception assessment

On the Motricity Index for upper limb, the PN+ patients obtained an average score of 55.4 (SD = 30.8, range 1-77), while the PN- obtained an average score of 47.0 (SD = 26.0, range 10-77). Mann-Whitney U test showed no significant difference between groups on motor impairment [PN-: mdn = 48, PN+: mdn = 65; U = 12.5, p = .66, r = .13].

One PN+ patient and 4 PN- patients showed impaired proprioception for movement and position conditions on the clinical assessment.

Table 6.2. Assessment for personal and extrapersonal neglect.

	%bias	Comb and Razor/ Compact Test		Fluff test	Letter cancellation		Star cancellation		Line bisection		Apple task	Complex Figure Drawing	Clock Drawing
		L	R		L	R	80mm	160mm	L	R			
<i>PN+ patients</i>													
TW	-0.21*	53/53	51/51	100	30/30	26/26	-3	5.2	0	0/5	0/12		
TA	-0.43*	29/53*	49/51	73.3*	22/30*	26/26	-9.5*	7.3*	-1	1.5/5*	6/12*		
ME	-0.20*	44/53*	51/51	93.3	20/30*	24/26	4.8	32.6*	50*	1.5/5*	1/12*		
PM	-0.38*	46/53*	49/51	86.7	18/30*	21/26	-7.0	1.3	3*	2.5/5*	3/12*		
MW	-0.21*	0/53*	36/51	73.3*	0/30*	21/26	na	na	na	na	0/12		
<i>PN- patients</i>													
CMG	0.04	53/53	46/51	100	25/30*	26/26	4.5	5.3	0	0.5/5*	0/12		
VE	0.06	53/53	51/51	93.3	27/30*	25/26	-9*	-1.2	0	0.5/5*	0/12		
CA	-0.02	52/53	49/51	100	26/30	23/26	4	7.1*	0	0/5	0/12		
GL	-0.08	53/53	51/51	93.3	28/30*	26/26	2.5	4.6	0	0.5/5*	0/12		
BO	-0.06	53/53	51/51	86.7	30/30	26/26	3.3	0.5	0	0/5	0/12		
MG	0.01	53/53	51/51	100	30/30	26/26	0	0.2	1	0/5	0/12		

* Defective performance, as compared with normative data.

Cancellation tasks: number of correct detections in the left/right (L/R) hand-side of the display.

Line bisection: percentage deviation (-/+leftward/rightward deviation) for lines of different length: 80 and 160 mm; complex figure and clock drawing: 0/5 and 0/12 indicate errorless performances, respectively.

All the five patients tested with evoked potentials presented altered somatosensory evoked potentials. PN- patients (CMG, VE, BO) and the PN+ patient TW showed normal median and ulnar N20 conduction time and amplitude for the right side of the body, while responses were absent on the left side. In one PN- patient (CA), responses were recorded bilaterally, normal on the right side, and altered in both latency and amplitude on the left one.

6.3.3.3 Experimental task

Before running any statistical analysis, grouping criteria (based on presence/absence of PN) was tested by correlating the patients' performance for the left hand with all quantitative demographic variables (reported in Table 1) and individual scores on the personal and extrapersonal neglect tasks (reported in Table 2). This was done to consider whether other possible factors were contributing to the aperture

Table 6.3. Correlation between LH performance and demographic/assessment scores variables

Variables	Spearman correlation (n =11)	
	ρ coefficient	p value
Age	-.456	.159
Education	.203	.549
Duration of disease	-.220	.516
Lesion volume	.169	.620
Motricity Index	-.156	.648
Hand Laterality	.101	.768
Comb and Razor/Compact test	.683	.021*
Fluff Test	.587	.058
Letter Cancellation	.599	.052
Star Cancellation	.469	.146
Line bisection 80mm ^a	-.292	.413
Line bisection 160mm ^a	-.377	.283
Apple task ^a	-.291	.226
Complex figure drawing ^a	-.421	.226
Clock drawing	-.491	.125

^a data from 1 patient were not available (n =10)

* indicates significant correlation

performance for the left hand. For this reason, a series of Spearman correlations were carried out, which showed that the judgment of passability for the left hand significantly correlated with the Comb/Razor test only. Fluff test and Letter Cancellation task showed a trend (Table 6.3). This confirmed that the presence/absence of PN was the critical aspect that better justify the grouping of the patient sample.

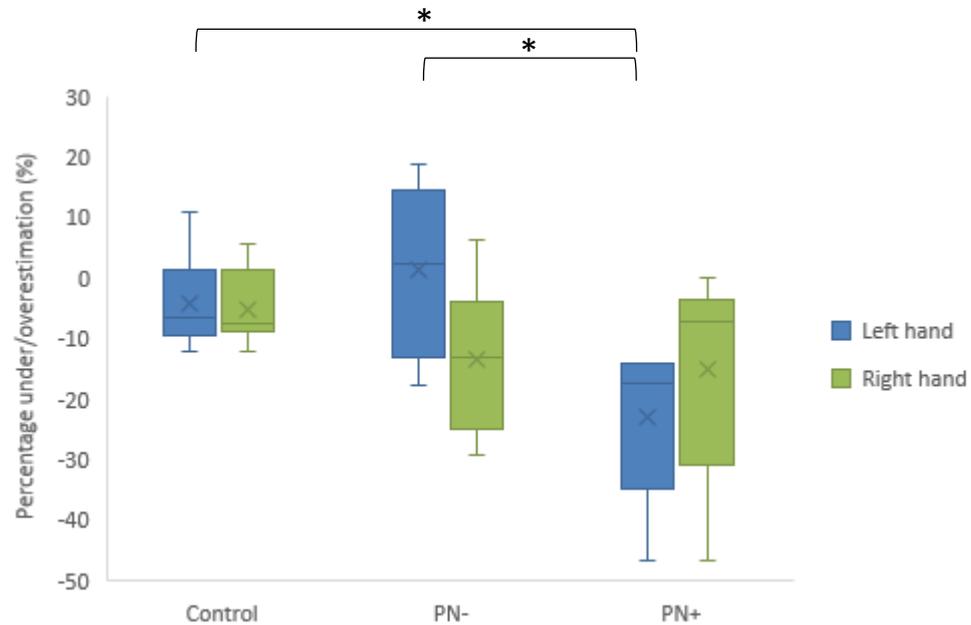
Then, the A/H ratios for the right ‘healthy’ hand were considered to evaluate the body-scaled nature of the aperture judgements. A median split approach was used to divide participants (both Controls and patients) into two major groups, *large-* (mean = 9.1 cm, SD = 1.21) and *small-*hand width (mean = 7.1 cm, SD = .32). Results showed that, the A/H ratio for the *small-*hand participants (mdn = .91) did not statistically differ from that for *large-*hand participants (mdn = .93) [U = 53.5, p = .48, r = .02]. The A/H ratios were also considered for each group. The three groups judged an aperture, for right hands, shorter than their hands width to be the boundary for hand passage (Control: mdn = .94; PN-: mdn = .93; PN+: mdn = .87); Kruskal-Wallis test did not indicate a significant difference [$\chi^2(2) = 2.17$, p = .34, $\eta^2 = .09$]. Overall, the consistency of this ratio suggests the use of body-scaled information for judging the apertures.

In light of the preliminary analysis discussed above, the under/overestimation for both hands and each of the three groups were then considered (see Figure 6.3). Descriptive statistics showed that Controls and PN+ tended to underestimate both right (Controls: mean = -5.24%, SD = 6.02; PN+: mean = -17.3%, SD = 20.56) and left (Controls: mean = -4.16%, SD = 7.52; PN+: mean = -24.58%, SD = 15.29) hands, while PN- underestimated the right (mean = -13.31%, SD = 12.6) but not the left hand (mean = 1.22%, SD = 15.23).

Kruskal-Wallis test for the three groups showed a significant difference for the left hand [$\chi^2(2) = 9.85$, p = .007, $\eta^2 = .45$] but not for the right [$\chi^2(2) = 2.21$, p = .33, $\eta^2 = .10$]. Dunn-Bonferroni pairwise comparisons for the left hand, highlighted a significant

difference between PN+ and Controls ($p = .011$), PN+ and PN- ($p = .019$) but not between PN- and Controls ($p = 1$).

Figure 6.3. Graphic representation of both left and right hands distortion for the three groups.



The middle line of the boxes represents the median, the x in the box represents the mean. The bottom line of the boxes represents the lower quartile, the top line the upper quartile. The vertical lines indicate the upper and lower extremes of each data set. * Significant difference between groups.

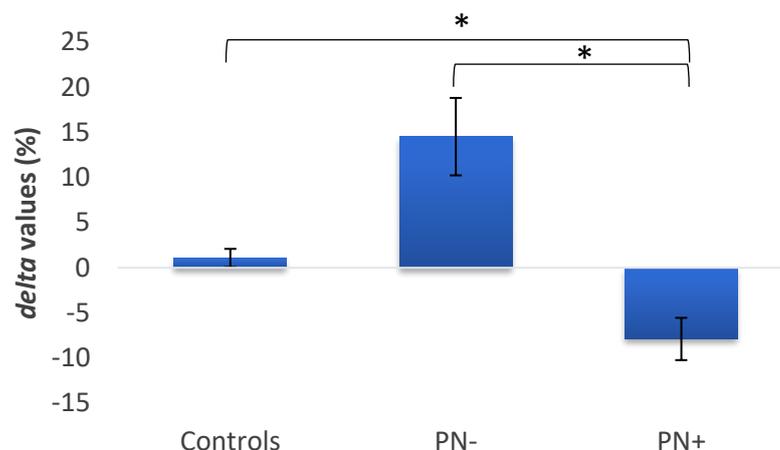
Data from the passability judgment were transformed into *delta* values by calculating the difference of under/overestimation between left and right differences hands (i.e. left hand *minus* the right hand) to highlight the degree of discrepancy among the two hands in the three groups (Figure 6.4). Specifically, negative *delta* values indicate that the left hand was perceived smaller than the right, positive values that left hand was perceived larger than the right, zero indicates no difference between left and right. Data were normally distributed by performing a Shapiro-Wilk test for each group [Controls: $W(12) = .911$, $p = .21$; PN+: $W(5) = .96$, $p = .81$; PN-: $W(6) = .97$, $p = .91$], so a parametric approach was adopted. Firstly, three one-sample t-test against zero were conducted to assess the significance of the discrepancy. Results were statistically significant for PN+ (mean = -7.89%, SD = 5.23) [$t(4) = -3.37$, $p = .028$, $d = 1.51$] and PN- (mean = 14.52%,

SD = 10.51) [$t(5) = 3.39, p = .020, d = 1.38$], but not for Controls (mean = 1.07%, SD = 3.51) [$t(11) = 1.06, p = .31, d = .31$].

Secondly, a one-way ANOVA showed a significant difference between groups [$F(2, 7.28) = 10.91, p = .006, \eta^2 = .64$]. Post-hoc analyses, adjusted for Games-Howell correction, were conducted comparing *delta* values between groups. Results revealed that *delta* values for the PN+ group were significantly different from PN- [$t(7.58) = 4.58, p = .005, d = 2.61$] and Controls [$t(5.57) = 3.51, p = .033, d = 2.01$]. The difference between Controls and PN- showed a trend close to significance [$t(5.57) = 3.05, p = .055, d = 2.32$].

As showed in Figure 6.4, the most interesting result was the opposite directions showed by the two patient groups.

Figure 6.4. Percentage difference (\pm SE) between left and right hands for the three groups.



Negative values indicate that the left hand is perceived smaller than the right hand, positive values that left hand is perceived larger than the right hand, zero indicates no difference between left and right.

* Significant difference between groups. Controls and PN- showed a trend ($p = .055$).

Finally, to further assess whether the direction of the discrepancy between the left and right hand might have been influenced by motor impairments, a Spearman's correlation between the *delta* values and the Motricity Index scores was carried out. Results showed a weak non-significant correlation ($\rho = -.153, p = .65$). When separate correlations were run for each group (PN- and PN+), only the PN- group showed a

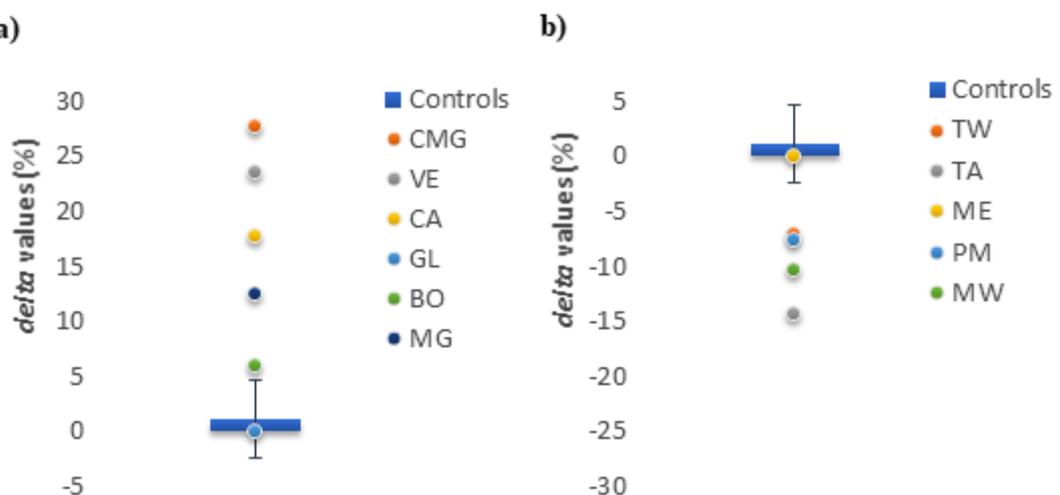
significant negative correlation with lower Motricity Index scores associated with higher *delta* values ($\rho = -.725$ $p = .05$; 1-tail); (PN+: $\rho = .700$ $p = .094$; 1-tail).

Single case analyses

To explore whether specific patients showed different patterns of responses, patients' individual performance on the Aperture task was considered. Individual results are illustrated in Figure 6.5 and show that PN+ patients tended to underestimate both hands but more the left hand with the exception of one patient (ME) who underestimated equally both hands. PN- patients showed a more heterogeneous performance in terms of under-over estimation but they tended to overestimate their left hand except for one patient (GL) who underestimated equally both hands (Figure 6.5).

To statistically investigate the difference between hands in PN+ and PN- patients, a Crawford's analysis was carried out on the *delta* values using SINGLIMS_ES.exe (Crawford & Garthwaite, 2002; Crawford & Howell, 1998). In the PN+ group, four patients out of five [TW: $t(1,12) = -2.23$, $p = .047$; TA: $t(1,12) = -4.18$, $p = .002$; PM: $t(1,12) = -2.39$, $p = .036$; MW: $t(1,12) = -3.10$, $p = .010$] showed a significant negative difference between left and right hand compared to controls. On the other hand, four patients out of six in the PN- group [CMG: $t(1,12) = 7.22$, $p < .0001$; VE: $t(1,12) = 6.11$,

Figure 6.5. Individual *delta* values for a) PN- group and b) PN+ group.



Controls' error bars indicate standard deviation.

$p < .0001$; CA: $t(1,12) = 4.48$, $p = .001$; MG: $t(1,12) = 3.11$, $p = .010$], showed significant positive *delta* values compared to controls (see Figure 6.5).

6.4 Discussion and Conclusion

Patients and controls were asked to imagine their hands with the palm wide open and the thumb stretched up almost perpendicular to the palm and decide whether the palm of their hands could fit into a series of vertical apertures. Results showed that the healthy controls exhibited an altered representation of their hands. They equally underestimated by about 5% the width of both their left and right hands, showing no evidence of hand dominance. Previous studies have reported that even healthy adults can misjudge the metric of their own body parts (Longo & Haggard, 2010; Longo, et al., 2010, Longo & Haggard, 2012; Fuentes et al., 2013; Linkenaguer et al. 2015; Cocchini et al., 2018; Caggiano & Cocchini, 2020) and the extent of the underestimation is in line with previous studies adopting a similar method of ‘passability’ (Warren & Whang, 1987; Ishak et al., 2008). Previous studies using apertures have found a tendency to undershoot the size of the hand in passability judgements, with participants trying to squeeze through apertures 7% smaller than their hand size (Ishak et al., 2008), and to underestimate the size of the whole body, with narrower apertures deemed as ‘passable’ (Warren & Whang, 1987).

In general, the majority of the patients showed a larger error than controls when estimating both hands. This could be due to various attentional and visuo-spatial factors that may have affected the patients’ ability to judge the apertures or to perform estimate tasks more generally. These factors may have affected their overall performance providing larger errors in estimating both hands. Interestingly, PN+ and PN- groups showed a profoundly different distortion of their left hand. The analysis of *delta* values showed that while PN- patients perceived their left hand larger than their right hand, PN+ patients showed the opposite pattern of data. It is, however, of particular interest to observe the significant difference between the PN+ and both groups (i.e. Controls and PN-). On the other hand, PN- showed a different representation of left and right hands

(i.e. *delta* different from zero) and a trend, close to significance, compared to Controls. The opposite pattern of results between the patient groups was also evident at individual level as shown in Figure 6.5 and following the single case analyses.

The discrepancy between the representation of the left and right hands in PN+ and PN- may be due to the combination of motor impairment and PN. Indeed, a recent study conducted by Muroi and colleagues (2017) seems to indicate that motor deficits after stroke, significantly impact on the ability to effectively walk through a narrow aperture (Muroi, Hiroi, Koshiha, Suzuki, Kawaki, & Higuchi, 2017). Critically, patients with hemiplegia not only make imprecise movements, but may have difficulties in correctly estimating the affected body size. Previous studies have shown that lack of somatosensory information, as in cases of hemiplegia or anaesthetisation, may lead to a perceived enlargement of the affected body part (Wallgren, 1954; Miles, 1956, Prevoznick & Eckenhoff, 1964; Melzack & Bromage, 1973; Nelles et al., 1999; Isaacson, Funderburk, & Yang, 2000; Gentili, Verton, Kinirons, & Bonnet, 2002; Paqueron, Leguen, Rosenthal, Coriat, Willer, & Danziger, 2003). Furthermore, some studies have reported that patients do have an illusion of swelling (i.e. increased width) of their entire upper or lower limb(s) following deafferentation. In these circumstances, perceived changes in body size may be explained by the removal of inhibitory background activity at different stages of the somatosensory pathway (Dykes & Lamour, 1988; Dykes & Craig, 1998), leading to a reorganization of overlapping sensory maps in the somatosensory cortex (Calford & Tweedale, 1988, 1991). Similarly, in hemiplegic patients the motor deficit associated with the ‘underused’ limb, impacts on the cortical representation of somatosensory and motor body maps, resulting in a form of maladaptive plasticity (Dohle et al., 2009).

In line with this literature, it is possible that hemiplegia may have led to a maladaptive plasticity effect, inducing a subjective ‘enlargement’ effect of the affected limb. As a result, PN- tended to represent their left hand larger than the right one. This

aspect is particularly important as also PN+ patients showed motor impairment and, based on this possible effect, a similar trend in the PN+ group should be expected. Yet, PN+ patients displayed the opposite trend with a significant underestimation of the affected hands. Individual results (see Figure 6.5 and single case analyses) show a consistent result across the PN+ patients who judged the left hand smaller than the right one. It seems therefore that, despite the possible ‘enlargement’ effect of the affected limb due to the associated motor impairment, PN has induced an opposite and larger impact on the representation of the neglected side of the body.

In the previous chapters it has been discussed how somatosensory information can modulate conscious body representation and how evidence of distorted body metrics can be explained in light of such assumption.

It should be noted that the frequency of patients showing sensory/proprioceptive deficits was larger in the PN- group compared to the PN+. This observation could suggest that PN- hand’s asymmetry could be the results of a primary motor and sensory deficit (bottom-up). However, if this explains the difference between the two patients’ group, it does not account for the difference between PN+ and controls. In fact, even in case of less impairment associated with a primary sensory deficit, PN+ patients performed significantly worse than controls, suggesting a primary disturbance of high-order body representation (top-down). Furthermore, it is reasonable to argue that the hand distortion observed in both patient groups cannot be the result of a general attentional deficit (de Vignemont, 2010) or allocentric neglect of the aperture, as in this case we would have observed a similar impact of passability responses for both hands and both patient groups. Also, the results cannot be interpreted as an effect of EN components as we would have observed the same pattern of distortion in both groups. On the contrary, the findings are better explained as a primary disturbance of body representation.

Lesion analysis on the PN+ sample, highlighted an involvement of the right insula, rolandic operculum, pre- and post-central gyri and occipital lobe. Recent studies have suggested that PN can be the consequence of a functional disconnection between regions that code motor and somatosensory input, such as the postcentral gyrus, and those which encode more abstract egocentric representation of the body in space (Coslett, 1998; Galati et al., 2001; Committeri et al., 2018). As a consequence, PN+ patients may find difficult to create a mental model of the *body image* and be aware of the configuration and motion of body in space (Galati et al., 2001). These observations, combined with evidence from recent studies (Committeri et al. 2007; Rousseaux et al. 2015; Baas et al., 2011), seem to further strengthen the hypothesis that a deficient body representation is the major mechanism underlying PN.

To summarize, the task consisted in imagining whether hands could fit into a series of vertical apertures; a control group and two patient groups used their '*judgment of passability*' to estimate the perceived subjective hand size. While the controls showed some degree of underestimation similar for both left and right hands, the patients' groups showed a larger degree of distortion of the contralesional hand and in opposite direction. Due to the heterogeneity of the sample and its relatively small size, results should be taken with caution. Nonetheless, the findings seem to be in line with the most recent literature on PN and open a new window for possible future studies on body metrics in disorders for the personal domain.

Chapter 7

General discussion

For long time, philosophers of the mind and cognitive scientists have considered the ‘body’ as of relatively marginal relevance in the quest to understand the nature of the mind and cognition, often confined within the boundaries of the mind-body dualism. Only in recent years, the debate on *embodied cognition* has become increasingly vivid in cognitive science (Adams, 2010; Aizawa 2007; Chemero, 2009; Shapiro, 2011). In a nutshell, embodied cognition posits that cognition is strongly influenced by aspects of an agent's body beyond the brain itself (Wilson & Foglia, 2011). In fact, it is through our bodies, and their perceptually guided motions, that we can achieve most our goals. In this view, cognition can be said to be embodied because it is affected by the way the body is represented in the mind (Gallagher, 2005).

In light of the above, it is rather surprising that the body, which should be central within this context, is often given for granted and very rarely explicitly investigated. Only recently new interest in the how the body is experienced has grown. Without entering into the debate of embodied cognition (which was not the primary aim of the present work), the current thesis has added an additional tile to the complex puzzle of the body representation. Understanding how body representation develops and its impact on the subjective experience, may ultimately help to understand cognition within the frame of embodied cognition.

In the following section, a summary of the main results reported in the studies presented in this thesis is will be outlined. In the second part of this general discussion, a broader argument on the principles behind the functional organisation of the body will be provided. Finally, to conclude the chapter, the implication of the findings will be discussed.

7.1 Summary of main findings

Study 1 confirmed previous results on bodily distortions and clearly highlighted a specific and stereotyped pattern according to which the upper and lower parts of the body appear to be asymmetrically represented. Specifically, it was reported that the forearms were considerably underestimated, whereas the lower legs were overestimated. The paradigm adopted consisted in a modified version of the BIT, originally proposed by Fuentes et al. (2013). In this particular version of the task, participants were asked to identify their own body parts *in* the extrapersonal space and in real scale by means of a laser pointer. With these two critical manipulations, it was possible to provide a novel insight into the nature of bodily distortion. Firstly, while Fuentes and collaborators (2013) did not find a significant correlation between the represented measures and true body size, such correlation was indeed found in the present study. Secondly, and perhaps more interestingly, it was observed a consistent correlation between the represented arms and torso length. The pattern of findings reported were interpreted as the result of how body parts are used in space when performing actions, which allowed to argue in favor of a *functional* dimension of the upper and lower body (Reed & Farah 1995; Fuentes et al., 2013).

This observation was further confirmed in a second experiment where the metrics of the body image were explicitly assessed by means of a depictive task. Critically, the perceived limbs length (i.e. arms and legs) maintained a similar degree of distortion with arms being shorter and legs longer. It was argued that the represented length of body parts can be defined by the relationship with other body parts rather than an intrinsic distortion of each part. Furthermore, it was stated that the asymmetrical representation for upper

and lower parts of the body could be interpreted considering the functional link between specific body parts and the actions we perform with them.

To further probe the *functional hypothesis*, in Study 2 a priming paradigm was adopted and a specific prediction was set. Specifically, if the representation of body parts carries information concerning their functional role, then the visual presentation of objects would facilitate visual recognition of the body part associated with the object. By means of a priming paradigm, behavioural data showed that participants performed better on trials in the object-Related compared to the object-Unrelated conditions (confirming the original hypothesis). However, the performance on the object-Neutral condition was not significantly different from the Related condition, showing only a trend. Despite the findings seemed to indicate a pre-existing link between an object and its related body effector, it was not possible to fully determine whether the priming elicited a facilitation for object-effector congruency or acted as a distractor for object-effector incongruence. In order to disentangle the possible underlying mechanisms involved in the priming effect, the same paradigm was adopted in a further experiment that looked at the electrophysiological correlates in a region strongly associated with full body and body parts visual perception (i.e. EBA). Results showed a differential modulation of the N200-P300 complex according to the different conditions. It was observed a systematic modulation of the N200 component during body part visual presentation with similar amplitudes for the Unrelated and Neutral conditions, which both significantly differed from the Related one. The data were interpreted as the result of possible early semantic processing according to which objects that are congruent with the effector facilitate the early visual recognition the of the subsequently presented body part involved in their use. On the other hand, the P300 component appeared to be larger for the Unrelated condition compared to the Related one. In light of this, data seemed to suggest that two processes might be involved: the object-body part congruency seems to facilitate early visual

recognition; however, this effect is quickly modulated by a second process that weights incongruence, strongly based on the previous knowledge of the objects. The relevance of these results is particularly noteworthy. In fact, while in literature there is substantial evidence suggesting that the observation of, for example, a hand activates motor information that can influence objects categorization (Borghi et al., 2007; Bub, Masson, & Lin, 2013; Vainio, Symes, Ellis, Tucker, & Ottoboni, 2008), the same cannot be said in regards to the role of objects in modulating body parts visual processing. By means of a priming paradigm, for the first time it was shown, both at a behavioural and electrophysiological level, that an object (with motor valence) can influence the recognition of its effector.

Bayesian inference and probabilistic integration of prior knowledge has been increasingly used to provide a new conceptual framework of body representation (Pitron et al., 2018; Pitron & de Vignemont, 2017; Blanke, Slater & Serino, 2015; Samad, Chung & Sham, 2015; Kammers, Mulder, de Vignemont & Dijkerman, 2009). In a nutshell, a Bayesian model starts with some a priori knowledge about the body and its constraints and it aims at computing the posterior probability, that is, the degree of belief in the prior hypothesis conditioned on the observation of sensory evidence. Within this view, and in light of the results provided, perceiving a body (part) is not merely based on visual characteristics, but influenced and dynamically modulated by interacting factors such as motor experience, expectation and attention. Therefore, these factors (i.e. the prior expectation elicited by the prime) may trigger the formation of the expected body part (i.e. the one functionally related to the prime), which can then be compared with the actual visual input. The finding reported in Study 2 provided additional support to this new reconceptualization of body representation and open a new window into the study of the weight of other potential contributors to body perception.

Study 3 sought to investigate, in three different experiments, the *functional hypothesis* by assessing the role of actions in shaping conscious body representation; specifically looking at its contribution in modulating both body metrics and body parts visual recognition. Results from Experiment 5 showed that a significant modulation of the perceived body parts' length occurred when participants were asked to perform a motor task on the floor (*Down-training* group) but not when the sorting occurred on a table (*Top-training* group). The training had an effect on the upper arms and torso, with both of them being significantly less underestimated in the post-training phase compared to the pre-training phase. While in literature consistent evidence has been reported on the effect of motor training in reshaping one's own body representation (e.g. extending peripersonal space and modulating the subjective length of related body parts), the effect of motor trainings in different sectors of the space has never been systematically explored. The results of Experiment 5 highlighted that, although motor training is relevant to modify the perceived length of body segments, the location in which the action occurs also plays a role. A central idea of the *functional hypothesis* is that the body is functional because specific actions need to be performed with specific body parts in order to appropriately interact with the environment. While Experiment 5 looked at the *where*, Experiment 6 looked at the *how*.

In Experiment 6, the weight of motor components (proximal versus distal), task demands (hit versus grasp) and tool-use (same goal versus different action) was assessed in respect to participants' performance on the forearm bisection task. For the very first time, the effect of specific motor programming was disentangled from the more general concept of motor training in the dynamic modulation of body representation.

Firstly, even in this task, it was observed an underestimation of the perceived forearms length at baseline. Secondly, after the proximal tasks, the post-training results showed that a shift of the perceived midpoint in the same direction occurred with and

without tool. This indicated that motor pattern (similar for the two proximal trainings with and without tool) was critical in driving the direction of the perceived arm length.

However, the effect was more pronounced with tool suggesting that tool-use can enhance a potential modification of body metric representation. Crucially, the observed proximal shift of the perceived midpoint after tool-use, openly contrast with the distal shift classically reported in other studies on tool-use (Garbarini et al., 2015; Sposito et al., 2012). As such, the results raised an intriguing consideration into others potential contributors to the body schema malleability such as the specific actions required by the agent for tool use. It was argued that the effect might be related to the agency experienced during the tool-use. Tool use involves several cognitive components, from the perceptual integration of somatosensory and visual input of the morphological and functional features of the tool, to the semantic aspects of tool recognition and the selection of motor patterns for the appropriate use of the tool (Maravita & Iriki 2004; Johnson-Frey Newman-Norlund, & Grafton, 2005; D'Angelo et al. 2018).

Along those lines, it was also shown that motor training does not only modulate body metrics (Experiment 6), but likewise lead to a selective advantage in recognising the body part used with during a training (Experiment 7). Findings indicated that the priming effect selectively emerged after a motor-training for the trained body part. This expands upon current literature as it shows that not only do visual objects activate motor information but that they are specifically linked with the representation of the effector. Such link can be potentially explained as a consequence of the pre-activation of the motor system following a training session.

Lastly, Chapter 6 investigated the perceived metric of the hand in Personal Neglect (PN). It was shown, for the first time, that PN patients not only may present an altered visuo-spatial body map (Guariglia & Antonucci, 1992; Marangolo et al., 2003; Canzano, et al., 2011; Palermo et al., 2014; Di Vita et al., 2016) and show an impaired performance

when asked to judge laterality of left hands (Baas et al., 2011); but that they dramatically underestimate their left hand size compared to both healthy controls and patients not showing PN. Furthermore, the analysis of left-right discrepancies showed a significant difference between the two patient groups. Interestingly, while in the patients group showing PN the left hand was more underestimated than the right, the patient group without PN showed the opposite pattern.

This result is of particular relevance for two main reasons. First, indicates that both bottom-up and top-down processes can differentially impact on the body representation. Second, it strongly suggests that PN is associated with a primary disruption of body representation. In fact, while motor and somatosensory impairment may explain the results from the PN-, it surely does not for the PN+ group. The frequency of patients showing sensory/proprioceptive deficits was larger in the PN- group (compared to the PN+), which could explain the difference between the two groups. However, although PN+ showed less impairment (compared to PN-), they showed a significant discrepancy between the left and right hand and, crucially, performed significantly worse than controls. It was stated that hemiplegia and/or anaesthetisation can result in acute increases in perceived size, and particularly in increased width (Gandevia & Phegan, 1999; Paqueron et al., 2003), potentially explaining the left/right hand asymmetry in the PN- group. This seems to suggest that while bottom-up sensory information can modulate body representation (as also clearly shown in Chapters 4 and 5) in the PN- group; in the PN+ patients, another mechanism (top-down) must be involved that explains the results. Arguably, motor and somatosensory impairments may have led toward an overestimation of the left hand compared to the right, in both patient groups. However, while the PN- group showed only the impact of motor and sensory deficit, the PN+ group showed an underestimation of the affected hand, which was at the net of the opposite trend due to motor impairment. In this sense, sensory information may have less weight due to the fact

that in PN is the body representation itself that is primarily disrupted (Gallagher, 2008; Guariglia & Antonucci, 1992; Di Vita et al., 2016).

A final consideration concerns the experimental procedure adopted in the study. The finding reported, indicates that the aperture task was effective at teasing out different body representation deficits in patients with and without PN. Further implementation and refining of the procedure mentioned above, can lead to the development of potential diagnostic tools aiming at evaluating the impact of different body representation deficits on affordance perception in patients with brain damage. This could have practical implication in better understanding and evaluating possible patients' difficulties in activities of daily living.

7.2 Function, integration and construction of the body representation(s)

Body representation plays a vital role in our interaction with the environment. To compute these movements, our brain needs to represent the configuration of our body segments in space. Taken together, the studies reported in this thesis provide a comprehensive investigation of the interaction between *body image* and *body schema* and evidence of the *functional* dimension of body representation.

The notion of a functional 'architecture' of body representation is not entirely new. Previous studies have suggested that the conceptual organization of the human body is based on its ability to perform action. For example, Reed et al. (2004) reported the emergence of specific clusters (arms, legs head/torso) following a sorting tasks in which participants had to place body parts that were similar into the same category. Interestingly, legs and feet were categorized together as also were arms and hands. The way body parts were clustered strongly indicated that the distinction was based neither on body part significance (i.e. cortical representation) nor on visual characteristic (such as size or contour discontinuity) but on the functional role of body parts in action (Reed et al., 2004). Similarly, Bläsing et al. (2010) investigated the mental representations of body

parts and body-related activities in individuals with congenitally absent limbs (with and without phantom sensations). In their study, the authors asked participants to group body parts and related activities according to whether or not they were considered related, based on their own body perception. While the control groups and the participants with phantom limb sensation revealed separate clusters for the lower and upper body, the participants without phantom sensations showed a different clustering pattern. Consistent with participants' specific way of using the foot for 'manual' and communicative activities, the conceptualization of, for example, the *big toe* was integrated with upper body parts (i.e. mouth, forehead, and chest) and activities such as talking, writing and pointing, suggesting that body representation can be strongly influenced by action concepts (Bläsing, Schack, & Brugger, 2010).

This thesis provided further evidence for a strong interaction of action-based and conceptual body representations on a functional level by means of Experiments 3, 4 and 7. Furthermore, and perhaps more importantly, it was shown that the 'functional' representation is not merely 'conceptual', but it is actually reflected in the way individuals represent the length and proportions of specific body parts (Experiments 1, 2, 5 and 6). Indeed, the visual perception (and representation) of our body cannot be reduced to the *mere* visual discrimination given by visual inputs (i.e. physical characteristics of the body). The experience of seeing and perceiving our own bodies is conditioned by our attitudes toward it, our physical posture, motor control as well as pragmatic intentions and responses to environmental stimuli (Gallagher, 2005).

Lastly, despite sensory input is pivotal in building our own body representation, it should be acknowledged, in this circumstance, the valence of an old adage, often associated with Gestalt psychology, '*the whole is more than the sum of its parts*'. In Chapter 6, the study on the clinical sample showed that in body representation, in particular the hand size, can be disrupted even in absence of primary evident

somatosensory and motor deficits. This highlighted how body representation involves higher-order cognitive processes not strictly reducible to individual lower-order sensory modalities.

In the introduction, it was discussed how different sensory modalities play a fundamental role in the way we construct the variety of multisensory representations that we use to perceive our bodies and that, ultimately, are critical to interact with the external environment. In Chapter 2, it was pointed out that a number of experimental evidence support the distinction of different body representations. This distinction has proven to be effective in implementing experimental paradigms and test hypotheses; however, it is evident that when perceiving the body, sensory information is not discrete nor comes in isolation, but it is rather integrated. Recently, scholars have started to question the strict differentiation proposed by the dyadic and triadic models of body representation. On one hand, there are approaches that favour multiple body representations (e.g. Longo et al., 2010; Medina & Coslett, 2010; Berlucchi & Aglioti, 2010); on the other, there are approaches that re-define the dichotomy in terms of online and offline body representation (Carruthers, 2008) or suggest an interaction between *body schema* and *body image* (De Vignemont, 2010). The idea of interacting body representations has been strongly supported and recently formalized by Pitron and colleagues (2010). The authors suggested that information coming from different sensory modalities determines the construction of body representation. In this sense, the action-based *body schema* and perception-based *body image* interact and reshape each other in a cyclic process of *co-construction*.

Both approaches (dissociation vs integration) are not necessarily, at least in principle, mutually exclusive. Indeed, identifying and dissociating multiple sensory processing mechanisms is effective at explaining the independence between representations. Identifying, instead, shared mechanisms help at explaining the

associations between representations of one's own body motricity and visual processing. In this view, rather than disregarding one or the other approach, the goal should be identifying what is the weight or impact of each modality on different body representations (i.e. *body schema* and *body image*) and, how these representations interact to produce an integrated body representation.

In the light of these statements and the studies reported in this thesis, there seems to be evidence for a strong interaction of action-based and conceptual body representations on a functional level. Throughout this thesis, it has been reiterated several times that the way we represent our body has profound implications in the way we perform appropriate actions. Yet, it is worth to note that action has not been, for long time, a central concept in the body representation literature. Only in the last decade, studies have started to specifically address the role of actions in body representation with a strong focus on tool-use (Bruno et al., 2019; Romano et al., 2019; Sposito et al., 2010; Cardinali, Frassinetti, et al., 2009; Maravita & Iriki, 2004). In this thesis, the role and the weight of actions was explicitly addressed under a different perspective: the way we perform actions affects our way of representing the body. It was shown that the plastic changes that happen after motor training are strictly depending on the functional use of the body part. Some of these changes rather than being short-termed can affect long-term properties of the body representation (such as body metrics) as consequence of experience. This was clearly evidenced in Chapter 4 and it is also supported by other studies that show that motor expertise can modulate and have profound and long-lasting effect on body representation. For example, it has been shown that expert magicians are more accurate in representing their own hands compared to naïve-to-magic individuals (Cocchini et al. 2018). On the other hand, a recent study on elite baseball players conducted by Coelho and collaborators (2019), showed that when compared to the controls, these professionals underestimated hand width and finger length of their hands.

So, while in some circumstances expertise can improve body representation, other times, it does not. Nonetheless, if the modulation of body representation is considered by factoring in the specific function (and purpose) of a training, it becomes possible to better understand the nature and direction of this modulation. Magicians have to pretend to perform an action while they are actually performing a different one, this does indeed require a relatively accurate representation of the hand (Cocchini et al. 2018). On the other hand, a smaller hand representation for baseball player can be beneficial in terms of increased control of precision movements, which would reduce the margin of error when catching a ball (Coelho et al. 2019). These observations, coupled with the data reported in the present work, seem to suggest that ‘functionality’ can be determinant factor in body representation (Caggiano & Cocchini, 2020; Bläsing et al., 2010). In this view, further studies on the role of expertise can provide an excellent opportunity to continue to explore the link between bodily distortions and the perceptual experience of the body parts.

By systematically evaluating the role of ‘actions’, the evidence reported in this thesis provided empirical support to the *co-construction* model (Pitron et al. 2018), in particular to two outstanding questions considered by the authors: i) a systematic interaction between the body image and the body schema with ii) the process of co-construction being serial rather than parallel. Contrary to the general assumption that *body image* is a stable representation compared to the *body schema*, it has been shown that both representations are relatively malleable. They can reciprocally influence each other with a possible primacy of motor information, which becomes engrained into the conscious body representation to reflect our experience and adaptation to the environment.

Critically, sensorimotor control is an ability that is acquired and refined over time and, as such, it is the result of an experiential process (Zoia et al., 2007). This point is of particular relevance when considering the results from Study 3 (Chapter 5). In Experiment 5 the modulation of body proportions occurred as result of the ‘less canonical’ position

where the task had to be performed. Participants ‘experienced’ a new setting according to which the subjective body representation had to be adjusted. In Experiment 6 the significant modulation occurred when participants had to operate a tool. In Experiment 7, a better performance was observed on the trials where the prime-target pairing was consistent with the previous motor experience with the object. Arguably, across the three experiments, the trainings engaged (and shaped) the action-based *body schema* yet, this effect was translated and reflected into the conscious body representation (*body image*). In fact, the adjustment of the represented body metrics and the visuo-perceptual modulation of body parts occurred, plausibly, because particular motor programs had to be implemented to accomplish the tasks at hand.

Notably, the present work has been exclusively focused on the role of *body schema* in modulating the conscious *body image*. However, as described in Chapter 2, the *co-construction* model postulates a feedback loop in which the *body image* also can influence and recalibrate the *body schema*. Therefore, the modulation of the *body image* as a consequence of a motor training - which involves the *body schema* -, should potentially lead to a subsequent modulation of other aspects of motor behaviour. A possible way of testing this hypothesis could be by expanding the methodology adopted in the present work. For instance, a future study could test whether the subjective change of the arm length, induced by a specific motor training (e.g. hitting a ball), can modulate the motor performance on a second task that is different, in both purpose and motor programming, from the one used to induce the subjective change (e.g. reach-to-grasp).

All these observations make a strong call for a reconceptualization of the empirical investigation of body representation. In literature, it has often been pointed out that body representation is susceptible to experimental task demands hence, different paradigms and measures may lead to different results (de Vignemont, 2010). Because the body representation is multimodal and extremely complex in its nature, this observation is not

entirely surprising but pose a significant question in regard to how overcome this potential limitation. One possible solution could be to start adopting a ‘comparative’ approach. So far, research has tackled body representation by devising studies that address *a* specific question with *a* specific experimental paradigm (for example, in the case of body metrics: BIT, bisection task, measure estimate tasks, perception of distances between tactile stimuli, etc.). In the few instances where different paradigms have been adopted in the same study, these have been used on different samples. Of course, by doing so it has been possible provide far more details about the specific experimental question under exam, but a ‘comparative’ approach can offer different perspectives and detect issues that would not emerge from using one paradigm in isolation. Therefore, it could be proposed to adopt a series of, now, well-established experimental paradigms to measure, for example, bodily distortions and evaluate the potential discrepancies between results obtained with different measures on the same sample. Such comparisons of would force researchers to ask questions such as why under the same experimental manipulation did a certain measure produce result R_1 and another measure a different result R_2 ? Even more interestingly, what are the consistent results between different measures? What these differences/consistencies tell us about the nature of body representation?

7.3 Limitations

The present work has addressed two particular aspects of body representation: body metrics and action. The possible link between these two components has been clearly investigated and the *functional hypothesis*, according to which action can impact on the conscious representation of the body, has been explicitly evaluated. It is however worth mentioning that other studies have not come to similar conclusions. For example, Tsakiris et al. (2011) suggested that interoceptive stimuli, rather than body practice, are of particular relevance for constructing the perception of body size estimation. Similarly, Tessari and colleagues (2012) argued that, although the body structural description represents the biomechanical constraints of the human body, it is mainly visuo-spatial in

nature and does not strongly rely on motor and proprioceptive (action-based) representations (Tessari, Ottoboni, Baroni, Symes, & Nicoletti, 2012).

Body representation is complex and multimodal, as also pointed out by Pitron and colleagues, in the process of its ‘construction’ many factors such as visual information, semantic knowledge, social and affective factors come into play. All these aspects have not been evaluated in the present thesis resulting in an important limitation of this work.

7.1 Concluding remarks

Our own body may seem to be the ‘object’ we know the best as we constantly receive a flow of information about it through bodily senses. Yet, although we constantly use our body, we rarely actively reflect upon it. As mentioned in the opening paragraph of the current chapter, within the field of embodied cognition, if bodily representation is pivotal in the implementation of basic cognitive skills, such as behaviour recognition, arbitration and imitation, sense of agency, and self–other distinction (Schillaci, Hafner, & Lara, 2016); it is then of critical importance to understand how the body is represented.

According to the embodied cognition framework, brain development is modulated by sensory information experienced by individuals while interacting with the external environment (Barsalou, 2008). It has been suggested that the meaning of concepts comes through embodied cognition; for example, physical concepts such as running and jumping, can be understood through the sensorimotor system, as they can be performed, seen, and felt (Lakoff, 2014). Indeed, evidence from fMRI studies showed that action words that are semantically related to different parts of the body activate the motor system in a somatotopic manner, suggesting relatively strong a functional connection between the language and regions and the sensorymotor system (Pulvermüller, 2005). Similarly, Varela, Thompson, and Rosch (1992) argued that the interactions between the body and the environment determine the way the world is experienced. The close link between body representation, action and external space has been highlighted, for example, in a study

conducted by Linkenauger, Bühlhoff, and Mohler (2015). By means of virtual-reality technology, the authors induced participants the illusion of having a long or short arm. Intriguingly, the modulation of the arm's reach (i.e. long or short) systematically influenced the perceived distance to targets: closer when the virtual arm was long, further away when their virtual arm was short. Likewise in another study, D'Angelo and colleagues (2019) induced a body-swap illusion with a tall (or small) mannequin and found that when participants experienced ownership of having a tall (or a short) body, this significantly modulated the representation of social and action space.

These considerations, combined with the results reported in this thesis, shed light on the close interconnection between body representation and action. The malleability of bodily experience, it can be argued, may well have implications in the rehabilitation domain. The variety and number of body awareness disorders reported in literature, encompassing both the neurological and psychiatric field, is curious and exceptional, to say the least. Does this mean that for each syndrome a specific body representation is disrupted? In the opening chapters it has been discussed how deficits in body representation helped to identify different body representation components, however it cannot be denied that deficits of *body schema* and *body image* are often associated and difficult to disentangle (de Vignemont, 2010). The complexity of body representation syndromes arises from simultaneous deficits of the *body schema* and the *body image*. It is therefore crucial to understand the interaction between these components in order to, potentially, take advantage of the interplay between body representations to ameliorate distorted body representations. Pushing a bit further, it can be speculated that these findings can have a potential impact in the field of augmentation technology such as limb prosthetics (Maimon-Mor, Schone, Moran, Brugger, & Makin, 2020; Maimon-Mor, Obasi, et al., 2020; Sato, Kawase, Takan, Spence, & Kansaku, 2017). Research has shown that we do not experience conscious ownership over most of the tools that we use

(Holmes, 2012). In Chapter 5 it was suggested that agency may have a possible influence in modulating body representation, as also indicated by other studies (Bruno et al., 2019; D'Angelo et al., 2018). Studies have reported that although both sense of ownership and sense of agency are, at least partially, independent mechanisms (Kalckert & Ehrsson, 2012; Braun, Thorne, Hildebrandt, & Debener, 2014; Cioffi, Hackett, & Moore, 2020), if they co-occur in experience, they may strengthen each other (Dummer, Picot-Annand, Neal, & Moore, 2009; Kalckert & Ehrsson, 2012; Braun, Emkes, Thorne, & Debener, 2016, Braun et al., 2014). Voluntary action provides important information about the sensory events that reflect what is my 'own body' and those ones that do not (Van Den Bos & Jeannerod, 2002; Synofzik et al., 2008b). Moving the body produces a distributed and integrated experience of the body (de Vignemont et al., 2009) therefore; actions may induce a stronger experience of ownership. By expanding our knowledge on the role of actions on body representation, we could possibly exploit agency to increase ownership of, for example, artificial limbs and achieve more complex and dynamic representations of motor abilities incorporated in one's own body representation.

Far from being conclusive, the present work has attempted to fill a gap in the current body representation literature. While some aspects have been addressed, many others need to be further investigated. This work represents a starting point for an empirical reconceptualization of this wide and rather complex puzzle.

References

- Adams, F. (2010). Embodied cognition. *Phenomenology and the Cognitive Sciences*, 9(4), 619–628.
- Aizawa, K. (2007). Understanding the Embodiment of Perception. *The Journal of Philosophy*, 104(1), 5-25.
- Albert, M. L. (1973). A simple test of visual neglect. *Neurology*, 23(6), 658–664.
- Ambroziak, K. B., Tamè, L., & Longo, M.R. (2018). Conceptual distortions of hand structure are robust to changes in stimulus information. *Consciousness and Cognition*, 61, 107–116.
- Anema, H.A., van Zandvoort, M. J., de Haan, E. H., Kappelle, L. J., de Kort, P. L. Jansen, B. P., & Dijkerman, H. C. (2009). A double dissociation between somatosensory processing for perception and action. *Neuropsychologia*, 47(6), 1615-2.
- Anstis, S. M. (1964). Apparent size of holes felt with the tongue. *Nature*, 203, 792–793.
- Asanuma, H., & Hunsperger, R. W. (1975). Functional significance of projection from the cerebellar nuclei to the motor cortex in the cat. *Brain Research*, 98(1), 73-92.
- Astafiev, S. V., Stanley, C. M., Shulman, G. L., & Corbetta, M. (2004). Extrastriate body area in human occipital cortex responds to the performance of motor actions. *Nature Neuroscience*, 7(5), 542-548.
- Baas, U., de Haand ,B., Grässli, T., Karnathd, H.O., Mueria, R., Perrig, W.J., Wurtz, P., & Gutbrod, K. (2011). Personal neglect - A disorder of body representation? *Neuropsychologia*, 49, 898–905.
- Barba, C., Frot, M., & Mauguière, F. (2002). Early secondary somatosensory area (SII) SEPs. Data from intracerebral recordings in humans. *Clinical Neurophysiology*, 113(11), 1778-86.
- Barbas, H. & Pandya, D. N. (1987). Architecture and frontal cortical connections of the premotor cortex (area 6) in the rhesus monkey. *Journal of Comparative Neurology*, 256, 211-228.
- Barsalou, L., W. (1999). Perceptual symbol system. *Behavioral and Brain Sciences*, 22, 577–660.
- Barsalou, L., W. (2008). Grounded cognition. *Annual Review of Psychology*, 59, 617–645.
- 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

- Benedet, M. J., & Goodglass, H. (1989). Body image and comprehension of body part names. *Journal of Psycholinguistic Research*, 18, 485-496.
- Berlucchi, G., & Aglioti, S. (2010). The body in the brain: neural bases of corporeal awareness. *Experimental Brain Research*, 200(1), 25–35.
- 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.
- Bisiach, E., Perani, D., Vallar, G., & Berti, A. (1986). Unilateral neglect: personal and extra-personal. *Neuropsychologia*; 24(6), 759-767.
- Bisiach, E., & Berti, A. (1995). Consciousness in dyschiria. In M. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 1331–1340). Cambridge: MIT-Press.
- Bisiach, E., & Rusconi, M.L. (1990). Break-down of perceptual awareness in unilateral neglect. *Cortex*, 26(4), 643–649.
- Bisiach, E., & Vallar, G. (2000). Unilateral neglect in humans. In F. Boller, J. Grafman, & G. Rizzolatti (Eds.), *Introduction/attention* (2nd ed., Vol. 1, pp. 459–502). Amsterdam: Elsevier Science B.V.
- Blanke, O., Slater, M., & Serino, A. (2015). Behavioral, Neural, and Computational Principles of Bodily Self-Consciousness. *Neuron*, 88(1), 145-66.
- Blankenburg, F., Taskin, B., Ruben, J., Moosmann, M., Ritter, P., Curio, G., & Villringer, A. (2003). Imperceptible stimuli and sensory processing impediment. *Science*, 299(5614), 1864.
- Bläsing, B., Schack, T., & Brugger, P. (2010). The functional architecture of the human body: assessing body representation by sorting body parts and activities. *Experimental Brain Research*, 203(1), 119-29.
- Bolognini, N., Casanova, D., Maravita, A., Vallar, G. (2012). Bisecting real and fake body parts: effects of prism adaptation after right brain damage. *Frontiers of Human Neuroscience*, 6, 154.
- Bonfiglioli, C. (2010). Association between objects and body parts mediated by function. *Quarterly Journal of Experimental Psychology*, 63(11):2106-12.
- Bonnier, P. (1905). L'Aschématie [Aschematia]. *Revue Neurologique (Paris)*, 13, 605–609.
- Borghi, A.M., Bonfiglioli, C., Lugli, L., Ricciardelli, P., Rubichi, S., Nicoletti, R. (2007). Are visual stimuli sufficient to evoke motor information? Studies with hand primes. *Neuroscience Letters*, 411, 17–21.
- Botvinick, M. M., & Cohen, J. (1998). Rubber hands ‘feel’ touch that eyes see. *Nature*, 391(6669), 756.

- Bowen, A., Gardener, E., Cross, S., Tyrrell, P., & Graham, J. (2005). Developing functional outcome measures for unilateral neglect: a pilot study. *Neuropsychological Rehabilitation*, 15(2), 97-113.
- Bracci, S., Caramazza, A., & Peelen, M.V. (2015). Representational Similarity of Body Parts in Human Occipitotemporal Cortex. *Journal of Neuroscience*, 35(38), 12977-12985.
- Bracci, S., Cavina-Pratesi, C., Ietswaart, M., Caramazza, A., & Peelen, M.V. (2011). Closely overlapping responses to tools and hands in left lateral occipitotemporal cortex. *Journal of neurophysiology*, 107, 1443–1456.
- Bracci, S., Ietswaart, M., Peelen, M. V., & Cavina-Pratesi, C. (2010). Dissociable neural responses to hands and non-hand body parts in human left extrastriate visual cortex. *Journal of Neurophysiology*, 103(6), 3389-3397.
- Bracci, S., & Peelen, M.V. (2013). Body and object effectors: the organization of object representations in high-level visual cortex reflects body-object interactions. *Journal of Neuroscience*, 33, 18247–18258.
- Braun, N., Emkes, R., Thorne, J. D., & Debener, S. (2016). Embodied neurofeedback with an anthropomorphic robotic hand. *Scientific Reports*, 6, 37696.
- Braun, N., Thorne, J. D., Hildebrandt, H., & Debener, S. (2014). Interplay of agency and ownership: the intentional binding and rubber hand illusion paradigm combined. *PLoS One*, 9, e111967.
- Brochier, T, Habib, M., & Brouchon, M. (1994). “Covert processing of information in hemianesthesia: a case report.” *Cortex*, 30(1), 135-44.
- Brozzoli, C., Makin, T. R., Cardinali, L., Holmes, N. P., & Farnè, A. (2012). Peripersonal space: a multisensory interface for body-object interactions. In: Murray MM, Wallace MT (eds) *The neural bases of multisensory processes*. CRC Press/Taylor & Francis, Boca Raton, p 2012.
- Brozzoli, C., Ehrsson, H. H., & Farnè, A. (2014). Multisensory representation of the space near the hand: from perception to action and individual interactions. *Neuroscientist*, 20, 122–135.
- Bruce, V., & Young, A. (1998). *In the eye of the beholder: the science of face perception*. Oxford University Press, Oxford.
- Bruno, V., Carpinella, I., Rabuffetti, M., De Giuli, L., Sinigaglia, C., Garbarini, F., & Ferrarin, M. (2019). How Tool-Use Shapes Body Metric Representation: Evidence From Motor Training With and Without Robotic Assistance. *Frontiers in Human Neuroscience*, 13, 299.

- Bub, D. N., Masson, M.E.J., Cree, G.S. (2008). Evocation of functional and volumetric gestural knowledge by objects and words. *Cognition*, 106, 27–58.
- Bub, D. N., Masson, M. E., & Lin, T. (2013). Features of planned hand actions influence identification of graspable objects. *Psychological Science*, 24(7), 1269–1276.
- Burton, H. (1986). Second somatosensory cortex and related areas. In: *Sensory Motor Areas and Aspects of Cortical Connectivity* (Jones, E. G., Peters, A. eds), pp. 31-98. New York: Plenum.
- Buxbaum, L. J., & Coslett, H. B. (2001). Specialized structural descriptions for human body parts: Evidence from autotopagnosia. *Cognitive Neuropsychology*, 18, 289–306.
- Buxbaum, L., Ferraro, M.K., Veramonti, T., Farne, A., Whyte, J., Ladavas, E., ... Coslett, H.B. (2004). Hemineglect: subtypes, neuroanatomy and disability. *Neurology*, 62(5), 749–756.
- Buxbaum, L., & Saffran, E.M. (2001). Knowledge of object manipulation and object function: Dissociations in apraxic and nonapraxic subjects. *Brain and Language*, 82, 179–199.
- Caggiano, P., Beschin, N., & Cocchini G. (2014). Personal neglect following unilateral right and left brain damage. *Procedia- Social and Behavioral Sciences Journal*, 140, 164–167.
- Caggiano, P., & Cocchini, G. (2020). The functional body: does body representation reflect functional properties? *Experimental Brain Research*, 238(1), 153-169.
- Caggiano, P., & Jehkonen, M. (2018). The ‘Neglected’ Personal Neglect. *Neuropsychology Review*, 28(4), 417–435.
- Calford, M.B., & Tweedale, R. (1988). Immediate and chronic changes in responses of somatosensory cortex in adult fying-fox after digit amputation. *Nature*, 332, 446-448.
- Calford, M.B., & Tweedale, R. (1991). Immediate expansion of receptive fields of neurons in area 3b of macaque monkeys after digit denervation. *Somatosensory & Motor Research*, 8, 249-60.
- Canzano, L., Piccardi, L., Bureca, I., & Guariglia, C. (2011). Mirror writing resulting from an egocentric representation disorder: a case report. *Neurocase*; 17(5), 447-460.
- Canzoneri, E., Ubaldi, S., Rastelli, V., Finisguerra, A., Bassolino, M., & Serino, A. (2013). Tool-use reshapes the boundaries of body and peripersonal space representations. *Experimental Brain Research*, 228(1), 25–42.

- 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*, 19(12), R478–R479.
- Cardinali, L., Brozzoli, C., & Farnè, A. (2009). Peripersonal space and body schema: two labels for the same concept? *Brain Topography*, 21, 252–260.
- Cardinali, L., Jacobs, S., Brozzoli, C., Frassinetti, F., Roy, A. C., & Farnè, A. (2012). Grab an object with a tool and change your body: tool-use-dependent changes of body representation for action. *Experimental Brain Research*, 218, 259–271.
- Carruthers, G. (2008). Types of body representation and the sense of embodiment. *Consciousness and Cognition*, 17, 1302–1316.
- Chakrabarti, S., & Alloway, K. D. (2006). Differential origin of projections from SI barrel cortex to the whisker representations in SII and MI. *Journal Comparative Neurology*, 498(5), 624–36.
- Chao, L. L., & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *Neuroimage*, 12, 478–484.
- Chemero, A. (2009). *Radical Embodied Cognitive Science*. Cambridge, MA: MIT Press.
- Cicirata, F., Angaut, P., Cioni, M., Serapide, M. F., & Papale, A. (1986). Functional organization of thalamic projections to the motor cortex. An anatomical and electrophysiological study in the rat. *Neuroscience*, 19(1), 81–99.
- Cioffi, M. C., Hackett, J., & Moore, J. W. (2020). Synchronous stimulation in the rubber hand illusion task boosts the subsequent sense of ownership on the vicarious agency task. *Consciousness and Cognition*, 80, 102904.
- Cocchini, G., Galligan, T., Mora, L., & Kuhn, G. (2018). The magic hand: effect of expertise on representation of own hand. *Quarterly Journal of Experimental Psychology*, 71(11), 2314–2324.
- Cocchini, G., Beschin, N., & Della Sala, S. (2018). Unawareness for motor impairment and distorted perception of tasks difficulty. *Journal of the International Neuropsychological Society*, 24(1), 45–56 (IF: 3.01).
- Cocchini, G., Beschin, N., Foutopolou, A., Della Sala, S. (2010). Explicit and implicit anosognosia for upper limb motor impairment. *Neuropsychologia*, 48, 1489–1494.
- Cocchini, G., Beschin, N., & Jehkonen, M. (2001). The Fluff Test: A simple task to assess body representation neglect. *Neuropsychological Rehabilitation: An International Journal*; 11(1), 17–31.

- Committeri, G., Piervincenzi, C., & Pizzamiglio, L. (2018). Personal neglect: A comprehensive theoretical and anatomo–clinical review. *Neuropsychology*, 32(3), 269–279.
- 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.
- Cole, J., & Paillard, J. (1995). Living without touch and peripheral information about body position and movement: Studies with deafferented subjects. In J. L. Bermudez, A. Marcel, & N. Eilan (Eds.), *The body and the self*. Cambridge, MA: MIT Press.
- Collins, D. L., Neelin, P., Peters, T. M., & Evans, A. C. (1994). Automatic 3D intersubject registration of MR volumetric data in standardized Talairach space. *Journal of Computer Assisted Tomography*, 18, 192–205.
- 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, 2879–2890.
- 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, 4162–4171.
- Coslett, H. B. (1988). Evidence for a disturbance of the body schema in neglect. *Brain and Cognition*, 37, 527–44.
- Costantini, M., Ambrosini, E., Scorolli, C., & Borghi, A. M. (2011). When objects are close to me: affordances in the peripersonal space. *Psychonomic Bulletin & Review*, 18, 302–308.
- Costantini, M., & Haggard, P. (2007). The rubber hand illusion: Sensitivity and reference frame for body ownership. *Consciousness and Cognition*, 16, 229–240.
- 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*, 40, 1196–1208.
- Crawford, J. R., & Howell, D. (1998). Comparing an individual's test score against norms derived from small samples. *The Clinical Neuropsychologist*, 12(4), 482–86.
- Creem-Regehr, S. H., & Lee, J. N. (2005). Neural representations of graspable objects: Are tools special? *Cognitive Brain Research*, 22, 457–469.

- Danckert, J., & Rossetti, Y. (2005). Blindsight in action: What can the different sub-types of blindsight tell us about the control of visually guided actions? *Neuroscience and Biobehavioural Reviews*, 29, 1035–1046.
- D'Angelo, M., di Pellegrino, G., & Frassinetti, F. (2019). The illusion of having a tall or short body differently modulates interpersonal and peripersonal space. *Behavioural Brain Research*, 375, 112146.
- 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), 13847.
- De Renzi, E., & Scotti, G. (1970). Autotopagnosia: Fiction or reality. *Archives of Neurology*, 23, 221–227.
- de Vignemont, F. (2010). Body schema and body image – Pros and cons. *Neuropsychologia*, 48, 669–680.
- 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*, 62(3), 500–512.
- de Vignemont, F., Ehrsson, H. H., & Haggard, P. (2005). Bodily illusions modulate tactile perception. *Current Biology*, 15, 1286–1290.
- Della Sala, S., Cocchini, G., Beschin, N., & Cameron, A. (2009). “VATAm: A new method to assess anosognosia for upper and lower limbs in left-and right brain damaged patients”. *The Clinical Neuropsychologist*, 11, 1–22.
- Demeurisse, G., Demol, O., & Robaye, E. (1980). Motor evaluation in vascular hemiplegia. *European Neurology*, 19(6), 382–9.
- Denes, G., & Pizzamiglio, L. (1996). *Manuale di neuropsicologia. Normalità e patologia dei processi cognitivi*. Bologna: Zanichelli.
- Dennis, M. (1976). Dissociated naming and locating of body parts after left anterior temporal lobe resection: An experimental case study. *Brain and Language*, 3, 147–163.
- Di Vita, A., Palermo, L., Piccardi, L., Di Tella, J., Propato, F., & Guariglia, C. (2016). Body Representation Alterations in Personal but Not in Extrapersonal Neglect Patients. *Applied Neuropsychology: Adult*, 24(4), 308–317.
- Dien, J., Frishkoff, G. A., Cerbone, A., & Tucker, D. M. (2003). Parametric analysis of event related potentials in semantic comprehension: evidence for parallel brain mechanisms. *Cognitive Brain Research*, 15, 137–153.

- Dijkerman, H., & De Haan, E. (2007). Somatosensory processes subserving perception and action. *Behavioral and Brain Sciences*, 30(2), 189-239.
- Diller, L., & Weinberg, J. (1977). Hemi-inattention in rehabilitation: The evolution of a rational remediation program. In E. Weinstein & R. Friedland (Eds.), *Advances in neurology* (Vol. 10). New York: Raven Press.
- 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, 209–217.
- Donchin, E. (1981). Surprise!...Surprise? *Psychophysiology*, 18, 493-513.
- Downing, P. E., Chan, A. W., Peelen, M. V., Dodds, C. M., & Kanwisher, N. (2006). Domain specificity in visual cortex. *Cerebral Cortex*, 16(10), 1453-1461
- Downing, P. E., Jiang, Y., Shuman, M., Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science*, 293, 2470–2473.
- Duignan, B. (2018). Occam’s razor. *Encyclopædia Britannica*, inc. Retrieved from <https://www.britannica.com/topic/Occams-razor>.
- Dummer, T., Picot-Annand, A., Neal, T., & Moore, C. (2009). Movement and the rubber hand illusion. *Perception*, 38, 271–280.
- Dykes, R.W., & Lamour, Y. (1988). An electrophysiological laminar analysis of single somatosensory neurons in partially deafferented rat hindlimb granular cortex subsequent to transection of the sciatic nerve. *Brain Research*, 449, 1-17.
- Dykes, R.W., & Craig, A.D. (1998). Control of size and excitability of mechanosensory receptive fields in dorsal column nuclei by homolateral dorsal horn neurons. *Journal of Neurophysiology*, 80, 120-129.
- Elsner, B., & Hommel, B. (2001). Effect anticipation and action control. *Journal of Experimental Psychology: Human Perception and Performance*, 27(1), 229-40.
- Evans, A. C., Collins, D. L., Mills, S. R., Brown, E. D., Kelly, R. L., & Peters, T. M. (1993). 3D statistical neuroanatomical models from 305 MRI volumes. *Proceedings of IEEE-Nuclear Science Symposium and Medical Imaging Conference*, 1813–1817
- Farné, A., Serino, A., & Ladavas, E. (2007). Dynamic size-change of perihand space following tool-use: determinants and spatial characteristics revealed through cross-modal extinction. *Cortex*, 43(3), 436–443.
- Faul, F., Erdfelder, E., Buchner, A., & Lang, A-G. (2009). Statistical power analyses using G*Power 31: Tests for correlation and regression analyses. *Behavioural Research Methods*, 41(4), 1149–1160.

- Felician, O., Romaguère, P., Anton, J. L., Nazarian, B., Roth, M., Poncet, M., et al. (2004). The role of the left superior parietal lobule in body part localization. *Annals of Neurology*, 55, 749-751.
- Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, 1(1), 1-47.
- Ferretti, G. (2016). Through the forest of motor representations. *Consciousness and Cognition*, 43, 177–196.
- Fisher, S. (1972). Body Image. In D. Sills (Ed.), *International Encyclopaedia of the Social Sciences* (Vol. 2, pp.113-116). New York: Collier-Macmillan.
- 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.
- Fossataro, C., Bruno, V., Giurgola, S., Bolognini, N., & Garbarini, F. (2018). Losing my hand. body ownership attenuation after virtual lesion of the primary motor cortex. *European Journal of Neuroscience*, 48, 2272–2287.
- Friedman, D. P., Murray, E. A., O'Neill, J. B., & Mishkin, M. (1986). Cortical connections of the somatosensory fields of the lateral sulcus of macaques: evidence for a corticolimbic pathway for touch. *Journal of Comparative Neurology*, 252(3), 323-47.
- Fuentes, C. T., Longo, M. R., Haggard, P. (2013). Body image distortions in healthy adults. *Acta Psychologica (Oxf)*, 144, 344–351.
- Gainotti, G., Messerli, P., & Tissot, R. (1972). Qualitative analysis of unilateral neglect in relation to laterality of cerebral lesion. *Journal of Neurology Neurosurgery & Psychiatry*, 35(4), 545-50.
- Galati G, Committeri G, Sanes JN, & Pizzamiglio L. (2001). Spatial coding of visual and somatic sensory information in body-centered coordinates. *European Journal of Neuroscience*; 14(4), 737–746.
- Gallace, A., & Spence, C. (2008). The cognitive and neural correlates of "tactile consciousness": a multisensory perspective. *Consciousness and Cognition*, 17(1), 370-407.
- Gallagher, S. (2005). *How the body shapes the mind*. New York: Oxford University Press.
- Gallagher, S. (1998). Body schema and intentionality. In *The Body and The Self*, eds J. L. Bermudez, A. Marcel, and N. Glan (Cambridge, MA: MIT Press), 225–24.
- Gallagher, S. (1986). Body image and body schema: A conceptual clarification. *Journal of Mind and Behavior*, 7, 541–554.

- Gallagher, S., & Cole, J. (1995). Body schema and body image in a deafferented subject. *Journal of Mind and Behavior*, 16, 369-390.
- Gallese, V., & Sinigaglia, C. (2010). The bodily self as power for action. *Neuropsychologia*, 48(3), 746–755.
- Ganea, N., & Longo, M. R. (2017). Projecting the self outside the body: body representations underlying proprioceptive imagery. *Cognition*, 162, 41–47.
- Garbarini, F., & Adenzato, M. (2004). At the root of embodied cognition: Cognitive science meets neurophysiology. *Brain and Cognition*, 56(1), 100–106.
- 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.
- Gardner, E. P., & Kandel, E. R. (2000). Touch. Kandel, E. R., Schwartz, J. H., & Jessell, T. M. (eds), *Principles of Neural Science*, 4th edn, McGraw Hill, New York.
- Gentili, M.E., Verton, C., Kinirons, B., & Bonnet, F. (2002). Clinical perception of phantom limb sensation in patients with brachial plexus block. *European Journal of Anaesthesiology*, 19, 105-108.
- Geyer, S., Schormann, T., Mohlberg, H., & Zilles, K. (2000). Areas 3a, 3b, and 1 of human primary somatosensory cortex. Part 2. Spatial normalization to standard anatomical space. *Neuroimage*, 11(6 Pt 1), 684-96.
- Giabbiconi, C. M., Jurilj, V., Gruber, T., & Vocks, S. (2016). Steady-state visually evoked potential correlates of human body perception. *Experimental Brain Research*, 234, 3133–3143.
- Gibson, J. (1979). *The ecological approach to visual perception*. Boston, MA: Houghton Mifflin.
- Gillmeister, H., Catmur, C., Liepelt, R., Brass, M., & Heyes, C. (2008). Experience-based priming of body parts: a study of action imitation. *Brain Research*, 1217, 157-70.
- Goodale, M. A., & Milner M. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, 15(1), 20-5.
- Gordon, M.S., & Rosenblum, L.D. (2004). Perception of sound-obstructing surfaces using body-scaled judgments. *Ecological Psychology*, 16(2),87–113.
- Goudge, M. E. (1918). A qualitative and quantitative study of Weber's illusion. *The American Journal of Psychology*, 29, 81–119.
- Grafton, S.T., Fadiga, L., Arbib, M.A., Rizzolatti, G. (1997). Premotor Cortex Activation during Observation and Naming of Familiar Tools. *Neuroimage*, 6, 231–236.

- Graziano, M. S. A. (2009). *The intelligent movement machine: An ethological perspective on the primate motor system*. New York, NY: Oxford University Press.
- Guariglia, P., Matano, A., & Piccardi, L. (2014). Bisecting or Not Bisecting: This Is the Neglect Question. Line Bisection Performance in the Diagnosis of Neglect in Right Brain-Damaged Patients. *PLoS One*, 9(6), e99700.
- Guariglia, C., & Antonucci, G. (1992). Personal and extrapersonal neglect: A case of neglect dissociation. *Neuropsychologia*, 30 (11), 1001-1009.
- Haggard, P. (2017). Sense of agency in the human brain. *Nature Reviews Neuroscience*, 18(4), 196-207.
- Haggard, P., & Chambon, V. (2012). Sense of agency. *Current Biology*, 22(10), R390-2.
- Halligan, P. W., Hunt, M., Marshall, J. C., & Wade, D. T. (1995). Sensory detection without localization. *Neurocase*, 1(3), 259-266.
- Halligan, P.W., Fink, G.R., Marshall, J.C., & Vallar, G. (2003). Spatial cognition: evidence from visual neglect. *Trends of Cognitive Science*; 7(3), 125-133.
- Head, H., & Holmes, H. G. (1911). Sensory disturbances from cerebral lesions. *Brain*, 34, 102–254.
- Holmes, N. P. (2012). Does tool use extend peripersonal space? A review and re-analysis. *Experimental Brain Research*, 218(2), 273-82.
- Holmes, N. P., & Spence, C. (2004). The body schema and multisensory representation(s) of peripersonal space. *Cognitive Processing*, 5, 94–105.
- Hommel, B. (2015). The theory of event coding (TEC) as embodied-cognition framework *Frontiers in Psychology*, 6, 1318.
- Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The theory of event coding (TEC): a framework for perception and action planning. *Behavioral Brain Science*, 24, 849–937.
- Horne, M. K., & Tracey, D. J. (1979). The afferents and projections of the ventroposterolateral thalamus in the monkey. *Experimental Brain Research*, 36(1), 129-41.
- Hluštík, P., Solodkin, A., Gullapalli, R. P., Noll, D. C., & Small, S. L. (2001). Somatopy in human primary motor and somatosensory hand representations revisited. *Cerebral Cortex*, 11, 312-321.
- Imamizu, H., Miyauchi, S., Tamada, T., Sasaki, Y., Takino, R., Pütz, B., Yoshioka, T., Kawato, M. (2000). Human cerebellar activity reflecting an acquired internal model of a new tool. *Nature*, 403(6766), 192–195.

- Iriki, A., Tanaka, M., Iwamura, Y. (1996). Coding of modified body schema during tool use by macaque postcentral neurones. *Neuroreport*, 7(14), 2325—2330.
- Isaacson, S., Funderburk, M., Yang, J. (2000). Regulation of proprioceptive memory by subarachnoid regional anesthesia. *Anesthesiology*, 93, 55-61.
- Ishak, S., Adolph, K.E, & Lin, G.C. (2008). Perceiving Affordances for Fitting through Apertures. *Journal of Experimental Psychology: Human Perception and Performance*; 34(6), 1501–1514.
- Ishibashi, H., Hihara, S., & Iriki, A. (2000). Acquisition and development of monkey tool-use: behavioral and kinematic analyses. *Canadian Journal of Physiology and Pharmacology*, 78(11), 958-66.
- Johnson-Frey, S. H., Newman-Norlund, R., & Grafton, S. T. (2005). A distributed left hemisphere network active during planning of everyday tool use skills. *Cerebral Cortex*, 15(6), 681–695.
- Jones, E. G. (1986) Connectivity of the primary sensory-motor cortex in cerebral cortex. In: *Sensory Motor Areas and Aspects of Cortical Connectivity* (Jones, E. G., Peters, A. eds, pp. 113-183. New York: Plenum.
- Kalckert, A., & Ehrsson, H. H. (2012). Moving a rubber hand that feels like your own: a dissociation of ownership and agency. *Frontiers of Human Neuroscience*, 6, 40.
- Kammers, M. P., de Vignemont, F., Verhagen, L., & Dijkerman, H. C. (2009). The rubber hand illusion in action. *Neuropsychologia*, 47(1), 204-211.
- Kammers, M. P., Kootker, J., Hogendoorn, H., & Dijkerman, H. C. (2010a). How many motoric body representations can we grasp? *Experimental Brain Research*, 202(1), 203- 212.
- Kammers, M. P., Mulder, J., de Vignemont, F., & Dijkerman, H. C. (2010b). The weight of representing the body: Addressing the potentially indefinite number of body representations in healthy individuals. *Experimental Brain Research*, 204(3), 333-42.
- Kandel, E. R., Schwartz, J. H., Jessel, M. T., Siegelbaum, S. A., Hudspeth, T. H., & Mack, S. (2013). *Principles of neuroscience* (5th ed.). London: McGraw-Hill Professional.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, 17(11), 4302-4311.
- Kemmerer, D., & Tranel, D. (2008). Searching for the elusive neural substrates of body part terms: A neuropsychological study. *Cognitive Neuropsychology*, 25, 601–629.

- Kiss, M., Driver, J., & Eimer, M. (2009). Reward priority of visual target singletons modulates event-related potential signatures of attentional selection. *Psychological Science*, 20(2), 245-51.
- Kwegyir-Afful, E. E., & Keller, A. (2004). Response properties of whisker related neurons in rat second somatosensory cortex. *Journal of Neurophysiology*, 92, 2083-2092.
- Lackner, J. R. (1988). Some proprioceptive influences on the perceptual representation of body shape and orientation. *Brain*, 111, 281–297.
- Laiacona, M., Allamano, N., Lorenzi, L., & Capitani, E. (2006). A case of impaired naming and knowledge of body parts: Are limbs a separate category? *Neurocase*, 12, 307-316.
- Lakoff, G. (2014). Mapping the brain's metaphor circuitry: is abstract thought metaphorical thought? *Frontiers of Human Neuroscience*, 8, 958.
- Lemon, R. (1988). The output map of the primate motor cortex. *Trends in Neurosciences*, 11(11), 501-6.
- Lenz, F. A., Dostrovsky, J. O., Tasker, R. R., Yamashiro, K., Kwan, H. C., & Murphy, J. T. (1988). Single-unit analysis of the human ventral thalamic nuclear group: somatosensory responses. *Journal of Neurophysiology*, 59, 299–316.
- Lhermitte, J. (1942). De l'image corporelle. *Revue Neurologique*, 74, 20-38.
- Lindell, A. B., Jalas, M. J., Tenovu, O., Brunila, T., Voeten, M. J. M., & Hämäläinen, H. (2007). Clinical assessment of hemispatial neglect: Evaluation of different measures and dimensions. *The Clinical Neuropsychologist*, 21(3), 479–497.
- Lingnau, A. & Downing, P. E. (2015). The lateral occipitotemporal cortex in action. *Trends in Cognitive Science*, 19, 268–277.
- Linkenauger, S. A., Wong, H. Y., Geuss, M., Stefanucci, J. K., McCulloch, K.C., Bülthoff, H. H., Mohler, B. J., & 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.
- Linkenauger, S. A., Bülthoff, H. H., Mohler, B. J. (2015). Virtual arm's reach influences perceived distances but only after experience reaching. *Neuropsychologia*, 70, 393-401.
- Longo, M. R. (2016). Types of body representation. In Y. Coello & M. H. Fischer (Eds.), *Foundations of Embodied Cognition, Volume 1: Perceptual and Emotional Embodiment* (pp. 117-134). London: Routledge.

- Longo, M. R., & Haggard, P. (2011). Weber's illusion and body shape: anisotropy of tactile size perception on the hand. *Journal of Experimental Psychology: Human Perception and Performance*, 37, 720–726.
- Longo, M. R., & Haggard, P. (2012a). A 2.5-D representation of the human hand. *Journal of Experimental Psychology: Human Perception and Performance*, 38, 9–13.
- Longo, M. R., & Haggard, P. (2012b). Implicit body representations and the conscious body image. *Acta Psychologica (Oxf)*, 141, 164–168
- Longo, M. R., Azañón, E., & Haggard, P. (2010). More than skin deep: body representation beyond primary somatosensory cortex. *Neuropsychologia*, 48(3), 655–668.
- Longo, M. R., & Haggard, P. (2010). An implicit body representation underlying human position sense. *Proceedings of the National Academy of Sciences, USA*, 107, 11727–11732.
- 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.
- Lourenco, S. F., & Longo, M. R. (2009). The plasticity of near space: Evidence for contraction. *Cognition*, 112(3), 451–456.
- Luck, S. J. (2005). *An introduction to the event-related potential technique*. Cambridge, Mass: MIT Press.
- Macaluso, E., & Maravita, A. (2010). The representation of space near the body through touch and vision. *Neuropsychologia*, 48, 782–795.
- Maimon-Mor, R. O., Schone, H. R., Moran, R., Brugger, P., & Makin, T. R. (2020). Motor control drives visual bodily judgements. *Cognition*, 196, 104120.
- Maimon-Mor, R. O., Obasi, E., Lu, J., Odeh, N., Kirker, S., MacSweeney, M., ... Makin, T. R. (2020). Communicative hand gestures as an implicit measure of artificial limb embodiment and daily usage. *medRxiv*. doi: <https://doi.org/10.1101/2020.03.11.20033928>
- Mancini, F., Longo, M. R., Iannetti, G. D., & Haggard, P. (2011). A supramodal representation of the body surface. *Neuropsychologia*, 49, 1194–1201.
- Manzoni, T., Barbaresi, P., & Conti, F. (1984) Callosal mechanism for the interhemispheric transfer of hand somatosensory information in the monkey. *Behavioural Brain Research*, 11, 155-170.
- Marangolo, P., Piccardi, L., & Rinaldi, M.C. (2003). Dissociation between Personal and Extrapersonal Neglect in a Crossed Aphasia Study. *Neurocase*; 9(5), 414-420.

- Maravita, A., & Iriki, A. (2004). Tools for the body (schema). *Trends in Cognitive Science (Regul. Ed.)*, 8, 79–86.
- Maravita, A., Spence, C., Kennett, S., & Driver, J. (2002). Tool-use changes multimodal spatial interactions between vision and touch in normal humans. *Cognition*, 83(2), B25–B34.
- Martín-Loeches, M. (2007). The gate for reading: reflections on the recognition potential. *Brain Research Reviews*, 53(1), 89-97.
- Martinaud, O., Besharati, S., Jenkinson, P. M., & Fotopoulou, A. (2017). Ownership illusions in patients with body delusions: different neural profiles of visual capture and disownership. *Cortex*, 87, 174–185.
- Mazzola, L., Isnard, J., & Mauguière, F. (2006). Somatosensory and pain responses to stimulation of the second somatosensory area (SII) in humans. A comparison with SI and insular responses. *Cerebral Cortex*, 16(7), 960-8.
- McCloskey, M. (2001). The Future of Cognitive Neuropsychology. In Brenda Rapp, *The Handbook of Cognitive Neuropsychology* (pp. 593-610), Hove: Psychology Press.
- 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.
- Medina, J., & Coslett, H. B. (2010). From maps to form to space: touch and the body schema. *Neuropsychologia*, 48(3), 645-54.
- Melzack, R., & Bromage, P.R. (1973). Experimental phantom limbs. *Experimental Neurology*, 39, 261-9.
- Miles, J. E. (1956). Phantom limb syndrome occurring during spinal anesthesia. *Journal of Nervous and Mental Disorders*, 123, 365-8.
- Milner, D. (1998). Unconscious visual processing for action: Neuropsychological evidence. *Towards a Science of Consciousness*, Third Conference, Tucson, 27 April 1998.
- Minnebusch, D.A., & Daum, I. (2009). Neuropsychological mechanisms of visual face and body perception. *Neuroscience and Biobehavioral Reviews*, 33, 1133-1144.
- Moore, J. W. (2016). What Is the Sense of Agency and Why Does it Matter? *Frontiers in Psychology*, 7, 1272.
- Mora, L., Cowie, D., Banissy, M. J., & Cocchini, G. (2018) My true face: unmasking one's own face representation. *Acta Physiol (Oxf)*, 191:63–68.

- Moreau, Q., Pavone, E.F., Aglioti, S.M., & Candidi, M. (2018). Theta synchronization over occipito-temporal cortices during visual perception of body parts. *The European Journal of Neuroscience*, 48(8):2826-2835.
- Muakkassa, K. F., & Strick, P. L. (1979). Frontal lobe inputs to primate motor cortex: evidence for four somatotopically organized 'premotor' areas. *Brain Research*, 177(1), 176-82.
- Muroi, D., Hiroi, Y., Koshiha, T., Suzuki, Y., Kawaki, M., & Higuchi, T., (2017). Walking through apertures in individuals with stroke. *PLoS One*, 12, e0170119.
- Murray, G. M., Zhang, H. Q., Kaye, A. N., Sinnadurai, T., Campbell, D. H., & Rowe, M. J. (1992) Parallel processing in rabbit first (SI) and second (SII) somatosensory cortical areas: effects of reversible inactivation by cooling of SI on responses in SII. *Journal of Neurophysiology*, 68, 703–710.
- Narici, M. V., Bordini, M., & Cerretelli, P. (1991). Effect of aging on human adductor pollicis muscle function. *Journal of Applied Physiology*, 71, 1277–1281.
- Nelles, G., Spiekermann, G., Jueptner, M., Leonhardt, G., Müller, S., Gerhard, H., & Diener, H.C. (1999). Reorganization of sensory and motor systems in hemiplegic stroke patients. A positron emission tomography study. *Stroke*, 30(8), 1510-6.
- Norrzell, U., Finger, S., & Lajonchere, C. (1999). Cutaneous sensory spots and the "law of specific nerve energies": history and development of ideas. *Brain Research Bulletin*, 48(5), 457-465.
- Ogden, J. A. (1996). *Fractured Minds: A Case-Study Approach to Clinical Neuropsychology*. Oxford: Oxford University Press.
- Ogden, J. A. (1985). Autotopagnosia: Occurrence in a patient without nominal aphasia and with an intact ability to point to parts of animals and objects. *Brain*, 108, 1009-1022.
- Oldfield, R.C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9(1), 97–113.
- Op de Beeck, H. P., Brants, M., Baeck, A., & Wagemans, J. (2010). Distributed subordinate specificity for bodies, faces, and buildings in human ventral visual cortex. *Neuroimage*, 49(4), 3414-3425.
- Orlov, T., Makin, T.R., Zohary, E. (2010). Topographic representation of the human body in the occipitotemporal cortex. *Neuron*, 68, 586–600.
- Ortigue, S., Mégevand, P., Perren, F., Landis, T., & Blanke, O. (2006). Double dissociation between representational personal and extrapersonal neglect. *Neurology*, 66 (9), 1414-1417.

- Paillard, J. (1999) Body schema and body image: A double dissociation in deafferented patients. In: *Motor control, today and tomorrow*, ed. Gantchev, G. N., Mori, S., & Massion, J., pp. 197–214. Academic Publishing House.
- Paillard, J., Michel, F., & Stelmach, G. (1983). Localization without content: A tactile analogue of ‘blind sight’. *Archives of Neurology*, 40, 548-551.
- Palermo, L., Di Vita, A., Piccardi, L., Trallesi, M., & Guariglia C. (2014). Bottom-up and top-down processes in body representation: a study of brain-damaged and amputee patients. *Neuropsychology*, 28(5), 772-81.
- 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, 702-712.
- Paré, A. (1551). *La Manière de Traicter les Playes Faictes tant par Hacquebutes que par fleches...* Paris, Jean de Brie.
- Parsons, L. M. (1987a). Imagined spatial transformation of one’s body. *Journal of experimental psychology General*, 116(2), 172-91.
- Parsons, L. M. (1987b). Imagined spatial transformations of one’s hands and feet. *Cognitive Psychology*, 19(2), 178–241.
- Pavlova, M., Sokolov, A. (2000). Orientation specificity in biological motion perception. *Perception & Psychophysics*, 62, 889–899.
- Peelen, M. V., & Downing, P. E. (2007). The neural basis of visual body perception. *Nature Reviews Neuroscience*, 8(8), 636-648.
- Peelen, M.V., & Downing, P.E. (2005). Selectivity for the human body in the fusiform gyrus. *Journal of Neurophysiology*, 93: 603–608
- Penfield, W., & Rasmussen, T. (1952). *The cerebral cortex of man*. Macmillan: New York.
- Penfield, W., & Boldrey, E. (1937). Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. *Brain: A Journal of Neurology*, 60, 389–443.
- Peru, A., & Pinna, G. (1997). Right personal neglect following a left hemisphere stroke. A case report. *Cortex*; 33 (3), 585-590.
- Peviani, V., Melloni, L. & Bottini, G. (2019). Visual and somatosensory information contribute to distortions of the body model. *Scientific Reports*, 9, 13570
- Pick, A. (1908). *Über Störungen der Orientierung am eigenen Körper, Arbeiten aus der Deutschen Psychiatrischen Universitäts-Klinik in Prag*, pp. 1-19. Berlin: Karger.

- Pick, A. (1915). Zur Pathologie des Bewußtseins vom eigenen Körper. *Neurologisches Centralblatt*, 34, 257-265.
- Pinel, J. P. J. (2010). *Biopsychology*. Harlow, Essex: Pearson Education Limited.
- Pitcher, D., Charles, L., Devlin, J. T., Walsh, V., & Duchaine, B. (2009). Triple dissociation of faces, bodies, and objects in extrastriate cortex. *Current Biology*, 19(4), 319-324.
- Pitron, V., & de Vignemont, F. (2017). Beyond differences between the body schema and the body image: insights from body hallucinations. *Consciousness and Cognition*, 53, 115–121.
- Pitron, A., Alsmith, A., & de Vignemont, F. (2018). How do the body schema and the body image interact? *Consciousness and Cognition*, 65, 352–358.
- Pizzamiglio, L., Cappa, S., Vallar, G., Zoccolotti, P., Bottini, G., Ciurli, P., Guariglia, C., & Antonucci, G. (1989). Visual neglect for far and near extra-personal space in humans. *Cortex*, 25(3), 471-477.
- Polich, J., & Kok, A. (1995). Cognitive and biological determinants of P300: An integrative review. *Biological Psychology*, 41, 103-146.
- Poncet, M., Pellissier, J. F., Sebahoun, M., & Nasser, C. J. (1971). Apropos of a case of autotopagnosia after a parieto-occipital lesion of the major hemisphere. *Encephale*, 60(2), 110-23.
- Porter, L. L., & White, E. L. (1983). Afferent and efferent pathways of the vibrissal region of primary motor cortex in the mouse. *Journal of Comparative Neurology*, 214(3), 279-89.
- Pourtois, G., Peelen, M.V., Spinelli, L., Seeck, M., & Vuilleumier, P. (2007) Direct intracranial recording of body-selective responses in human extrastriate visual cortex. *Neuropsychologia*, 45, 2621–2625.
- Prevoznick, S. J., & Eckenhoff, J. E. (1964). Phantom sensations during spinal anesthesia. *Anesthesiology*, 25, 767-70.
- Proske, U., & Gandevia, S. C. (2012). The proprioceptive senses: Their roles in signaling body shape, body position and movement, and muscle force. *Physiological Reviews*, 92, 1651-1697.
- Proverbio, A.M. (2012). Tool perception suppresses 10–12 Hz mu rhythm of EEG over the somatosensory area. *Biological Psychology* 91, 1– 7.
- Pulvermüller, F. (2005). Brain mechanisms linking language and action. *Nature Reviews Neuroscience*, 6, 576–582.

- Punt, T. D., & Riddoch, M. J. (2006). Motor neglect: Implications for movement and rehabilitation following stroke. *Disability and Rehabilitation*, 28(13–14), 857–864.
- Purves, D., Augustine, G.J., Fitzpatrick, D., Hall, W.C., LaMantia, A-S., & White, L.E., (2012) *Neuroscience* (5th Edition). Sunderland: Sinauer Associates, Inc. Publishers.
- Ramachandran, V. S., & Hirstein, W. (1998). The perception of phantom limbs. *Brain*, 121, 1603–1630.
- Rathelot, J. A., & Strick, P. L. (2006). Muscle representation in the macaque motor cortex: an anatomical perspective. *Proceedings of the National Academy of Science of the United States of America*, 103(21), 8257-62.
- Reed, C. L., & Farah, M. J. (1995). The psychological reality of the body schema: a test with normal participants. *Journal of Experimental Psychology: Human Perception and Performance*, 21, 334–343.
- Reed, C. L., Stone, V.E., Bozova, S., & Tanaka, J. (2003). The body-inversion effect. *Psychological Science*, 14(4), 302-8.
- Reed, C. L., McGoldrick, J. E., Shackelford, R., & Fidopiastis, C. (2004). Are human bodies represented differently from other animate and inanimate objects? *Visual Cognition*, 11, 523–550.
- Reed, C. L., Stone, V. E., Grubb, J. D., & McGoldrick, J. E. (2006). Turning configural processing upside down: part and whole body postures. *Journal of Experimental Psychology: Human Perception and Performance*, 32(1), 73.
- Reep, R. L., Goodwin, G. S., & Corwin, J. V. (1990). Topographic organization in the corticocortical connections of medial agranular cortex in rats. *Journal of Comparative Neurology*, 294(2), 262-80.
- Romano, D., Uberti, E., Caggiano, P., Cocchini, G., & Maravita, A. (2018). Different tool training induces specific effects on body metric representation. *Experimental Brain Research*, 237(2), 493–501.
- Ronchi, R., Heydrich, L., Serino, A., & Blanke, O. (2017). Illusory hand ownership in a patient with personal neglect for the upper limb, but no somatoparaphenia. *Journal of Neuropsychology*, 12(3), 442-462.
- Rorden, C., & Brett, M. (2000). Stereotaxic display of brain lesions. *Behavioural Neurology*, 12(4), 191-200.
- Rousseaux, M., Allart, E., Bernati, T., & Saj, A. (2015). Anatomical and psychometric relationships of behavioral neglect in daily living. *Neuropsychologia*; 70, 64-70.

- Rossetti, Y., Rode, G., & Boisson, D. (1995). Implicit processing of somesthetic information: A dissociation between where and how? *NeuroReport*, 6, 506-510.
- Rossion, B., & Jacques, C. (2008). Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. *Neuroimage*, 39, 1959–1979.
- Rugg, M. D., & Curran, T. (2007). Event-related potentials and recognition memory. *Trends in Cognitive Science*, 11(6), 251-7.
- Sadeh, B., Pitcher, D., Brandman, T., Eisen, A., Thaler, A., & Yovel, G. (2011). Stimulation of category-selective brain areas modulates ERP to their preferred categories. *Current Biology*, 21(22), 1894-9.
- Sadibolova, R., Ferrè, E. R., Linkenauer, S. A., & Longo, M. R. (2019). Distortions of perceived volume and length of body parts. *Cortex*, 111, 74–86.
- Samad, M., Chung, A. J., & Shams, L. (2015). Perception of Body Ownership Is Driven by Bayesian Sensory Inference. *PLoS ONE*, 10(2): e0117178.
- Sato, Y., Kawase, T., Takano, K., Spence, C., & Kansaku, K. (2017). Incorporation of prosthetic limbs into the body representation of amputees: Evidence from the crossed hands temporal order illusion. *Progress in Brain Research*, 236, 225-241.
- Schillaci, G., Hafner, V. V., Lara, B. (2016). Exploration Behaviors, Body Representations, and Simulation Processes for the Development of Cognition in Artificial Agents. *Frontiers in Robotics and AI*, 3, 39.
- Schneider, W., Eschman, A., Zuccolotto, A. (2002). E-Prime (Version 2.0). *Computer software and manual*. Pittsburgh, PA: Psychology Software Tools Inc.
- Schwarzlose, R. F., Baker, C. I., & Kanwisher, N. (2005). Separate face and body selectivity on the fusiform gyrus. *Journal of Neuroscience*, 25(47), 11055-11059.
- Schilder, P. (1935). *The image and appearance of the human body*. New York: International Universities Press.
- Schwoebel, J. & Coslett, H. B. (2005). Evidence for multiple, distinct representations of the human body. *Journal of Cognitive Neuroscience*, 17, 543–553.
- Semenza, C. (1988). Impairment in localization of body parts following brain damage. *Cortex*, 24, 443–449.
- Shapiro, L. (2019). Flesh matters: The body in cognition. *Mind and Language*, 34(1), 3-20
- Shapiro, L. (2011). *Embodied Cognition*. New York: Routledge Press.
- Sherrington, C. S. (1906). *The Integrative Action of the Nervous System*. C Scribner's Sons; New York, NY.

- Sirigu, A., Grafman, J., Bressler, K., & Sunderland, T. (1991). Multiple representations contribute to body knowledge processing. Evidence from a case of autotopagnosia. *Brain*, 114(Pt 1B), 629-42.
- Soechting, J. F. (1982). Does position sense at the elbow reflect a sense of elbow joint angle or one of limb orientation? *Brain Research*, 248, 392–395.
- Soltani, M., & Knight, R. T. (2000). Neural origins of the P300. *Critical Review in Neurobiology*, 14, 199-224.
- Soria Bauser, D.A., Suchan, B., & Daum, I. (2011). Differences between perception of human faces and body shapes: Evidence from the composite illusion. *Vision Research*, 51, 195–202.
- Spaccavento, S., Cellamare, F., Falcone, R., Loverre, A., & Nardulli, R. (2017). Effect of subtypes of neglect on functional outcome in stroke patients. *Annals of Physical and Rehabilitation Medicine*, 60(6), 376-381.
- 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.
- Sposito, A.V., Bolognini, N., Vallar, G., Posteraro, L., Maravita, A. (2010). The spatial encoding of body parts in patients with neglect and neurologically unimpaired participants. *Neuropsychologia*, 48(1), 334–340.
- 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 (Amst)*, 185, 22-32.
- Sumi, S. (1984). Upside-down presentation of the Johansson moving light-spot pattern. *Perception*, 13(3), 283-6.
- Suzuki, K., Yamadori, A., & Fujii, T. (1997). Category-specific comprehension deficit restricted to body parts. *Neurocase*, 3, 193–200.
- Synofzik, M., Vosgerau, G., & Newen, A. (2008a). Beyond the comparator model: a multifactorial two-step account of agency. *Consciousness and Cognition*, 17, 219–239.
- Synofzik, M., Vosgerau, G., and Newen, A. (2008b). I move, therefore I am: a new theoretical framework to investigate agency and ownership. *Consciousness and Cognition*, 17, 411–424.
- Tamè, L., Azañón, E., & Longo, M. R. (2019). A conceptual model of tactile processing across body features of size, shape, side, and spatial location. *Frontiers in Psychology*, 10, 291.

- Tamè, L., Bumpus, N., Linkenauger, S. A., & Longo, M. R. (2017). Distorted body representations are robust to differences in experimental instructions. *Attention, Perception and Psychophysics*, 79, 1204–1216.
- 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.
- Taylor-Clarke, M., Jacobsen, P., & Haggard, P. (2004). Keeping the world a constant size: Object constancy in human touch. *Nature Neuroscience*, 7, 219–220.
- Tessari, A., Ottoboni, G., Baroni, G., Symes, E., & Nicoletti, R. (2012). Is access to the body structural description sensitive to a body part's significance for action and cognition? A study of the sidedness effect using feet. *Experimental Brain Research*, 218(4), 515-25.
- Thierry, G., Martin, C., Downing, P., & Pegna, A. (2007). Controlling for interstimulus perceptual variance abolishes N170 face selectivity. *Nature Neuroscience*, 10(7), 801-802.
- Tosi, G., Romano, D., Maravita, A. (2018). Mirror box training in hemiplegic stroke patients affects body representation. *Frontiers of Human Neuroscience*, 11, 617.
- Townsend, J.T., & Ashby, F.G. (1983). *Stochastic modelling of elementary psychological processes*. Cambridge University Press; New York.
- Tsakiris, M., & Haggard, P. (2005). The Rubber Hand Illusion Revisited: Visuotactile Integration and Self-Attribution. *Journal of Experimental Psychology: Human Perception and Performance*, 31(1), 80-91.
- Tsakiris, M., Prabhu, G., & Haggard, P. (2006). Having a body versus moving your body: How agency structures body-ownership. *Consciousness and Cognition*, 15(2), 423-32.
- Tsakiris, M., Tajadura-Jiménez, A., & Constantini, M. (2011). Just a heartbeat away from one's body: interoceptive sensitivity predicts malleability of body-representations. *Proceedings of the Royal Society B*, 278, 2470–2476.
- Turman, A. B., Ferrington, D. G., Ghosh, S., Morley, J. W., & Rowe, M. J. (1992). Parallel processing of tactile information in the cerebral cortex of the cat: effect of reversible inactivation of SI on responsiveness of SII neurons. *Journal of Neurophysiology*, 67, 411–429.
- Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. Ingle, D. J., Goodale, M. A., & Mansfield R. J. W. (eds.). *Analysis of visual behavior.*, (pp. 549 586). Cambridge,MA: MIT Press.

- Urgesi, C., Berlucchi, G. & Aglioti, S. M. (2004). Magnetic stimulation of extrastriate body area impairs visual processing of non-facial body parts. *Current Biology*, 14, 2130–2134.
- 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.
- Vainio, L., Symes, E., Ellis, R., Tucker, M., & Ottoboni, G. (2008). On the relations between action planning, object identification, and motor representations of observed actions and objects. *Cognition*, 108, 444–465.
- Vallar, G. (1998). Spatial hemineglect in humans. *Trends of Cognitive Science*, 2(3), 87-97.
- Vallar, G., Sterzi, R., Bottini, G., Cappa, S., & Rusconi, M.L. (1990). Temporary remission of left hemianesthesia after vestibular stimulation. A sensory neglect phenomenon. *Cortex*, 26(1), 123-131.
- van Beers, R. J., Sittig, A. C., & Denier van der Gon, J. J. (1998). The precision of proprioceptive position sense. *Experimental Brain Research*, 122, 367–377.
- Van Den Bos, E., & Jeannerod, M. (2002). Sense of body and sense of action both contribute to self-recognition. *Cognition*, 85, 177–187.
- Varela, F. J., Thompson, E. T., & Rosch, E. (1992). *The Embodied Mind: Cognitive Science and Human Experience*, New Edn. Cambridge, MA: The MIT Press.
- Wallgren, G. R. (1954). Phantom experience at spinal anaesthesia. *Annales Chirurgiae et Gynaecologiae Fenniae Suppl*, 5, 486-500.
- Warren, W., & Whang, S. (1987). Visual Guidance of Walking Through Apertures: Body-Scaled Information for Affordances. *Journal of Experimental Psychology Human Perception and Performance*, 13(3), 371-83.
- Weber, E. (1834). *E. H. Weber on the tactile senses*, 2nd ed. London: Academic.
- Weinberg, J., Diller, L., Gordon, W.A., Gerstman, L.J., Lieberman, A., Lakin, P., ... Ezrachi, O. (1977). Visual scanning training effect on reading-related in acquired right brain damage. *Archives of Physical Medicine and Rehabilitation*, 58, 479-86.
- Weiner, K. S., & Grill-Spector, K. (2011). Not one extrastriate body area: Using anatomical landmarks, hMT+, and visual field maps to parcellate limb-selective activations in human lateral occipitotemporal cortex. *Neuroimage*, 56(4), 2183-2199.
- Weinstein, S. (1968). Intensive and extensive aspects of tactile sensitivity as a function of body part, sex and laterality. In *the First Int'l symp. On the Skin Senses*, 1968.

- Weiskrantz, L. (2004). Roots of blindsight. *Progress in Brain Research*, 144, 229-241.
- Wilson, B., Cockburn, J., & Halligan, P. (1987). Development of a behavioral test of visuospatial neglect. *Archives of Physical and Medical Rehabilitation*; 68(2), 98-102.
- Wilson, M. (2002). Six views of embodied cognition. *Psychonomic Bulletin & Review*, 9, 625-636.
- Wilson, R. A., & Foglia, L. (2011). Edward N. Zalta (ed.). *Embodied Cognition*. The Stanford Encyclopedia of Philosophy (Fall 2011 Edition).
- Yovel, G., Pelc, T., & Lubetzky, I. (2010). It's all in your head: why is the body inversion effect abolished for headless bodies? *Journal of Experimental Psychology: Human Perception and Performance*, 36, 759-767.
- Zeki, S. M. (1993). The visual association cortex. *Current Opinion in Neurobiology*, 3, 155-159.
- Zhang, H. Q., Zachariah, M. K., Coleman, G.T., & Rowe, M.J. (2001). Hierarchical equivalence of somatosensory areas I and II for tactile processing in the cerebral cortex of the marmoset monkey. *Journal of Neurophysiology*, 85(5), 1823-35.
- Zimmermann, M., Mars, R. B., de Lange, F. P., Toni, I., & Verhagen, L. (2018). Is the extrastriate body area part of the dorsal visuomotor stream? *Brain Structure & Function*, 223(1), 31-46.
- Zimmermann, M., Meulenbroek, R. G. J., & de Lange, F. P. (2012). Motor planning is facilitated by adopting an action's goal posture: an fMRI study. *Cerebral Cortex*, 22, 122-131.
- Zimmermann, M., Verhagen, L., de Lange, F. P., & Toni, I. (2016). The extrastriate body area computes desired goal states during action planning. *eNeuro*, doi:10.1523/ENEURO.0020-16.2016.
- Zoccolotti, P., & Judica, A. (1991). Functional evaluation of hemineglect by means of a semistructured scale: Personal and extrapersonal differentiation. *Neuropsychological Rehabilitation*, 1(1), 33-44.
- Zoia, S., Blason, L., D'Ottavio, G., Bulgheroni, M., Pezzetta, E., Scabar, A., & Castiello, U. (2007). Evidence of early development of action planning in the human foetus: a kinematic study. *Experimental Brain Research*, 176, 217-226.