Valeria Bellan

BODY REPRESENTATION, BODY LOCALISATION AND BODY SIZE PERCEPTION:

A STUDY OF BODILY MODULATIONS

Doctoral thesis promoted by
dr. Alberto Gallace

University of Milano-Bicocca, Department of Psychology
Doctoral program in Experimental Psychology, Linguistics,
and Cognitive Neuroscience, XXVI cycle.

Summary

People are generally quite good at adapting to changes in body shape and size because of the flexibility of their body representation. By means of bodily illusions, it is possible to experimentally induce updating of body representation and, thus, manipulate the sense of self. The main aim of this thesis is to investigate important aspects related to the sense of self through bodily illusions. Firstly, we investigated the relationship between the sense of ownership and self-localisation (Study 1). The results from this study are taken to suggest that the proprioceptive drift (i.e. a bias in the localisation of a given body part) is more likely related to the visual capture of touch rather than being a reliable measure of a shift in the sense of body ownership. In fact, our data show that the proprioceptive drift occurs not only in the absence of a shift in the sense of ownership, but even in the absence of body-like objects. Secondly, we investigated self-localisation of body parts by means of a novel illusion, the Disappearing Hand Trick. In particular, we explored the role of vision and proprioception (Study 2), as well as the role of attention and sensory incongruence (Study 3), in locating one's own hands when visual and proprioceptive information regarding the body are incongruent. Our data (Study 2) are in line with previous research, confirming a predominant role of vision over proprioception. In addition, they show that, after a certain amount of time, proprioception is weighted more heavily than vision. That is, our results demonstrate that the cortical representations of body position can be updated even when there is no real need to do it (i.e. no movement is required). This might be seen as an evolutionarily convenient response to keep the body ready for a possible quick reaction. In Study 3, we ruled out the possibility that this effect was only driven by spatial attention being directed towards the side of the space where the hand was actually located. In fact, no difference in localisation accuracy was found when the direction of spatial attention was manipulated. Finally, by asking the participants to reach across for their hidden right hand (Study 3), we confirmed that a motor act bearing a sensory incongruence

accelerates the reliance on proprioception, most likely by aligning the motor and perceptual coordinates in order to plan the movement.

In the first three studies, vision was manipulated in order to trick self-localisation. In Study 4, proprioception was manipulated, showing that incongruent proprioceptive information coming from the same joint does not affect the perceived size of that body part, but does lead to a more accurate estimation of its position. However, we wondered whether these same changes in the way people perceive their body might also occur at a more implicit level, just triggered by vision. The preliminary results obtained would seem to suggest that body perception is more vulnerable to change in women than in men after exposure to same-sex ideal bodies.

Taken together, the results of the studies reported in this thesis suggest that, by manipulating bodily signals, both explicitly, by means of a variety of bodily illusion, and even implicitly, by generating subtle incongruence between one’s own real body and how the body “should” be, it is possible to establish the relative importance of different sensory signals in shaping our body representation. Our studies also shed some light on the temporal dynamic of these sensory interactions.

Originality statement

I, Valeria Bellan, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

Doctoral thesis promoted by:
Dr. Alberto Gallace,
Department of Psychology, University of Milano-Bicocca

Table of contents

Acknowledgements

There are not enough words (in English or in Italian), to thank all the people that, in one way or in another, contributed to this thesis, and, even more, to make these last four years a mesmerising adventure. First of all, a very grateful thanks to my supervisor, Alberto Gallace. Alberto, thank you for having me as a PhD student. Without your help, your support and your teachings, not even a word of this thesis could have been written. Also, I would like to thank Carlo Reverberi, who “picked me up” when I was a little lost, and Alessio Toraldo, my very first mentor, who never stopped encouraging me. A huge thanks to Lorimer Moseley, the Body in Mind team and the University of South Australia, for they all made me feel simply “one of them”. Lorimer, I cannot imagine a more complete and edifying life experience than the one I had the privilege to live in Adelaide. Working with highly experienced, extremely brilliant and incredibly humble people like you, Tasha and the whole group encouraged me in constantly trying to improve, never give up, but most of all, in believing in myself. Heartfelt thanks to all of you, my dear Australian family.

A special thanks, then, to the wonderful and tireless Tracy Jones and Mrs De Marco: without you, we would all be lost.

Thanks from the bottom of my heart to my Bicocca’s friends and “travel buddies”, Valentina, Giulio, Silvia and Mirella, who made me feel at home, even being on the other side of the world. Thanks also to Federica, Elena, Elisa and Veronica, for listening to me, encouraging me and advising me, and to Chiara and Pina, you have been to me teachers and true friends.

Thanks to my wonderful family: Mum, Dad, Benni, but also Aunts and Uncles, Grandparents and cousins. Thank you for all the Skype calls, trying to slot in time zones and various commitments. The last but not the least, Davide: you bravely followed me literally to the end of the world, providing, every day of my life, unconditioned love and endless patience. Probably I would not be here without you. Thank you.

Publications, presentations and awards

Publications:

Bellan V, Reverberi C, & Gallace A (2012). Evidence for " Visual Enhancement of Touch " Mediated by Visual Displays and Its Relationship with Body Ownership. Haptics: Perception, Devices, Mobility, and Communication. Lecture Notes in Computer Science, 7282/2012, 58–66.

Bellan V, Moseley GL, & Gallace A, *Percezione del dolore*. In: Papagno, C., & Gallace, A. (a cura di), *Psicobiologia del comportamento normale e patologico*, 1ª ed., Bologna, Il Mulino, 2014, cap. VI

Gilpin HR, **Bellan V**, Gallace A, & Moseley GL (2014). Exploring the roles of body ownership, vision and virtual reality on heat pain threshold. European Journal of Pain, 18(7), 900–901.

Manuscripts currently under review:

Bellan V, Gilpin HR, Stanton TR, Newport R, Gallace A, & Moseley GL (under review). Untangling visual and proprioceptive contributions to body localization.

Bellan V, Wallwork SB, Stanton TR, Reverberi C, Gallace A, & Moseley GL (under review). No telescoping effect with dual tendon vibration

Conference presentations during candidature:

Bellan V, Gilpin HR, Stanton TR, Newport R, Gallace A, Moseley GL. "Where does it hurt? Untangling multisensory inputs for awareness of body location". *International Association for the Study of Pain: 15th World Congress on Pain.* Buenos Aires, October 2014. *Poster presentation.*

Boesch E, **Bellan V**, Moseley GL & Stanton TR. “The effect of bodily illusions on clinical pain: A systematic review and meta-analysis”. *International Association for the Study of Pain: 15th World Congress on Pain.* Buenos Aires, October 2014. *Poster presentation*

Bellan V, Etzi R, Gallace A. “Evaluating the effect of seeing human body images on people’s ability to estimate their own body size and on body satisfaction”. *15th International Multisensory Research Forum.* Amsterdam, June 2014. *Poster presentation.*

Bellan V, Reverberi C, Gallace A, Moseley GL. “Modulation of tactile information processing by ‘visual body touch”. *PainAdelaide.* Adelaide, April 2013. *Poster presentation.*

Bellan V, Reverberi C, Gallace A. “Watching touch increases people’s alertness to tactile stimuli presented on body surface”. *13th International Multisensory Research Forum.* Oxford, June 2012. *Poster presentation.*

Bellan V, Reverberi C, Gallace A. “Evidence for’ Visual Enhancement of Touch’ mediated by visual displays and its relationship with body ownership”. *Eurohaptics.* Tampere, June 2012. *Poster presentation.*

Bellan V, Piroddi C, Scarpa P, Pelle F, Cascardo B, Volpi S, Zanardi G, Francione S, Quattropani C, Bergese S, Lo Russo G, Bottini G. “Does the postsurgical clinical outcome influence the cognitive function of children with Drug Resistant Frontal Focal Epilepsy*?”. Developmental Neuropsychology Workshop*. Bressanone, January 2011. *Poster presentation and topical workshop proposal accepted.*

Invited talks during candidature:

Bellan V. “Bodily illusions and hypnosis: building a bridge?”. *South Australian Society of Hypnosis: Annual Meeting.* Adelaide, October 2014. *Invited speaker.*

Bellan V. “What if…a part of your body suddenly disappears*?”. Australian Physiotherapy Association: Annual Meeting.* Adelaide, August 2014. *Invited speaker.*

Bellan V. “Why do haptics matter? A look at the ‘visual’ body touch”. *Australasian Neuroscience Society: 34th Meeting.* Adelaide, January 2014. *Topical workshop proposal accepted*, *International Invited Speaker.*

Awards:

International Association for the Study of Pain. Poster presentation: *Where does it hurt? Untangling multisensory inputs for awareness of body location*. Travel grant and Registration grant. October 2014.

Royal Society of South Australia’s Postgraduate Prize. Oral presentation: *Feeling touch in empty space.* September 2013.

Preface

This thesis is arranged in seven chapters, such that each chapter can be read independently. Study 1, described in Chapter II, has been conducted in collaboration with Alberto Gallace (University of Milano-Bicocca and NeuroMI), Carlo Reverberi (University of Milano-Bicocca and NeuroMI) and G. Lorimer Moseley (University of South Australia and Neuroscience Research Australia and PainAdelaide). Study 2, described in Chapter III, and Study 3, described in Chapter IV, have been conducted in collaboration with Helen R. Gilpin (University of South Australia), Tasha R. Stanton (University of South Australia and Neuroscience Research Australia), Roger Newport (University of Nottingham), Alberto Gallace (University of Milano-Bicocca and NeuroMI) and G. Lorimer Moseley (University of South Australia, Neuroscience Research Australia and PainAdelaide). Chapter III manuscript is presently under review, and Chapter IV is submission-ready and will be submitted upon acceptance of the Chapter III manuscript. Study 4, described in Chapter V, has been conducted in collaboration with Sarah B. Wallwork (University of South Australia), Tasha R. Stanton (University of South Australia and Neuroscience Research Australia), Alberto Gallace (University of Milano-Bicocca and NeuroMI) and G. Lorimer Moseley (University of South Australia, Neuroscience Research Australia and PainAdelaide). Chapter V's manuscript is currently under review.

Chapter I is an introduction to the thesis and provides an overview of the relevant literature regarding the concept of body representation. Chapter II is a study investigating the existence of a visuo-tactile ventriloquist effect. Chapter III and IV describe two studies conducted with a piece of equipment called Mirage, that allows to manipulate the visual appearance of the participants' hands. Chapter III received a positive response to a submission enquiry at *Experimental Brain Research*, and is presently under review at this journal. Chapter V concerns a study that explores the effect of opposite and inconsistent proprioceptive cues coming from a limb to the self-localisation of that limb. Chapter V as well received a positive response to a submission enquiry at *Journal of Experimental Psychology: Human Perception and Performance*, and is currently under review at this journal. Chapter VI is a pilot study investigating the possibility that an implicit manipulation of body representation might occur only by showing the image of ideal bodies. Future directions are discussed. Chapter VII is a conclusions chapter, which consists of an overview of the main findings, the implications of these findings, and recommendations for future research.

Reference list, appendices and supplemental material are included at the end of the thesis.

CHAPTER I

INTRODUCTION

Abbreviations used in this chapter:

RHI, Rubber Hand Illusion; S1, Primary Sensory Cortex; EBA, Extrastriate Body Area; FBA, Fusiform Body Area; TMS, Transcranial Magnetic Stimulation; PPc, Post Parietal cortex; TPJ, Temporo-Parietal Junction; vPMc, ventral PreMotor cortex;SCR, Skin Conductance Response; CNS, Central Nervous System.

1. The body representation(s)

For centuries philosophers, scientists and thinkers have been trying to define the concept of “self”. From an ontogenetic perspective, newborns spend a lot of time exploring their own body during the first months of life. But what makes a “self”? Over the last two centuries different definitions and explanations have been proposed. Some authors chose to focus on one aspect of the self, that is, how the body is represented in the brain, i.e. the “body representation”. In this first chapter, the concept of body representation will be explored.

1.1. The dualism of the body representation

In 1905 for the first time the word “body schema” appears in a scientific work, describing the spatial organisation of the internal body sensations. However, it is only with Head and Holmes (1911) that this term acquires more specific connotations. These authors are also the first to have attempted to describe how the brain processes these aspects. Importantly, their approach started a long and still going terminological and theoretical speculation. In particular, they proposed that two different body schemata might describe how the body is represented: one body schema accounting for the localisation of tactile stimuli delivered on the body surface, and another body schema accounting for the posture and the movements. According to this theory (Head & Holmes, 1911), at each moment in time, new schemata are created in order to provide a “plastic model of oneself” that is independent by any changes driven by movement, variation in posture or tactile stimuli. Lately, Schilder (1923, 1936), even though from a psychoanalytic perspective, used the words “image” (i.e. “the animated image”) and “schema” (i.e. “the expression of the body schema”) to describe the phenomenon of the phantom limb (i.e. the sensation, after the amputation of a limb that the limb is still present). Nevertheless, the term “body schema” is not employed here with the same meaning originally suggested by Head and Holmes (1911). Furthermore, by using the terms “image” and “schema” interchangeably, he accidentally contributed to the creation of a murky interpretation of two different concepts (Gallagher & Meltzoff, 1996).

Merleau-Ponty (1945) outlined his idea of *schema corporèl* with a particular focus of the acquired and innate aspect of it. According to his interpretation, the newborns do not possess any external perceptual ability, such as their earliest experiences are utterly interoceptive. It is only between the third and sixth month of life that they “submerged from chaos” and a fruitful collaboration between the intero- and extero-ceptive domains can start. Merleau-Ponty justified this vision from a neurological point of view, as the myelinisation process occurs between three and six months of age and gradually, namely with some body part completely myelinated before others. Within this context, the body schema (or *schema corporèl*) is created and integrated gradually and dynamically, in a way that it is more and beyond a mere “sum of associations” established during the experiences.

However, various research regarding the study of congenital aplasia rejected Merleau-Ponty’s view (Weinstein & Sersen, 1961, 1963; Poek, 1964; Vetter & Weinstein, 1967; Ramachandran, 1993; Lacroix, 1992; Saadah & Melzack, 1994; Melzack, Israel, Lacroix, & Schultz, 1997), by reporting that a considerable number of patients with limb aplasia (i.e. congenital limb deficiency) show phantom limb. The fact that being born without a limb does not eliminate the sensation of the absent limb suggests that at least some parts of those brain mechanisms that subserves the somatic perception and representation of one’s own body are genetically determined. In other terms, following this view, the representation of the body would seem to be innate (Melzack et al., 1997).

The debate about the nurture/nature genesis of the body representation, still, does not shed light on the meaning of the concepts themselves. As highlighted by Critchley first (1979) and by Gallagher later (1986), a lack of clear definitions still persists. In fact, diverse terms are used interchangeably to define the same concept, such as body image, body schema, corporeal schema, *image de soi*. Within this necessity of clarity, it is possible divide the different views in two big categories. The first one includes all those authors who chose to support the idea of a discrete number of body representations. A different group of authors instead prefer a more holistic vision of the issue, proposing a unified and dynamic representation of the body.

1.2. Body schema vs. body image(s)

The authors that support a discrete approach justify their position in two ways: (1) comparing this dichotomy with other neurocognitive dichotomies; (2) exploiting the so-called "double dissociation" in the clinical field (Berlucchi & Aglioti, 2010).

In fact, according to some authors (Paillard, 1991, 1999; Dijkerman & de Haan, 2007) the functional distinction between perception and action, already shown for other sensory modalities (e.g. vision, Milner & Goodale, 1995; audition, Belin & Zatorre, 2000; touch and proprioception, Dijkerman & de Haan, 2007), can also explain how the body is represented. For example, as far as vision is concerned, a visual stimulus can lead to different reactions according to the task. For example, in the picture below (Fig. 1), it is shown the traditional Titchener circles illusion (also known as Ebbinghaus illusion). In both configurations, the central circle is exactly the same size, but, because of the contrast due to the difference in size between the internal and external circles, the central circle in the left configuration appears to be bigger than the one in the right configuration.

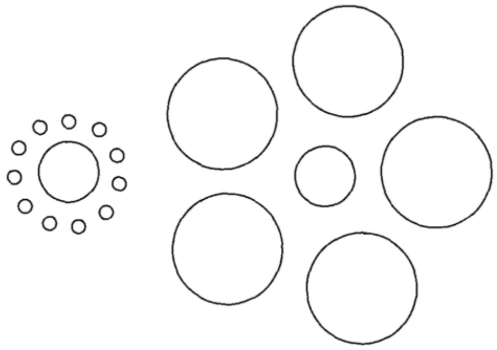


Figure 1 - The Titchener circles or Ebbinghaus illusion. (Adapted from Aglioti et al., 1995)

However, it has been shown that if the participants are asked to grasp the central circle, even if they still report to visually perceive the difference in size, the hand aperture during grasping does not differ whether they are asked to attempt to grasp one central circle or the other (Aglioti, DeSouza, & Goodale, 1995). The anatomo-functional dichotomies found in the field of vision – that is, on one side the "what" (perception of the object) and "where" (location of the object) paths theory (Ungerleider & Mishkin, 1982), and, on the other side, the "vision for perception" and "vision for action" dichotomy (Milner & Goodale, 1995) – inspired Paillard in the definition of body schema and body image. In fact, the body schema is conceived by this author as a sensorimotor map of the body that is mainly guided by proprioception. The body image, on the other hand, is a graphic description of the body and it is mainly built on the basis of visual inputs (Paillard, 1999).

Later Gallagher proposed another definition for the body image and schema (Gallagher, 2005). In particular, according to this author, the body schema allows the agent to interact with his/her surrounding world, providing all the postural and sensory-motor cues without the need of any perceptual monitoring. The body image, instead, guarantees the sense of body ownership and self-consciousness, gathering the perceptions and the beliefs about one's own body. In other words, in both Paillard (1999) and Gallagher (2005)'s descriptions, the difference in the concept of the body schema vs. body image is interpreted on the basis of the aim that each representation has for the agent.

Both Paillard (1983, 1999) and Gallagher (2005), provide support for their theories using the results arising from clinical neuropsychology. Within this field, a double dissociation is known as a basic neuropsychological principle, where if a patient (or a group of patients) shows an impairment in the task A but not in the task B and another patient (or group of patients) shows an impairment in the task B but not in the task A, and A and B evaluate the same construct, for example the body representation, then it is possible to affirm that A and B measure two different and independent aspects of that same construct.

Further findings, supporting the dichotomy between body image and body schema, are also represented by the neuropsychological syndrome called “unilateral spatial neglect”. As a consequence of a right parietal lesion, some patients “neglect” their left limbs (i.e. they fail “to report, respond, or orient to novel or meaningful stimuli presented to the side opposite a brain lesion, when this failure cannot be attributed to either sensory or motor defects”; p. 279, Heilman, Watson, & Valenstein, 1993), but, in absence of paralysis, they can engage in bimanual tasks (Denny-Brown, Meyer, & Horenstein, 1952). According to Gallagher (2005) this represents a case of intact body schema and damaged body image. On the contrary, Gallagher and Cole (2005) reported that patients that experience lack of proprioceptive cues coming from the body, need to rely on vision and attention in order to perform goal-directed actions. These actions based on the body image (intact) seem to be slower and less accurate than the actions that are usually based and controlled by the body schema (damaged in these patients) (Gallagher & Cole, 2005). Other authors found inspiration from these works (Paillard et al. 1999; Rossetti et al. 2001) in order to attempt to provide solid neural correlates to the definition of the body image and body schema based on the dichotomy between “perception and action” (Dijkerman & de Haan, 2007). In general, all the dichotomies proposed so far agree on two facts. The first is that the body schema is unconscious, while the body image is conscious; the second regards the fact that the body schema serves action. As well highlighted by de Vignemont (2010), though, both these points are quite problematic. In fact, as far as consciousness is concerned, it has been suggested that it is possible to become aware and conscious of ones’ own body schema, for example through motor imagery (Schwoebel & Coslett, 2005). In this sense, consciousness does not represent a solid point to disentangle body image and body schema. Nevertheless, it can be questioned whether, through the motor imagery, one does not rather become conscious of just one aspect of the body schema, that is the body part's position.

However, on the other hand, the general agreement about the "active" nature of the body schema cannot be confuted. Nonetheless, the body image is often conceived by means of a mutually exclusive form of reasoning: everything that is not action-directed (e.g. everything that does not fit into the definition of body schema) is body image. It appears quite clear that this cannot be considered a real scientific definition, *tertium non datur*.

Some other authors, therefore, tried to better define the nature of the body image, maintaining the general structure based on the double dissociation, but proposing a triadic taxonomy of body representation. In particular, these authors (Schwoebel & Coslett, 2005; Sirigu, Grafman, Bressler, & Sunderland, 1991) would seem to agree on the existence of a sensorimotor representation (i.e. the body schema), but also propose to split the concept of body image into two different representations: one based on body structural description and the second based on body semantics. The first one can be described as a visuospatial map of one's own body, providing the structural relationship between body parts; this representation is mainly guided by vision and somatic perceptions. The second representation concerns the meaning and the linguistic label of each body part, and its categorical relationship with the other parts.

However, even considering this approach, the problem of defining body representation remains unsolved, mainly because it would be possible to dissociate the body image into a virtually infinite number of sub-functions. This would seem to be in opposition with the aim of the theories previously presented, in which the tendency is to enumerate a finite number of possible solutions. Importantly, the scientific knowledge proceeds by "decomposing" an initial theory analysing different aspects in order to integrate all of them in a novel, more effective, theory, eventually. In addition to this, the “Perception-Action” functional distinction per se has been widely criticised from both empirical and theoretical perspectives. In particular it has been claimed that it would be impossible for these two pathways to work totally independently (de Vignemont, 2010).

Other approaches to the problem of defying the body representation, such as the enactive approach (e.g., Thompson, 2005), suggests that the whole dichotomy between body schema and body image is pointless. This is due to the fact that, ultimately, each perceptual experience is bonded to the sensorimotor aspects and there would be no reason to dissociate them into body image and body schema (also, it would not be possible) (for an overview see de Vignemont, 2011).

1.2.1. Bayesian model: is it the solution?

In order to solve the problem about how many representations of the body are present in our neurocognitive system, some authors (Kammers, Mulder, de Vignemont, & Dijkerman, 2010) proposed to look at the problem from a different perspective. In fact, in order to study the body representation in healthy individuals, they proposed to look not only at the output of the processes that lead to certain behaviours, but also to consider the type of input used for these behaviours to be accomplished, and how the output and input are related. Besides, they suggested to consider different types of theoretical models at the same time and to compare them. In order to identify the best model among all those described in the extant literature they proposed to apply the Bayesian rule. With such a method they would be able to test the models against each other and to identify the one that has the higher probability to be correct. More specifically, this approach allows identification of the model that is more supported by the data, even though it does not reveal it to be the “best” possible model. Their reasoning, thus, suggested that the experiments on this topic should focus on how the body is represented by the neurocognitive system rather than on how many representations of the body can be maintained.

Even though this approach is interesting and its future development should probably be highly regarded, the authors did not take into account those models that, refusing a discrete vision of body representations, proposed a more holistic view to the matter. The first conceptualisation of this holistic view of body representation has been suggested, back in the late 1980’s, by Ronald Melzack.

1.3. A new conceptual model: the neuromatrix (Melzack, 1989)

In 1989 Melzack highlighted the lack of theories that could really explain the phenomenon of phantom limb (see above). Authors such as Simmel (1958) and Weinstein and colleagues (1963) described it as completely related to the ‘body schema’ (Head and Holmes, 1911). That is, the representation of the phantom limb, as the whole body, is conceived as completely represented at the somatosensory cortex level (according to the homunculus mapped by Penfield and Boldrey, 1937). However, this idea has been criticised in three ways (Melzack, 1989). First, the concept of “body schema” per se, especially in its original description, is far too vague to constitute the basis of such a complex and misunderstood phenomenon as the phantom limb. Second, in phantom limb, vision has been shown to play an important role: in fact, there is a clear dissociation between the “seen” and the “perceived” body shape. Since Head and Holmes did not include a connection between body schema and body image, the role of vision is left unexplained. Third, there is no support to the idea that the phantom limb is generated into the post central somatosensory cortex. In fact, surgical ablation of this area has been reported not to affect the phantom limb symptoms (Merzenich & Kaas, 1980; White & Sweet, 1969). However, as wisely pointed out by Melzack (1989), even supposing that the identification of the phantom limb with the somatosensory cortex is correct, it is now acknowledged that there are several projections coming from the body receptors to the cortex, to the brainstem, to the limbic system and to the cerebellum, and, obviously, all of them are likely to play a role in the phantom limb phenomena. Moreover, it remains unclear how this process could work. This lack of a clear description of the phantom limb phenomena, thus, led Melzack to suggest a new conception not only of the phenomenon itself, but also of the functioning of the entire nervous system. This new conceptual model is based on four observations about the phantom limb symptoms and signs:

- The phantom limb feels totally real. This suggests that “We don’t need a body to feel a body” (p. 4, Melzack, 1989).
- The quality of experience such as pain, warmth, cold, are created by neural networks within our nervous system and are triggered by inputs coming from the body. This means that the quality of an experience does not exist outside our brain – “outside” exists just an experience that triggered that particular quality of sensation (for example, the external experience of touching an ice cube triggers the neural network for the sensation of cold, but the quality “cold” is not an inherent quality of the ice per se).
- The body is always perceived as a unity and identified as the self, as compared with the non-self (e.g. other people or the surrounding world). This suggests that the central nervous system is able to process a quantity of different information coming from the body as a whole.
- The finding that the phantom limb can actually be experienced by aplasic patients, suggests that the brain processes, underpinning the “body-self” are

> genetically determined. This, however, does not exclude the possibility that the "body-self" is malleable and can be modified by experience.

Following Melzack's view, the nervous system includes four main functional and conceptual components: the body-self neuromatrix, the neurosignature (i.e. Cyclical Processing and Synthesis, CPS), the Sentient Neural Hub (SNH) and the neuromodules. The neuromatrix can be defined as the "anatomical substrate of the body-self" and it is represented by a large and widespread network of neurons that create loops between the thalamus and the cortex, and between the cortex and the limbic system. These loops diverge (to allow a parallel processing of the information in different components of the neuromatrix) and converge (in order for the products of the processing to interact) creating cyclical processing and synthesis of nerve impulses through the neuromatrix. This is process produces what it is called the neurosignature. The neurosignatures are produced by patterns of synaptic connections in the entire neuromatrix. They are both genetically predetermined (i.e. the normal growth of synapses), but they are also modified by the environment (i.e. the inputs coming from the body select which synapses are functionally needed and which ones are not). In particular, there are some portions of the neuromatrix that are specialised in processing particular types of information. These portions are called neuromodules and they impress subsignatures on the larger, general neurosignatures. The final neurosignature (i.e. the product of the neuromatrix plus the intervention of the neuromodules that carry the input properties) is synthesised, by means of a process called Cyclical Processing and Synthesis (CPS), and converges into the areas of the Sentient Neural Hub (SNH). According to Melzack's model, the SNH is located centrally in the brainstem and it is where the inputs coming from the neuromatrix are translated into awareness. This means that the SNH assigns to the neurosignature patterns a specific quality of experience (i.e. the sensation of cold by touching an ice cube).

So far, we described how, on the basis of Melzack's theory, the quality of sensations is generated. However, it should be said that an important aspect of the quality of an experience is the ability to respond to it (e.g. retreating one's own hand from the fire that is causing the sensation of pain). In order to respond to a sensory stimulus (e.g. a potentially dangerous one), the individual should need to detect – non necessarily at a conscious level – the stimulus itself. In other words, a behavioural response can occur just after the input has been identified in order to represent a meaningful experience (e.g. postural adjustments in body position naturally occur in everyday life without the need of a conscious experience, instead they are automatically activated to avoid joint or muscular stress). However, at the same time, the response to the stimulus from the individual should be prompt, thus, as soon as the inputs from the body start to be analysed within the neuromatrix and, while the CPS works to identify the class of input, several possible action – neuromodules need to be activated. As far as the input is progressively better defined, the more effective action – neuromodules are narrowed down until one is finally chosen. When the appropriate action patterns are activated (both relying on genetically predetermined and experience based patterns), the input carried by the firing neurons is transmitted to the dorsal horns that activate, in turn, the appropriate set of muscles. When the final action is performed, the experience of movement is recorded back to the neuromatrix and this is where the phantom limb sensation occurs. In fact, the part of the neuromatrix that is innate still carries the neuromodules for the missing limb and for its movements.

Melzack's theory constituted a great step forward in the understanding of a variety of medical conditions involving pain. His idea that "a genetically determined template for the body-self is modulated by powerful stress system and the cognitive functions of the brain, in addition to the traditional sensory inputs" (p. 93, Melzack, 2005) represented a strong theoretical framework for previously unexplained phenomena such as the phantom limb pain, the chronic back pain and the Complex Regional Pain Syndrome (CRPS, a highly disabling condition in which a certain body part – usually a limb – is in pain, often swollen and reddened, without the presence of any evident tissue damage). In fact, the main idea underpinning these unusual pain experiences is that, far from being "psychogenic", the experience of pain, that normally has a protective meaning, can be generated even in absence of a real danger. On the basis of Melzack's suggestion, this can be explained by conceiving a neuromatrix in which genetics, hormonal stress-related mechanisms and neural mechanisms for the processing of sensory inputs are interrelated and work in cooperation.

Even though Melzack's theory had the undoubtedly advantage to pave the way to a new conceptualisation of the nervous system, it has been heavily criticised and still is. In particular, according to some authors (Keefe et al., 1996) Melzack's theory failed to offer a mechanism for the SNH idea. Although there are correlates in motor control of the idea of a bifurcated message to action and perception (i.e. the SNH), there is no centre that has been identified.

1.4. From the neuromatrix to the Body Matrix

If Melzack's starting point was the consideration about the lack of a theory that could explain the phantom limb phenomenon, Moseley, Gallace and Spence (2012) begun their studies on the mechanisms behind body representation starting from the phenomenon of the Rubber Hand Illusion (RHI). A full description of the RHI is widely covered in paragraph 4 of this chapter. Briefly, when one of the participants' arm is out of view and, in its usual place, is shown a fake arm, a simultaneous stroking of the real and fake hand results into the sensation that the fake hand belongs to the participant (Botvinick & Cohen, 1998). A lot was written in order to try to explain this illusion. In particular, Makin (2008) underlined the importance of a multisensory representation of the so-called “peri-hand space”, (i.e. the space that is around one’s own hand) to produce the illusion. The finding that the RHI can be induced when the fake hand is placed no more than 30 cm apart from the real hand seems to support this idea: the RHI is in fact explained as the consequence of multisensory integration of cues in the peri-hand space. In particular, according to Makin, the peri-hand space is shifted from the real hand to the fake hand. This drift is driven by the conjunction of tactile and visual events centred on the hands. In conclusion, the author proposes that the illusion is due to a representation of the space around the body that is body part-centred, in this specific case, thus, hand-centred. However, as pointed out by Moseley and colleagues (2012), this model cannot explain some other phenomena. In fact, it has been demonstrated that during the RHI the hand involved in the illusion (i.e. the ‘disowned’ hand) cools down (Moseley et al., 2008), meaning that a change in thermoregulation occurs, following a change in the sense of ownership. In addition to this, in patients affected with CRPS usually one side of their body is cooler than the other. Moseley et al.(2009) reported that when the cool hand, crossing the midline, is placed in the other side of the space, it warms up. At the same time, when the affected hand is shifted to the ‘unaffected’ side, it cools down and a slightly decrease in pain it has also been reported (Moseley, Gallace, & Spence, 2009). These results are supported by research on healthy volunteers using experimental pain (Gallace, Torta, Moseley, & Iannetti, 2011; Sambo et al., 2013; Torta et al., 2013). In particular, these studies support the idea that the spatial representation of the body (together with the anatomical representations, of course) plays an important role in the processing of the stimuli delivered on the body surface. That is, a model that is body part-centred, such the one proposed by Makin (2008) does not account for these spatially-related phenomena. For this reason, Moseley and collaborators proposed the more comprehensive concept of

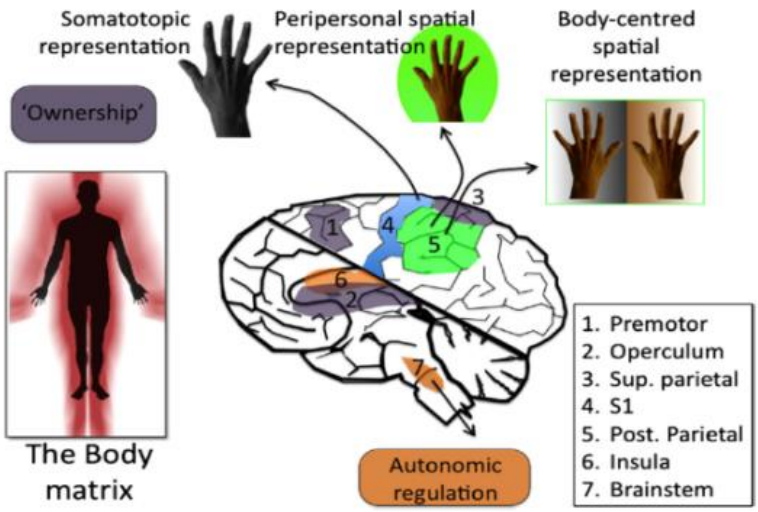


Figure 2 - The Body Matrix (from Moseley et al., 2012)

body matrix as a "multisensory representation of peripersonal space and of the space directly around the body" (p.39).

The most important and innovative aspect of this fairly new concept, compared to the previous descriptions of peripersonal space, is that the body matrix is aligned with a body-centred (rather than a hand- or body part-centred) frame of reference. In particular, all the sensory events occurring on the right side of the space are mapped as 'right', even if they involve a body part that is usually located in the left part of the space (such as a left hand). This idea of a body-centred representation (even though it is still unclear if it is centred on the torso or on the head) provides a putative explanation for disturbances such as the CRPS. In fact prolonged inaccurate input coming from a body part that is usually located in a certain part of the space (i.e. the right hand) would affect the representation of that specific part of the space (i.e. the right side) (Moseley, Gallace, & Spence, 2012). Another important feature of the concept of body matrix is that it resolves the "body image and body schema" problem. In fact, the concept of body matrix includes (and entails) a direct connection between cognitive representations (e.g. the sense of ownership) and homeostatic functions (e.g. thermoregulation), approaching the body representation issue in an holistic way. As highlighted before, the concept of Body Matrix at the moment might be conceived as the peak of the evolution of theory about the body representation. While including all the valid characteristics proposed by the previous theories, the concept of body matrix provides explanations for most recent findings (i.e. the analgesic effect of crossing the arm).

In regard to thermoregulation, specifically, the body matrix model can account for the cooling effect observed during the RHI (Moseley et al., 2008). That is, it is possible to observe the RHI from two different perspective. First, the participants feels a sense of ownership towards a new (fake) hand, but, in the meantime, in order to own a new body part, they might “disown” the old (real) hand. So, what happens to the replaced part? According to Moseley et al., the observed decrease in temperature in the real hand can be explained as follows: during the illusion, two main and complementary changes occurs within the body matrix: the neural activation for the representation of the space where the rubber hand is increases, and that space is now considered a part of the body, such that protection, ownership and homeostatic control are now focussed on that spot. In the meantime, though, the neural activation supporting the representation of the space where the real (unseen) hand is placed, decreases, together with the sense of ownership, protection and homeostasis over that area of the space (Moseley et al., 2012). This bidirectional link between the body matrix and the body itself is also supported by findings showing that artificially cooling down the hidden hand increases the vividness of the illusion, while warming it up decreases the vividness of the illusion (Kammers, Rose, & Haggard, 2011).

1.4.1. The neural correlates of the body matrix

The precise neural mechanisms underpinning the concept of body matrix and the relationship between the cognitive representations and the homeostatic functions of the body, certainly need to be further investigated by means of neuroimaging studies. Nonetheless, the authors suggested a putative cerebral organisation for the body matrix. As shown in Fig. 3, a widespread network is thought to be involved. First of all, the Primary Sensory Cortex (S1) is acknowledged to contain the somatotopic representation of the body (Penfield & Boldrey, 1937). Besides, areas, such as the Premotor Cortex, the Superior Parietal Cortex (Ehrsson, Spence, & Passingham, 2004), the Operculum and the Insula (Tsakiris, Hesse, Boy, Haggard, & Fink, 2007), have been found to be involved in the sense of ownership towards one's own body. The Posterior Parietal Cortex instead, has been shown to be important in the processing and integration of spatially based information coming from the body (Fechir et al., 2010), therefore, the authors (Moseley et al., 2012) proposed that the representation of peripersonal space, as well as the body-centred spatial representation of the body might reside here. Interestingly, this area has strong connections with the Insular Cortex, which, amongst the other several functions and together with the brainstem, plays a relevant role in interoceptive awareness, homeostasis and autonomic regulation (Craig, 2003; Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004). Moseley and colleagues crucially pointed out that the body matrix might also be seen as a "coarse representation of the body and the space around it" common to different individuals (Moseley et al., 2012). After all, as described by Darwin more than one and a half centuries ago (1854), all the mammals share the basic anatomical structures. In other terms, it is possible to speculate that there is a general sketch of a body matrix common not only across all the humans, but also across different species. This idea might find support in the results that arise from virtual realities studies, in which the participants have been shown to adapt very quickly to even important changes to their body shapes (Banakou, Groten, & Slater, 2013) even implausible ones (Kilteni, Bergstrom, & Slater, 2013; Steptoe, Steed, & Slater, 2013).

1.4.2. Body matrix and neuromatrix: differences and commonalities.

The concept of body matrix and that of neuromatrix certainly share some communalities. Melzack's main trigger for conceptualising his new idea of body representation was the study of the phantom limb phenomenon, for which a satisfying and neat explanation was not available. The body matrix model proposed by Moseley and colleagues started from the need to find an explanation to the results coming from bodily illusion such as the Rubber Hand Illusion (Botvinick & Cohen, 1998) and the more peculiar and perplexing clinical presentations of people in pain. In particular, new physiological data coming from the study of body representation in neurologically intact participants required a revision of previous concepts.

The body matrix is conceived, as well as the neuromatrix, as a holistic and widely comprehensive view of the representation of one's own body and of the space around it. In addition to this, both models, describe a widespread Hebbian-like neural representation, involving different neural structures. However, the body matrix description is more detailed, especially as far as the role fulfilled by a number of cortical areas (i.e. the premotor cortex, the operculum, the parietal cortex and S1) are concerned. Another important common feature to the two models, is the partially innate nature of the neuromatrix and the body matrix. In fact, they share the concept that a coarse, general representation of one's own body is somehow predetermined. Melzack (1989) also describes a built-in neuromatrix phylomatrix, common the all the human beings, that then develops into an ontomatrix for each individuals. The body matrix goes above and beyond this concept, by proposing that a common sketch of the body matrix is not only common within the human species, but it extends to all the mammals. This can be supported by the concept of homology (Owen, 1843) according to which an organ that developed into different functions in different animals has in fact a common ancestor (e.g. the fin of a whale, the wing of a bat and the hand of a human).

The body matrix and the pain matrix are equally effective in explaining many features of chronic pain conditions. However, Melzack's explanation relies mainly on the idea of 'injury' as a stressor event that disrupts the body homeostasis (and this, on the other hand, also represents a psychological stress that facilitates the establishment of a chronic condition; Melzack, 2005). The explanation provided by Melzack is fascinating, but it does not take into account that the nociceptive signals have been demonstrated to have a spatial substrate. In particular, different studies now agree on the fact that the sensory stimuli presented on the body surface are encoded in a spatial frame of reference (Gallace et al., 2011; Sambo et al., 2013; Torta et al., 2013; Yamamoto & Kitazawa, 2001). In addition to this, as reported by Moseley at al. (2012), CRPS patients reports changes in the temperature and in the pain level of the affected limb when it is moved to the non affected side of the body. To date, the body matrix is the only description of the body representation that integrates different features already present in the previous descriptions, with the important and innovative idea of a body-centred (rather than body part centred) representation that is described on the basis of spatial coordinates.

In conclusion, it is possible to affirm that the body matrix is today among the most accurate and promising description of how the body is represented in the neurocognitive system. Nevertheless, there is still room for improvements and of course further research will be needed (i.e. a criticism of the neuromatrix that also applies to the body matrix is the lack of defined biological substrate, although the body matrix has perhaps stronger inferential data).

1.5. Beyond the concept of body matrix

Despite the large number of papers published in the last thirty-five years (Critchley, 1979; Gallagher, 1986; Melzack, 1989; Berlucchi & Aglioti, 2010; de Vignemont, 2010; Moseley et al. 2012) that, more or less explicitly criticize the use of a dichotomy (body schema vs. body image) and suggested the need for more effective and unequivocal descriptions of body representation, the terms “body schema” and “body image” remain widespread and still in use in the scientific literature.

The concept of body matrix represented a big step forward towards a new holistic approach to the study of body representation, even though a lot of issues still remain to be addressed. In particular, neuroimaging studies need to dig into the complexity of the neural correlates of the body matrix. Moreover, in order to support the view that the neurocognitive representation of the body is mainly based on spatial (more than somatotopic) features it would be necessary to clarify whether such representation is centred on the head or on the torso. Also, it would be important to unravel the way in which the body is localised in space, that is, how self-localisation actually works. This would shed light on the connections between chronic pain and disorders in the body representations, including the ability to localise one’s own affected limb without using visual monitoring.

2. The body in the brain

How is the body represented in the brain? The very first attempt to answer this question has been done by Penfield and colleagues, who mapped the sensory-motor cortex, assigning to each body part a portion of it, according to the how precisely that part was represented (such that the very sensitive lip occupies a larger portion of the somatosensory cortex that, let say, the back) (Penfield & Boldrey, 1937; Penfield & Rasmussen, 1950). However, in the last decades a lot of studies have investigated this topic and a more detailed description of the body representation in the brain has become available.

One of the most important discoveries was related to the multisensory nature of this representation. In fact, if only the unisensory areas of the brain that encode for the different body parts are considered, the question at the very beginning of this paragraph would be just partially (and not correctly) addressed. Considering each sensory channel independently, different brain areas are active. For example, the primary somatosensory cortex in the post-central gyrus is active when different body parts are touched (Marshall, Woolsey, & Bard, 1937; Penfield & Boldrey, 1937), while the Extrastriate Body Area (EBA; Downing, Jiang, Shuman, & Kanwisher, 2001) and the Fusiform Body Area (FBA; Downing & Peelen, 2004; Schwarzlose, Baker, & Kanwisher, 2005) is active when different body parts are seen. When hearing someone clapping his hands or, in general, body-related sounds, portions of the Inferior Frontal Gyrus and Inferior Parietal Lobe are activated and smelling someone else’s body odour activates the posterior and anterior cingulate cortex, the occipital gyrus and the angular gyrus (Aglioti & Pazzaglia, 2011).

According to some authors, these unisensory representations alone are not sufficient to provide a complete representation of the body (Serino et al., 2013). In support to this view, two findings are relevant. First, studies on brain damaged patients showed that the damage of one (or more) of these unimodal areas leads to sensory specific deficit, while the overall bodily experience remains intact (Ronchi & Vallar, 2010). Second, when the unisensory signals are somehow manipulated (by stimuli that activate the senses in a separate way, for example only visual stimuli), the perception of the whole body is not affected (Serino et al., 2013). A synergic activation of different cortical and subcortical regions, involving different sensory channels is most likely necessary to support a complete representation of the body.

In the next paragraphs the different areas that have been found to be involved in the body representation will be described.

2.1. The occipito-parietal cortex

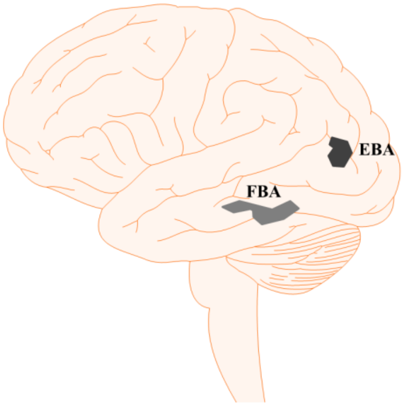


Figure 3 - Extrastriate Body Area (EBA) and Fusiform Body Area (FBA)

Over ten years ago, Downing and colleagues (Downing et al., 2001) found in the occipito-parietal cortex two areas that significantly responded to visually presented bodies/body parts stimuli compared to objects/object parts or faces/face parts. These two areas are located in the posterior inferior temporal sulcus/middle temporal gyrus (EBA, Extrastriate Body Area) (Downing et al., 2001) and ventrally in the fusiform gyrus (FBA, Fusiform Body Area) Downing & Peelen, 2004; Schwarzlose, Baker, & Kanwisher, 2005). Several studies, including neuroimaging, TMS (Transcranial Magnetic Stimulation) and clinical lesional studies, supported these findings (Moro et al., 2008; Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009; Pourtois, Peelen, Spinelli, Seeck, & Vuilleumier, 2007; Urgesi, Berlucchi, & Aglioti, 2004; Urgesi, Candidi, Ionta, & Aglioti, 2007). In fact, the two areas seem to have quite distinct functions: the EBA responds to local body parts (e.g. single fingers), while FBA processes own bodies or largest body parts (e.g. torso, limbs) (Taylor, Wiggett, & Downing, 2007). This dissociation suggests that EBA and FBA might be involved in higher-level processes, such as those involved in the processing of goal-directed actions and, in turn, to the distinction between the self and the others (Astafiev, Stanley, Shulman, & Corbetta, 2004; Costantini et al., 2005; Kühn, Keizer, Rombouts, &

Hommel, 2010; Marsh et al., 2010; Moro et al., 2008; Saxe, Jamal, & Powell, 2006). However, there is still contradictory evidence about the exclusiveness of these two areas and probably other brain regions, such as the insula, are best candidates for the sense of agency and sense of ownership, both essential for the self-consciousness (Berlucchi & Aglioti, 2010). Recently, though, it has been suggested that these areas might simply contains neural populations that encode for basilar visual characteristic of the human bodies (e.g. posture or shape), but the real processing of meaningful actions is actually distributed into a wider neural network (Downing & Peelen, 2011). As suggested by Amoruso and collaborators, this network is likely to include frontal, insular and temporal areas (Amoruso, Couto, & Ibáñez, 2011).

In conclusion, to date, the extrastriate and fusiform body areas are known to be implicated in the processing of body parts. In particular, the area called EBA seems to encode for smaller body parts, while the area called FBA seems to encode for the whole body or bigger body parts. Recently, some authors found that this is true not only for visually presented body parts, but also for haptically encoded body parts, that is during the recognition by touch of human faces, hands and feet (Kitada, Johnsrude, Kochiyama, & Lederman, 2009).

2.2. The insular cortex

Another very important way that allows one to perceive his/her own body is by mean of “interoception”, namely the internal sense of the body. This includes all the physiological and homeostatic conditions of the body, such as pain, temperature, itch, sensual touch, and thirst, just to cite a few of them (Berlucchi & Aglioti, 2010).

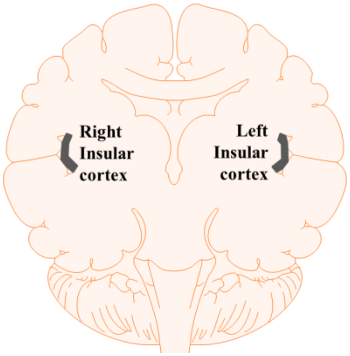


Figure 4 - Insular cortex

The role played by interoception is orchestrated together with proprioception –

“the senses of limb position and movement, the sense of tension or force, the sense of effort, and the sense of balance” (Proske & Gandevia, 2012) – and exteroception – “the convergence of multi-sensory information about the external world from vision, touch, hearing, etc.” (Mussap & Salton, 2006) – in order for the brain to determine a complete set of information about the body.

Interoception is thought to be processed and represented in the insula cortex (Craig, 2003). In particular, the primary sensory inputs (e.g. gustatory, somatosensory, vestibular and visceral) are projected to the posterior insula where they are elaborated and integrated in an across-modal fashion. Then, following the caudal-rostral organisation of the insular cortex, they are projected to the anterior insula, that is interconnected with the “emotional” network (i.e. the limbic insular component and the cingulate cortex). Recent findings would seem to suggest that the anterior insular cortex is crucial in order to integrate the homeostatic conditions of the body together with the emotional experiences and the awareness of the surrounding environment (Craig, 2009). These are thought to be key features to build a complete and stable sense of “self”. According to Craig (2009), in fact, the anterior insular cortex is implicated not only in the interoception, but also in the awareness of body movement (i.e. feeling of agency and awareness of body control during movements), self- recognition and emotional awareness.

In line with the concept of Body Matrix, the insular cortex plays a crucial role in the representation of the body (Moseley et al., 2012).

2.3. The fronto-temporo-parietal cortex

It has long been recognised that the key components that make up the concept of body representation are reducible to two: the sense of ownership towards a body part and the self-localisation – namely, I know that this is my body and I know its position in space (Serino et al., 2013). These two components would seem to be strictly interconnected, even if some studies revealed that they can be anatomically and cognitively dissociated.

The posterior parietal cortex (PPc) and the ventral premotor cortex (vPMc) have been found to be active when the sense of ownership is manipulated by means of visuotactile stimulation (i.e. the same used to enhance the RHI, in this case delivered not only on the hand but on the abdomen as well). However, only the activation of vPMc correlates with the strength of the illusion and does not change when the hand versus the abdomen are stimulated (Petkova et al., 2011). This findings would seem to suggest that the population of neurons present in this area is in fact crucial for the multisensory experience of a unique body to be supported.

In addition to the areas highlighted so far, other studies, involving full body illusions, have underlined the importance of another area, active when the self-localisation of one’s own body in space is concerned. In particular, the temporal parietal junction (TPJ) has been found to be involved in localising one’s one body parts (Ionta et al., 2011). In line with these findings, left parietal lesions have been shown to be responsible for autotopagnosia (i.e. the inability to correctly locate one’s own body part and the relationship between one and another) (Corradi-Dell’Acqua, Hesse, Rumiati, & Fink, 2008).

2.4. A widespread network

In line with both the concept of neuromatrix (Melzack, 1989) and the more recent concept of body matrix (Moseley et al., 2012), the representation of the body is a widespread network including different areas of the brain. According to Serino and colleagues (2013)

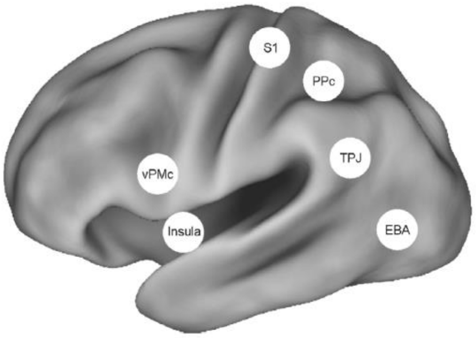


Figure 5 - from Serino et al. (2013)

(see Fig. 5), all the signals coming from the body through different sensory channels, end up in unisensory brain regions, in particular in S1 and in the EBA. At this point, these unisensory signals are integrated in the parietal, premotor and visual areas, and a synergic cooperation between other areas complete the representation. These additional areas are the vPMc, that is involved in providing a sense of ownership towards the body, the PPc, that provides an online map of the body, allowing the agent to know the location of the body parts in respect to each other (body-centred), and the insula, that provides an "offline" representation of the body from the inside (i.e. interoceptive and guided by proprioception). Finally, the processing occurring in the TPJ, provides a world-centred perspective, allowing the agent to navigate in the external space.

3. Illusions and pathologies involving the body representation

As reported in the first paragraph of this chapter, the body representation has been described in various ways, highlighting the presence of a number of sub-representations. However, how do different aspects of the body representation work together? What are the mechanisms that allow to perceive a leg as belonging to one's own body? What happens when something goes wrong and a body part is not perceived as one's own anymore?

3.1. Embodiment, ownership and self-localisation

Concepts such as the "sense of ownership", "feeling of disownership", "embodiment", "self-localisation" are frequent in the literature on bodily illusions. Quite surprisingly, however, these terms have not always been employed in an unidirectional and unambiguous way.

It has been proposed, that the term "embodiment" can be conceived as an umbrella term that includes, between others, also the concept of "ownership" itself (de Vignemont, 2011b; Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008). In particular, according to de Vignemont (2011b), the embodiment expresses what is like to have a body and, in this sense, it represents a *conditio sine qua non* for the sense of ownership to develop. Conversely, not everything that is embodied is actually considered as belonging to one's own body. For example, we really care for our body and we show defensive responses when one of our body parts (or what we believe to be one) is threatened. That is, during the RHI, when the rubber hand is threatened, the skin conductance response in the hidden hand is increased (Armel & Ramachandran, 2003) and a cortical anxiety response is elicited (Ehrsson, Wiech, Weiskopf, Dolan, & Passingham, 2007), just as if the rubber hand actually belongs to the participants (and it is not just embodied). On the other hand, we use tools in order to extend a part of our body, for example, a spoon to stir a boiling soup. In this case, the spoon *might* be embodied (as representing an extension of one's own body with the aim of performing a certain motor act), but no feeling of ownership is expected, in fact, we do not feel threatened by the spoon being hurt by the hot soup because we judge the spoon is not in danger. According to de Vignemont (2011b), thus, both a prosthetic hand (during the RHI) and a tool can be embodied, but in different ways. For example, the embodiment of prosthetic hand during the RHI is thought to be passively induced by the so-called "visual enhancement of touch" (Press, Taylor-Clarke, Kennett, & Haggard, 2004). In fact, it has been demonstrated that watching a hand being touched enhances the tactile processing of the stimulus delivered on that body part and this has been shown to influence body representation as well (Press et al., 2004). Also, the embodiment of a tool is a more active process, namely a certain amount of tool using and motor learning is needed for this effect to occur (Iriki, Tanaka, & Iwamura, 1996). Moreover, the participants feel that the prosthetic hand is "incorporated" in their body, while they consider the tool just as an "extension" of their body. However, the most important difference between embodying a tool versus embodying a rubber hand is that a sense of ownership is felt just in the latter case. According to de Vignemont (2011b), thus, different types of embodiment are likely to exist. It is now clear what the “embodiment” is, while the “sense of ownership” over a body part is still to be defined. In order to clarify this issue, it is possible to consider “ownership” together with its opposite, that is, the concept of “disownership”. How do we know that we own a body part? It would be possible to say that I know that this arm is mine because I can feel its presence. However, as a matter of fact, I do not feel my liver, but I know that I own one. We can speculate that the real difference between owing an arm and owning a liver is that I know I own a liver because I have learnt that, being a healthy human, I must have a liver. However, I have no sense of ownership over my liver. Conversely, I own my arm in a deeper way: I can see it, I can feel it. In other words, I have a multisensory knowledge of my arm and all my senses agree on saying that “that is my arm”. Back to the liver – and, more generally, to all the internal organs – a specific perception of it is not actually possible: in other words, it is not possible to distinctly “feel” one’s own liver. This is because sensations we refer to internal organs are in fact attributed to portions of the body surface, distributed according to dermatomes (Netter & Colacino, 1989) (see Fig. 6).

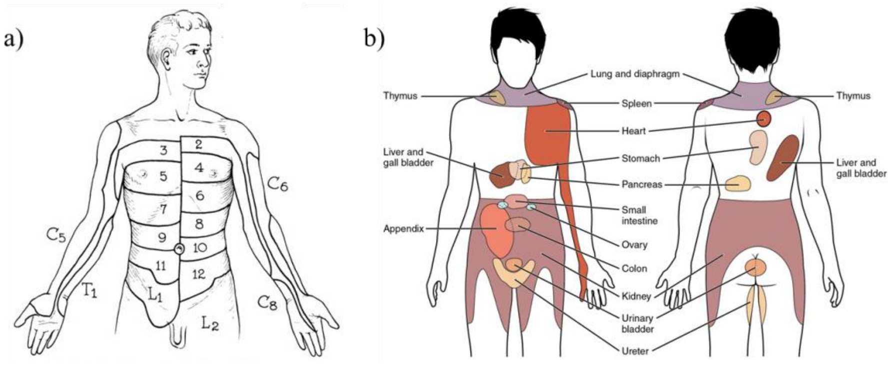


Figure 6 – (a) Torso dermatomes (adapted from Grant, 1962). (b) The perception of visceral sensations according to specific portions of the body is shown. The internal organs sensations can be felt locally, while some others are located in areas even distant from the organ itself (retrieved from http://cnx.org/contents/0bae7483-e6a1-47eb-8571-723ea8ed4131@2/Autonomic_Reflexes_and_Homeost).

Both internal receptors, carrying signals from internal organs, and dermatomes, carrying signals from portions of the body surface, have common synapses on the same interneurons, providing a unique signal to the CNS. In this way a signal coming from, namely, the liver, is merged together with the signals coming from the surface body portion located above the liver itself (however, it is worth to note that this is the assumed mechanism of referred pain, but it does not always happen. So, there is clearly convergence, but perhaps also divergence).

If we consider the same issue from the opposite side, one might start doubting over the ownership of a body part when a number of sensory signals coming from the body are in conflict. This is what happens, for example, during the RHI, in which the participants feel their arm being stroked but, instead, they see a prosthetic arm being stroked. In order to preserve that fundamental sense of ownership and to maintain the integrity of the body representation, the brain shifts the sense of ownership towards the rubber hand. The other side of the coin, thus, is that, if a sense of ownership does exist, it must exist a sense of disownership as well. In this sense, what happens to the hidden hand during the RHI has been extensively studied. In particular, Moseley et al. (2008) demonstrated that, during the RHI, the real hand cools down. This homeostatic effect has been interpreted along with the concept of body matrix (see paragraph 1.4; Moseley et al., 2008, 2012). It seems quite intuitive, then, that the sense of ownership and the sense of disownership are complementary and cannot be dissociated (notably, however, Moseley et al., 2008 did not measure disownership and it remains possible that both hands remain owned). In other words, it seems quite unlikely to disown a part of one's own body without substituting that part with another one (as in the case of the RHI). However, this is not always true. In fact, in some pathologies, patients simply feel that a part of their body do not belong to them, thus experiencing a sense of both disembodiment and disownership over one or more body parts (e.g. Vallar & Ronchi, 2009). In all of these pathological conditions, for one reason or another, the usual representation of one's own body does not match with the real appearance of the body. This leads to a dissociation between ownership and disownership, meaning that it is theoretically possible to disown a part of the body without substituting it with a new one, as in the cases described above. However, it is important to underline that this dissociation represents a pathological and unusual condition, in which the representation of the body is somehow disrupted. The neurological substrate of most of these conditions is still not clear, mainly because they are quite rare and a number of comorbities often occurs.

Here are some examples.

- *Somatoparaphrenia* was firstly described as a group of “illusions or distortions concerning the perception of and confabulations or delusions referring to the affected limb or side” (p.895) (Gerstmann, 1942). In other words, patients report that one of their limbs does not belong to them anymore and often they provide implausible explanations concerning the ownership of the limb (i.e. it belongs to a relative or a previous patient that was in the same bed or to the doctor/nurse) ((Vallar & Ronchi, 2009)).
- *Body Integrity Identity Disorder* (BIID) is a rare condition in which the individuals report an intense desire to have one or more limbs amputated or paralysed. The aetiology of this disorder is still unknown, but it has been interpreted as a mismatch between the mental body representation and the real appearance of the body (Blom, Hennekam, & Denys, 2012). This condition has been proven to be unrelated to any psychiatric or neuropsychological disorders (e.g. schizophrenia or somatoparaphrenia) and it might be congenital. Patients report sensations of disownership towards their own limb/s (e.g. “My limbs do not feel like they belong to me, and should not be there”) and quite often they can identify exactly the level at which the stump should begin (for a review see Blom et al., 2012). To date, treatments other than surgery have not been shown to be always effective. The surgery intervention is aimed to “realign” the mental representation of the body with its real appearance by means of amputation of the alien limb.

- *Depersonalisation*, according to the DSM-IV, is an "alteration in the perception or experience of the self so that one feels detached from, and as if one is outside observer of, one's mental processes or body". Patients report also lack of emotional feelings and autonomic response, even though the motor expression of the emotions appears appropriate (Sierra & Berrios, 1998).
- *Deafferentation* occurs when large sensory fibres are interrupted or destroyed, while smaller ones (< 7 μm) and all the motor nerves remained intact. People suffering from this condition experience a loss of tactile and proprioceptive information coming from the point of the lesion down, while the movement control and the body image are not affected (Proske & Gandevia, 2012). This sensory loss leaves these patients unable to move and with the sensation of floating in the air. The body, then, is not actually disowned but a sense of disembodiment occurs (Cole & Paillard, 1995; Vignemont, 2011b; Proske & Gandevia, 2012).

This last disorder introduces another important aspect of how one's own body is represented and how the sense of awareness towards one's own body develops: the self-localisation. For long time in the study of body representation, knowing where one's own limb was in space has been strictly connected with the sense of ownership. For example, the so-called proprioceptive drift (i.e. the shift in the perceived position of one's own body part towards a new body part) has been adopted as measure of the strength of the illusion over the prosthetic hand during the RHI (Botvinick & Cohen, 1998). However, some authors have more recently criticised this method as they found a significant drift in the perceived location of one's own arm even after the asynchronous hand stroking condition (when the illusion is not induced) or when no hand is displayed at all (Rohde, Di Luca, & Ernst, 2011). Moreover, by comparing different imaging studies, some authors outlined that the sense of ownership and the self-location of a limb may underpin different neural substrates, suggesting, then, a putative dissociation between these two components (Serino et al., 2013).

At the very basis of the concept of self-localisation is proprioception, that includes "the senses of limb position and movement, the sense of tension or force, the sense of effort, and the sense of balance" (Proske & Gandevia, 2012, p. 1651). Proprioceptive sensations are very complex to be explicitly described by a naïve person, because we are totally unaware of them for most of the time. According to the modern view, when a willed movement is planned, the sensory input that should be generated by such movement is anticipated. When this predicted sensory input matches the real sensory input generated by the actual action, no discrepancy is detected and we know exactly the position of the limb moved. However, when the predicted and actual sensory inputs do not match, the ability to localise one's own limb is momentarily disrupted and self-localisation becomes less accurate. Importantly, it is possible to induce an artificial proprioceptive signal that mismatches one's own predictions by means of the tendon vibration (see paragraph 4.2).

At a more physiological level, it is commonly recognised that the muscle spindles are the principal proprioceptors, namely, the receptors responsible to signal position of the limb when it moves. Others sensors, such as joint and skin receptors, once believed to carry most of the job, as a matter of fact, play only a minor role in identifying one's own limb position in space (for a recent and extensive description about this issue see Proske & Gandevia, 2012).

- The *Phantom Limb* is another condition in which the flexibility of the body representation is challenged and it does not keep up with sudden changes in the body, as a limb amputation. Individuals affected by this condition, experience that a missing limb is still present, sometimes with pain or 'cramping' (Flor, 2002). That this phenomenon can be also found in aplasia (i.e. the congenital absence of a limb) (Gallagher & Meltzoff, 1996; Melzack et al., 1997; Melzack, 1989) shows, however, that it does not depend on sudden changes in the body.

This condition again supports the idea that the sense of ownership is not necessary linked to the presence of a body object. In fact, perceptual sensations over a body part can exist even when that body part does not exist anymore or it has never existed at all. Accepting this idea that the sense of ownership is independent by the physical presence of a body-like object means also to disprove the idea that "ownership" is part of "embodiment", because in phantom pain-like phenomena this does not occur.

In summary, self-awareness of the body involves many processes that are rather difficult to disentangle. Nonetheless, it is possible to identify at least three strong and independent components: the sense of embodiment, the sense of ownership and the self-location.

4. Some bodily illusions

Neurologically intact people can be induced to believe that their body is not as it appears. In particular, by means of some simple bodily illusions, it is possible to manipulate both body ownership and self-localisation. In the present paragraph the most frequently used bodily illusions will be illustrated (see Table1).

The *Rubber Hand Illusion* (RHI) (Botvinik & Cohen, 1998) is possibly one of the most known and employed bodily illusions of the last 15 years. The participants are asked to sit comfortably on a chair and to place both hands and arms on a table. While one of the two arms is hidden behind a screen, a fake hand is placed in front of the participants, in an anatomically plausible position. The experimenter, then, begins to stroke the

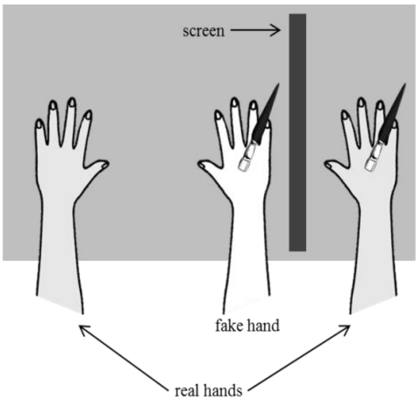


Figure 7 - The Rubber Hand Illusion

fake hand (visible) and the participants' real hidden hand at the same time in correspondent spots, while the participants are asked to look at the fake hand being stroked. After a few seconds, the participants start to perceive that the fake hand has replaced their own real hand and that the tactile stimuli originate from the position occupied by the fake hand (rather than from that occupied by their own hand, where they actually originate).

The effects induced by the RHI have been widely investigated. The key outcome is that the sense of ownership towards one's own hand is transferred to the fake hand and, as a consequence of this, a sense of disownership arises towards the real hand. This "ownership effect" (and its "disownership" counterpart) has a series of implications.

(1) The real hidden hand, during the illusion, cools down and the processing of tactile stimuli delivered on that hand is decreased (Moseley et al., 2008). This effect can be explained in term of dynamic modifications occurring in the representation of the real hand. In fact, during the RHI the real hand is somehow neglected, in favour of the rubber hand, that, in turn, has now acquired the status of "new" real hand.

(2) When the blindfolded participants are asked to localise their hidden hand, they point to a spot between the real and the fake hand. This effect, called "proprioceptive drift", has been reported to positively correlate with the strength of the illusion as measured by a questionnaire. The "proprioceptive drift" can be described as a displacement of the perceived position of one's own hand towards the rubber hand after the RHI, compared to a baseline measure of this perceived position (Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005).

In the RHI as well as in other bodily illusions, at least two components can be clearly identified as relevant for the effects to occur, namely, a multisensory integration between visual and tactile sensations and a substantial change in the body representation. It has been proposed that the first component (i.e. the multisensory integration between visual and tactile sensations) is due to a bottom-up process in which visual and tactile stimulation are provided in a synchronised and spatially congruent fashion (Tsakiris & Haggard, 2005). Importantly, a milestone of multisensory research is the finding that vision plays a dominant role over the other senses (such that, in case of uncertainty, people tend to rely on vision other than on proprioception or touch, for example; Ernst & Banks, 2002). The second component (i.e. change in body representation as the self-attribution of the rubber hand) is thought to be due to a top-down process (Tsakiris & Haggard, 2005), in which the CNS, prioritising vision over other senses, reorganises the body representation in order to best match the reality. Thus, by weighting more heavily the visual information (i.e. the seeing of the rubber hand being stroked) the tactile information (i.e. the feeling of one's own hand being stroked) is reinterpreted and "realigned" with the visual cue, such that a new representation of the hand is created. This new representation is the best match with the reality, from a multisensory perspective.

Furthermore, according to Tsakiris and Haggard (2005), the mere correlation between tactile and visual perception is not sufficient for the self-attribution of a fake body part. Rather, in a series of experiments they showed how the RHI can be effectively induced only when the rubber hand is in a congruent posture or matches the participant's identity. However, this might seem to be in contrast with other findings, in which the sense of ownership was induced not only with incongruent posture, but even towards neutral objects (i.e. without a veridical anatomical part present; e.g. Armel & Ramachandran, 2003) (see Tsakiris & Haggard, 2005 for a complete discussion about this issue).

The changes in body representation, sense of ownership and self-localisation have been also successfully induced using other kind of illusions. Here some examples are reported.

Mirror box (Ramachandran & Rogers-Ramachandran, 1996). In this illusion the participants see the reflection of one limb into a mirror while the contralateral limb is beyond the mirror. In this way, after appropriate tactile and motor stimulation, the reflection of the limb is perceived as the image of the participant's real hidden limb seen beyond the mirror. If the illusion is induced in amputee patients experiencing phantom limb, the missing limb placed beyond the mirror is reported to be "resuscitated" by its visual image (which is in fact the reflection of the intact limb).

Virtual and augmented reality. A promising method to induce bodily illusion is to reproduce part of or entire body within a virtual reality environment. This method has the advantage to create full-body illusions and to easily manipulate different visual aspects of the body (i.e. colour or size). The clear limits of this method are the relatively high cost of the equipment and the programming abilities necessary to implement a virtual environment.

Vestibular caloric stimulation. By irrigating with warm or cold water (or air) the external auditory channel, it is possible to induce a convective current in the endolymph of the semicircular channel. This activation can lead to the sensation that the head is turning. In particular, by injecting cold water (30° C or less) a perceived sensation that the head is turning to the same side of the stimulated ear is induced, while the eyes turns towards the contralateral side. On the contrary, with warm water injections (44° C or more), the perceived sensation is the opposite (i.e. head turning on the opposite side of the stimulated ear) and the eyes turn towards the ipsilateral side (Bárány, 1906; Silberpfennig, 1941; Bárány, 1967). This illusion reportedly relieved phantom limb pain in amputees and spinal cord injured patients (Rade, Perenin, Honoré, & Boisson, 1998) and temporary remission of visual and personal aspects of the hemispatial neglect (Rubens, 1985) (for a review see Rossetti and Rode, 2002).

Prism adaptation. The prism goggles are special glasses the lenses of which are modified in a way that, once worn, they can make the participant perceiving that the visual world has turned upside down or has shifted to one side (Stratton, 1897). The interaction with the surrounding environment becomes inaccurate, because the visual and proprioceptive maps, that are usually aligned, become, after wearing the prisms, misaligned (Newport & Schenk, 2012). However, thanks to the extreme flexibility of the sensory motor system, the motor performance is accustomed accordingly after some practice. Interestingly, the new alignment of the proprioceptive and visual maps lasts for some time after the goggles are dismissed (after effects), meaning that the accuracy of the sensory-motor system in interacting with the actual world remains impaired for a while. This effect has been exploited in the study and rehabilitation of the spatial neglect, after Rossetti and colleagues (1998) reported a substantial reduction of some of the neglect symptoms consequent to prisms adaptation (for a review on the effect of prism adaptation in unilateral neglect see Newport & Schenk, 2012).

The illusions presented in this Chapter are summarised in Table 1. In the following chapters two other illusions will be taken into account: the *Disappearing Hand Trick* (Newport & Gilpin, 2011) (Chapter II and III) and *the Tendon Vibration Illusion* (Eklund, 1972; Goodwin, McCloskey, & Matthews, 1972) (Chapter IV). They both have been included in Table 1 with a brief description, as well as fully described below.

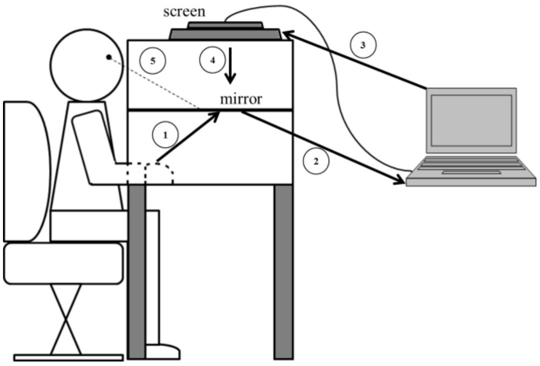


Figure 8 - Mirage general setup

4.1. The Mirage: Multisensory Illusions

The Mirage Multisensory box has been designed and firstly described by Newport and colleagues (Newport, Preston, Pearce, & Holton, 2009). The general setup of the machine is represented in Fig. 8. The participants are comfortably seated on an adjustable chair, with their hands kept inside the Mirage box. (1) The image reflection of the hands on the above mirror is recorded by a camera and (2) sent to a laptop controlled by the experimenter. An in-house program manipulates the image of the hands and (3) sends this new image to a screen placed on the top of the Mirage box, face down.

The image displayed by the screen is thus projected on the upper surface of the mirror (4), such that, the participants, looking inside the Mirage box, see an online (manipulated) image of their hands. Different in-house software have been created in order to produce various effects and illusions. For example, the embodiment of supernumerary limbs (e.g. the sensation of owing more than two arms) has been successfully induced (Newport, Pearce, & Preston, 2010). In another study, Newport and his colleagues reported that patients suffering from hand osteoarthritis experienced a relief from painful sensations when seeing and feeling their painful joint being stretched (Preston & Newport, 2011).

The Mirage box has been employed in Studies 2 (see Chapter III) and 3 (see Chapter IV) of the current thesis. In both of these studies, other bodily illusions have been used, namely the Disappearing Hand Trick (DHT) (Newport & Gilpin, 2011) (Study 3) and a slightly modified version of it (Study 2, see details in Chapter III).

In the DHT, the participants see two blue bars moving around their hands. They are told to hover their hands a few centimetres above the surface of the table and to keep them within the black space between the blue bars, trying not to touch the bars on either side. The image of the hands is manipulated such that the participants see their hands moving inwards, while they are actually forced to move them outwards (in order to fit them between the bars), without realising it. This adaptation procedure is concluded when the blue bars stop moving and the participants are allowed to rest their hand on the surface of the table. At this point the right hand disappears from view and the participants are asked to reach across with their left hand in order to touch their hidden right hand.

As represented in Fig. 9e, though, the participants simply miss their hand (and often report a shocked reaction) as if the right hand was actually disappeared. Newport and Gilpin in the first report of this illusion (2011), investigated the physiological effects induced on the disappeared hand and they found that, when the disappeared hand was threatened (both in its real position and in its seen position), no significant Skin Conductance Response (SCR) was detected. The authors interpreted this result as a sense of disownership towards the disappeared hand, i.e. the right hand was not perceived as in danger, therefore no protection response was activated. However, one can argue that it is not possible to provide protection for one’s own body if the position of the body itself is unknown. Study 2 will address this and other issues.

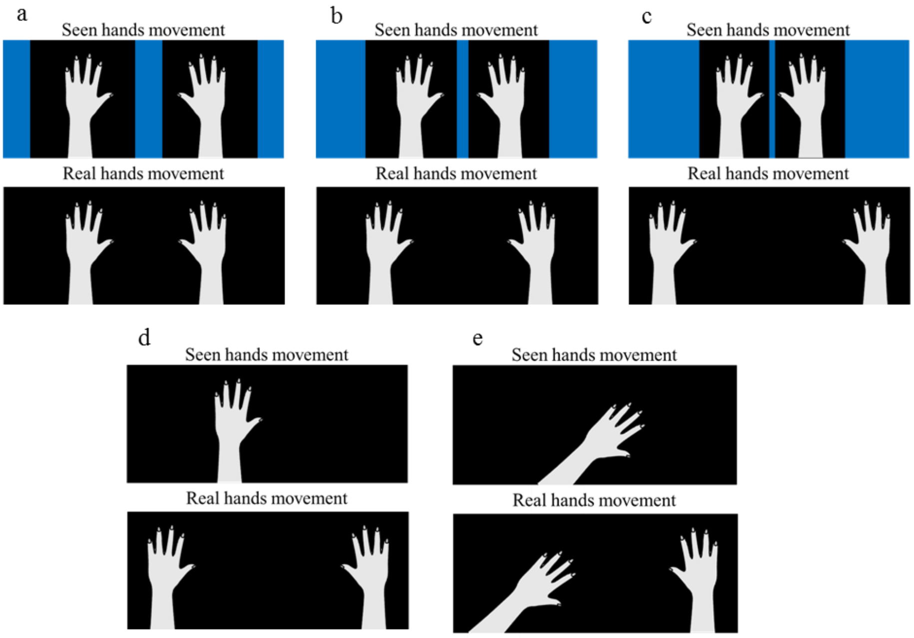
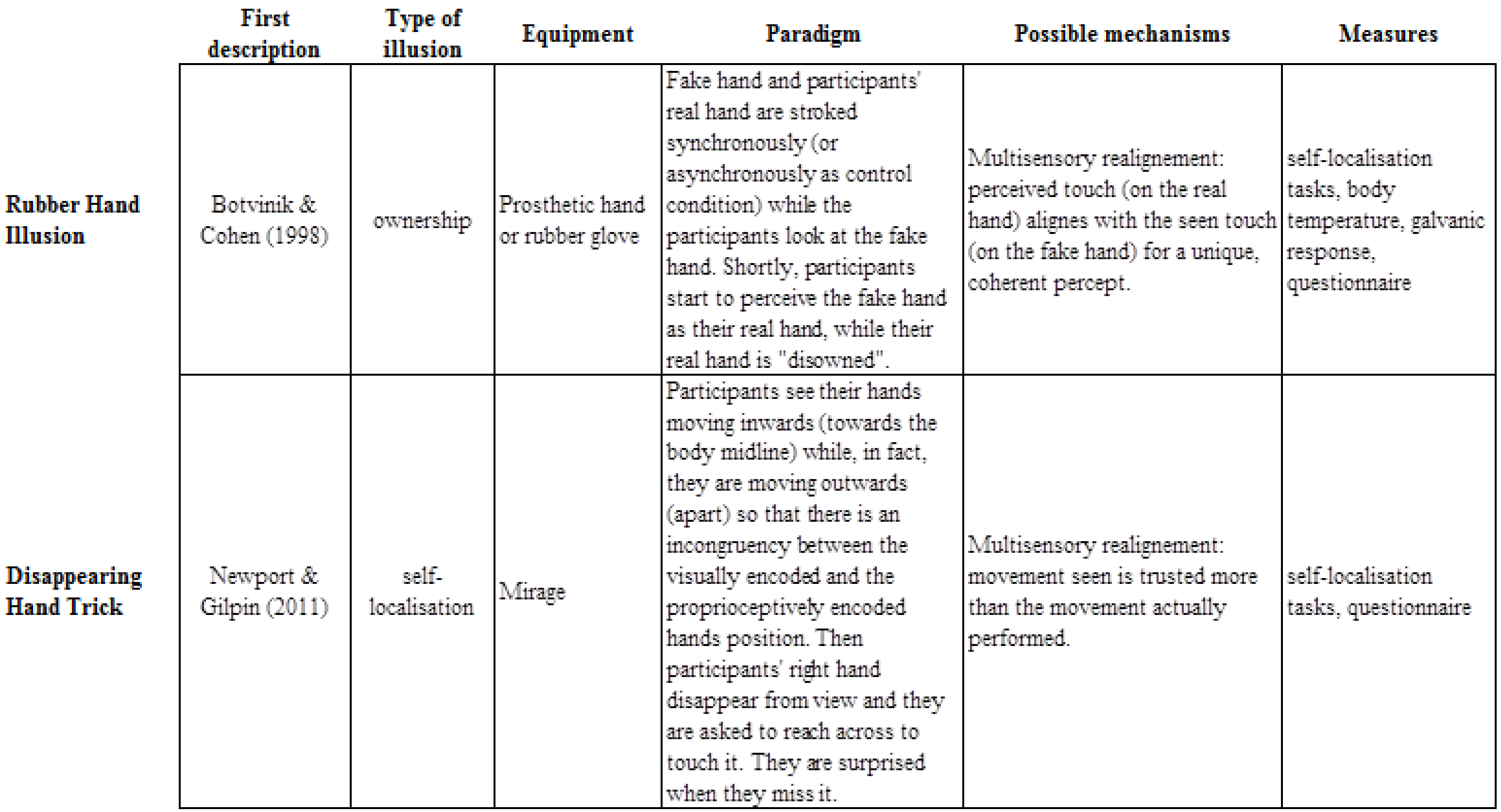


Figure 9 - The images a, b and c represent the adaptation procedure, i.e. the first part of the illusion during which the blue bars sliding in induces the participants to move their hands outwards, while the image of the hands is moving inwards. In this way (as shown in c) the hands end up further apart than where they appeared to be. Then (d) the right hand disappears from view and the participants (e) reach across to touch their right hand with their left hand, without finding it.

4.2. The tendon vibration illusions

In 1966 Eklund and Hagbarth reported that the “mechanical stimulation of muscle receptors can give rise the movement illusions (length change) indicating that these receptors might be able to signal steady length – that is, position” (Eklund, 1972, p. 606). However, the first complete description of the effects of the tendon vibration on the arm was provided in 1972, separately, by Eklund’s and by Goodwin’s groups (Eklund, 1972; Goodwin, McCloskey, & Matthews, 1972). Specifically, it was shown that by vibrating a tendon, the spindle receptors start firing, therefore the CNS interpret this signal as muscle extension. Thus, a 80-100 Hz vibration delivered on the biceps or triceps tendons induces an illusion of movement and the position of the limb is displaced in a direction that would elongate the vibrated muscle. Crucially, a vibration over the elbow does not induce any illusion. However, when the vibratory stimulus is set at lower frequencies and larger amplitude, the illusion of displacement alone is induced (McCloskey, 1973). A number of different illusions might be induced using this method (see Lackner, 1988), which together attest to the importance of muscle spindles as principal proprioceptive receptors (Proske & Gandevia, 2012).

Table 1 – some commonly used bodily illusions.



	First description	Type of illusion	Equipment	Paradigm	Possible mechanisms	Measures
Rubber Hand Illusion	Botvinik & Cohen (1998)	ownership	Prosthetic hand or rubber glove	Fake hand and participants' real hand are stroked synchronously (or asynchronously as control condition) while the participants look at the fake hand. Shortly, participants start to perceive the fake hand as their real hand, while their real hand is "disowned".	Multisensory realignement: perceived touch (on the real hand) alignes with the seen touch (on the fake hand) for a unique, coherent percept.	self-localisation tasks, body temperature, galvanic response, questionnaire
Disappearing Hand Trick	Newport & Gilpin (2011)	self-localisation	Mirage	Participants see their hands moving inwards (towards the body midline) while, in fact, they are moving outwards (apart) so that there is an incongruency between the visually encoded and the proprioceptively encoded hands position. Then participants' right hand disappear from view and they are asked to reach across to touch it. They are surprised when they miss it.	Multisensory realignement: movement seen is trusted more than the movement actually performed.	self-localisation tasks, questionnaire

Tendon vibration	Eklund (1972); Goodwin, McCloskey, & Matthews (1972)	self-localisation body size(?)	80-100 Hz frequency vibrator device	Vibratory stimuli is applied to participants' tendon. Illusions of movement and displacement over the vibrated limb is experienced by the participants.	The vibratory stimulus induce a firing in the muscle spindles that, in turn, are interpreted by the CNS as an activation of the muscle and, thus, a motor and displacement illusion is perceived.	self-localisation tasks, questionnaire
Prism adaptation	Stratton (1897)	self-localisation	Prisms glasses	Participants wear a pair of goggles whose lenses (prisms) have been modified such as the external world appears as shifted on one side. Shortly, participants adapt accordingly to the new coordinates. The effect temporarily lasts when the goggles are removed.	Multisensory realignment: sensory motor system is quickly updated to new shifted coordinates.	self-localisation tasks, questionnaire
Mirror box	Ramachandran & Rogers-Ramachandran (1996)	ownership	Mirror box	A mirror is placed between participants hands, in a sagittal position, such as their hands are placed on opposite sides of the mirror. Participants are asked to perform different motor routines with the seen hand and with the hidden hand. The reflection of the seen hand is soon perceived as the opposite (real) hand that is in fact hidden behind the mirror.	Multisensory realignment: the mechanisms are likely to be very similar to the RHI, but in this case the realignment occurs between a seen and a performed movement and it does not involve any external or fake hand.	self-localisation tasks, body temperature, galvanic response, questionnaire

Caloric Vestibular Stimulation	Barany, 1906	self-localisation	Needleless syringe filled with warm/cold water	Either warm or cold water is injected into participants' external auditory channel, leading them to perceive as the head is turning.	The warm or cold water induce a convective current in the endolymph of the semicircular channel, provoking the sensation of turning head.	self-localisation tasks
Virtual and augmented reality	various authors from 1990s	ownership, self-localisation, body appearance	VR goggles and/or environment	Participants are immersed in a computer designed environment in which their body or part of their body look different than usual (e.g. different skin colour, different size…). Participants are asked to interact in different way within the new reality and perform various task.	Multisensory realignment: the body representation is enough malleable to be able to embody a new avatar (or part of) and successfully interact with the environment in new spatial coordinates.	questionnaire and other measures depending on the study purposes

5. What can bodily illusions teach us?

Bodily illusions are a powerful and feasible tool to investigate different aspects related to the way in which the body is represented in our neurocognitive system. While inducing an illusion, diverse components of the body representation can be involved and it has been proposed that the crucial ones are a shift in the sense of ownership (as part of the sense of embodiment) and a failure of self-localisation: in other words, which body is mine and where is my body (Serino et al., 2013). Even if illusions might differ for various characteristics, these two components have been invariably analysed in any case.

5.1. What does the body feels like: questionnaires and self-reports

Intuitively, the most straightforward way to investigate an illusion is to simply ask the participants to report their sensations when experiencing it. In order to do this, questionnaires are often used. Participants are asked to respond to a number of questions in a standardised fashion and specific issues that are of interest for each specific experiment are addressed. For example, in order to explore the effect of the RHI a 9-item questionnaire was developed by Botvinik and Cohen (1998).

In fact, even if this is undoubtedly an easy and "cheap" (in terms of both time and resources) method to assess an illusion, it is obviously subject to individual differences due to the complexity of the illusory experience itself (Longo et al., 2008).

Nonetheless, even with its limits, the questionnaire still represents the most popular tool to assess illusions. In fact, Botvinik and Cohen's first questionnaire has been extensively used and modified to be employed in other kinds of experimental context, such as, for example, in virtual reality environments (e.g. Hänsel, Lenggenhager, von Känel, Curatolo, & Blanke, 2011). In order to minimise the individual biases related to this technique, experimenters often also decide to briefly interview the participants after completion of the questionnaire (e.g. Petkova & Ehrsson, 2008). In the Disappearing Hand Trick (Newport & Gilpin, 2011), as well, a questionnaire similar to that adopted by Botvinik and Cohen (1998) was employed. The participants, after the illusion, were asked to read 20 statements and to express their level of agreement with each of them. Questionnaires and self –reports represent, thus, an effective and cheap tool to explore bodily sensations as experienced by the participants during the illusion. However, individuals might describe (and perceive) these sensations differently, leading to a rich but sometimes not entirely reliable description of what their body felt like.

5.2. What does the body feels like: physiological responses.

It has been shown that, during the RHI, statistically significant drops in the temperature of the real hand occurs (Moseley et al., 2008). This has been interpreted as a proof of an ongoing sense of disownership towards one's own real hand, while the rubber hand is embodied and the sense of ownership is therefore transferred to it. Conversely, it has also been reported that by cooling down the participants' hand, the effects of RHI can be strengthened (Kammers, Rose, & Haggard, 2011). For its physiological nature, the collection of thermal data is immune from all the biases carried by the other methods. However, more studies might be needed in order to specify the exact conditions under which the change in temperature can be detected, most notably careful control of room temperature. Currently, however, a dropping in the temperature of a limb involved in a bodily illusion has been taken to suggest (perhaps wrongly) that that limb has been disowned and probably replaced with a new (fake) limb, as in the case of the RHI. Another physiological signal of ownership towards a body part is the protective response enhanced by a threatening stimulus directed to that body part. An automatic protection mechanism implemented by the CNS is to increase the amount of sweating in case of psychological arousal (e.g. danger). The amount of arousal-related sweating can be physiologically measured by means of the Skin Conductance (or galvanic) Response (SCR). Armel and Ramachandran (2003) reported that participants, after the induction of the RHI, displayed higher SCR when the rubber hand was threatened. Later, this finding has been confirmed and extended showing that, when the rubber hand is threatened after the illusion, a cortical anxiety response is elicited (Ehrsson, Wiech, Weiskopf, Dolan, & Passingham, 2007).

Taken together, these findings support the idea that it is possible for the CNS to incorporate a new body part "by functionally suppressing the existing hand" (Longo et al., 2008, p. 992) in order to maintain the body constancy. Crucially, then, to "acquire" a new body part it is compulsory to "dismiss" the old one. On the other hand this also means that when an illusion (such as the DHT) fools the CNS in thinking that a body part is gone, it is highly unlikely that a sense of disownerhisp would arise towards the missing body part, as this would breach the principle of body constancy. This issue will be further explored in Chapter II.

When the body representation is somehow modified by a bodily illusion, then, the CNS is able to signal these changes. Interestingly, in some pathological conditions in which the body representation is thought to be involved, such as the CRPS, the body part in pain has been shown to display abnormalities in some physiological features as temperature regulation, sweating or hair grow (Marinus et al., 2011). This again support the close connection between updates in body representation and physiological responses.

5.3. Where is the body: self-localisation.

As reported above, another important component of the self-body-awareness is the localization of the position that the body occupies in the surrounding space. Not being able to correctly localise one's own body part can be interpreted as a sign body representation disturbances (i.e. in deafferented or chronic pain patients;

Cole & Paillard, 1995; Lotze & Moseley, 2007).This component can also be affected when body representation is disrupted in neurologically normal participants by means of an illusion. In fact, going back to the RHI paradigm, Botvinik and Cohen (1998) reported that, after the synchronous stimulation of the real and the fake hand, when the blindfolded participants are asked to localise their real hand, they point to a position that is between the real and the rubber hand. This "proprioceptive drift" towards the rubber hand correlates with the strength of the illusion as measured via questionnaire procedures (Botvinik & Cohen, 1998). The authors suggested that the proprioceptive drift represents a valid and bias-free method to assess the strength of the illusion. However, this method has been often criticised. In fact, according to various authors, people are generally not very accurate in localising their own hands when they cannot see them (e.g. Jones, Cressman, & Henriques, 2010; Wann & Ibrahim, 1992). Besides, it has been demonstrated that the proprioceptive drift can be evoked also not only as a consequence of the asynchronous stimulation in the RHI, but also in total absence of a prosthetic hand (Rohde, Di Luca, & Ernst, 2011).

In the following chapters of this thesis we will try to answer a number of unresolved questions related to the mechanisms of body representation. In particular,

in Chapter II will be addressed the question: "Does the proprioceptive drift measure the sense of ownership towards a fake hand?". During the bodily illusions, incongruent cues are coming from the external world and the CNS has the role to merge the information to produce a coherent and unique percept. Nonetheless, not always evaluation made by the CNS corresponds to the reality, in fact, for example, in the RHI the real hand is disowned and in the DHT the hidden hand is mislocalised. Thus, which and how many factors play a role in localising one's own body part under conditions of uncertainty? This issue has been interrogated in the past by selectively distorting visual information, e.g. via prism glasses (Rossetti et al. 1998), or proprioceptive information, e.g. via tendon vibration (Lackner, 1988). Thus, what is the relative role of vision and proprioception in correctly locating one's own body part? Several studies have investigated this issue (Ernst and Banks 2002; Ernst and Bülthoff, 2004; Smeets et al. 2006; van Beers et al. 1999, 1998; van Beers et al. 2002) and most of them supports the idea that the CNS optimises the estimated position by integrating visual and proprioceptive signals. But what happens when incongruent information are provided?

In Chapter III the question "What is the role of vision and proprioception during when the information they are providing are conflicting?" will be addressed. In particular, by means of a new version of the Disappearing Hand Trick (Newport & Gilpin, 2011), incongruence between the visually encoded and proprioceptively encoded position of the participants' right hand will be induced. The localisation of the participants' own hidden right hand will be measured over time.

In Chapter IV the question "What is the role of attention and sensory incongruence in self-localisation?" will be addressed. The Disappearing Hand Trick (Newport & Gilpin, 2011) will be employed, this time trying to manipulate the visual attention in order to evaluate its role in self-localising the hidden right hand. Furthermore, in this same chapter, the effect of realising that an illusion had been performed (i.e. reaching across with the left hand to touch the right hand and failing in finding it) on the self-localisation accuracy will be explored.

In Chapter V the question "Is it possible to manipulate the body size by providing contrasting proprioceptive information?" will be addressed. By means of the tendon vibration illusion (see above), it is possible to manipulate one's own proprioception. In this Chapter this issue will be explored, by trying to replicate previous results (Longo et al., 2008). However, previous research (e.g. Gilhodes et al., 1986) showed that vibrating both tendons at the same time nullified any illusion of movement and led to a sensation of stabilised position of the arm.

Chapter VI will present some preliminary data from a pilot study, designed to investigate how one’s body representation can be implicitly modulated. Eventually, in Chapter VII general conclusions about the present thesis will be drawn. In particular, this thesis presents some innovative findings, having explored the body representations and how bodily illusions can deceive these representations in terms of self-localisation and size perception. These findings will help to better understand cases in which one’s own body representation does not coincide with the actual body appearance.

CHAPTER II

STUDY I

Abbreviations used in this chapter:

RHI, Rubber Hand Illusion; HS, Hand Synchronous condition; HA, Hand Asynchronous condition; NH, No Hand condition.

Study 1: "Feeling touch in empty space: When the proprioceptive drift does not measure body"

Study 1 has been conducted in collaboration with Alberto Gallace (University of Milano-Bicocca and NeuroMI), Carlo Reverberi (University of Milano-Bicocca and NeuroMI) and G. Lorimer Moseley (University of South Australia and Neuroscience Research Australia and PainAdelaide).

1. Introduction

In the extant literature on body localization, the proprioceptive drift has been described as the tendency to mislocalise one's own body part when it is hidden from view (Block, 1890; Paillard and Brouchon, 1968; Craske and Crawshaw, 1975; Wann & Ibrahim, 1992). The proprioceptive drift has been extensively used in experiments involving the Rubber Hand Illusion (RHI). In the RHI, a fake hand is stroked synchronously with the participant's hidden real hand. After a while (between a few seconds to 30 minutes), the participant starts to report ownership towards the fake hand (Botvinick & Cohen, 1998). In this context, the proprioceptive drift has been used as a measure of the sense of ownership towards the rubber hand. Consistent with this assumption, after synchronous stimulation, the participants start to localise their own real hand in a spatial position that is significantly shifted towards the rubber hand (Botvinick & Cohen, 1998; Makin, Holmes, & Ehrsson, 2008; Tsakiris & Haggard, 2005). However, it is worth noting here that a proprioceptive drift has also been reported, although to a lesser extent, not only after the asynchronous stroking of the rubber and real hands, but also after the stroking of an object (Armel & Ramachandran, 2003; Tsakiris & Haggard, 2005). Moreover, other studies have shown that a proprioceptive drift can be found not only during a synchronous visuo-tactile stimulation of the real and fake hand, but also when the stimulation is asynchronous, or even when there is no stimulation at all - participants just look at the fake hand (Rohde, Di Luca, & Ernst, 2011). On the basis of these observations, it remains unclear what exactly the proprioceptive drift measures and whether or not it can be considered a direct consequence of a shift of body ownership towards a fake body part, as has been assumed.

In this study, we investigated the role of visuo-tactile stimulation in eliciting the proprioceptive drift. In particular, the question addressed here is whether or not the presence of synchronous vs. asynchronous multisensory stimulation alone is sufficient to elicit a shift in the perceived body position, regardless of the presence of a virtual body part (and regardless of shifts in the sense of body ownership). Our main hypothesis is that the proprioceptive drift should be considered a consequence of a visuo-tactile form of the ‘ventriloquist effect’ (i.e., a phenomenon where auditory events are mislocalized towards the position of simultaneously-presented visual events; Bertelson, 1998) . Therefore, mislocalizations of the body should be equally strong with or without the presence of the rubber hand illusion and whenever visual information suggests that tactile stimuli originate from a certain position in external space whether or not an object is located in that space.

2. Materials and methods

We investigated how the ability to estimate the location of one’s own arm degrades when visuo-tactile information is modulated. In two experimental conditions, a video of a virtual finger touching a left hand was displayed on a monitor. Synchronously (first condition) or asynchronously (second condition) with the touch seen on the monitor, a vibrotactile stimulus was delivered to the participant’s left hand, at the same location on the hand as the stimulus depicted on the monitor (a setup similar to that adopted in the classic rubber hand illusion; Botvinick & Cohen, 1998). Before and after watching the monitor, the participants were asked to evaluate the perceived position of their left hand by pointing with their right hand at their left index finger while blindfolded (Botvinick & Cohen, 1998; Makin, Holmes & Ehrsson, 2008;

Tsakiris & Haggard, 2005). In a third experimental condition, a video of a virtual finger crossing a blank space and stopping in the middle of the monitor, exactly where the hand was shown in the first two conditions, was presented. When the finger stopped, a vibrotactile stimulus was delivered to the participants' hidden left hand. In this condition we aimed at evaluating the specific role of the presence of a body part in influencing the proprioceptive drift. The participants were equally divided into three groups and each group was randomly assigned to one of the three conditions, namely: Hand Synchronous (HS), Hand Asynchronous (HA) and No Hand (NH)

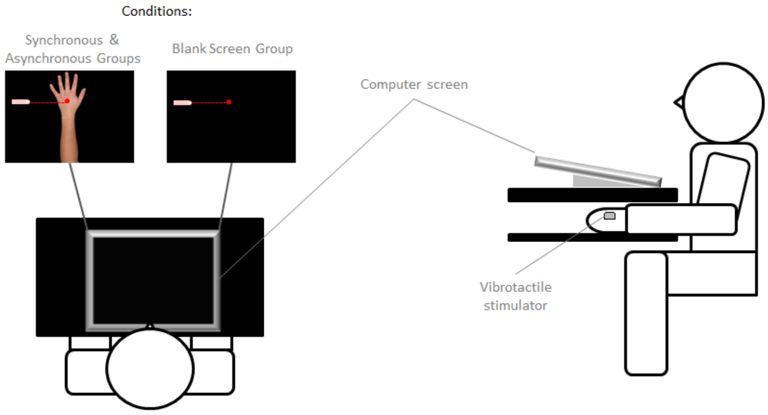


Figure 10 - Experimental setup.
The participants rested both forearms on a shelf placed 10 cm below a desk. A pc monitor was placed on the desk aligned with the participant's body midline. A picture of a left arm and hand was displayed on the screen to the groups undertaking the Hand Synchronous and Hand Asynchronous conditions. In the NH condition, participants watched a blank screen. A vibrotactile stimulator was placed on the dorsum of the participants' left hand.

Participants

Forty-two right-handed volunteers (35 female, mean age: 22±2 years, education: 16±1 years) participated in this study. All of them had normal or corrected to normal visual acuity, no current or past neurological impairment involving the upper limbs, and no current pain or history of significant pain disorder. All the participants were also naïve about the purpose of the study. All the participants gave written consent prior to their participation to the experiment. The study was performed in accordance with the ethical standards laid down in the 1991 Declaration of Helsinki and was approved by the Institutional Ethics Committee.

A schematic representation of the experimental setup is showed in Figure 1. Each participant was seated at a desk, with both forearms resting on a shelf placed 10 cm below the desk, such that the hands were equidistant from the body midline. A 17' LCD monitor was placed on the desk aligned with the participant's body midline. A picture of a left arm and hand (the whole arm was 26.5 cm long and 4 cm wide, the hand was 10 cm wide) was shown to the groups undertaking the HS and HA conditions on the centre of the monitor. The gender of the arm on the monitor was matched with the participant's gender. No such picture was presented in the NH condition, whose participants watched instead a blank screen. A vibrotactile stimulator (Audiological Engineering Corporation) was placed on the dorsum of all participants' left hand by means of Velcro tapes. Each experimental session involved five steps:

1. The participants were asked to place their left hand on a shelf, below the desk, so that their index finger was exactly positioned on a plastic dot marked on the surface of the shelf. The coordinates along the X and Y axis, indicating the dot position on the above desk were previously measured, so that the exact position of the participant's left index finger was precisely tracked. The plastic dot represented the origin of the measuring axis, when drift was later measured. The participant's right hand rested on the participants' right thigh.
2. On the left side of the desk, about 30 cm from the body midline, a white A3 size paper sheet was placed, in order to cover all the possible hand localisation points. At this stage the participants, blindfolded and guided by the experimenter, placed their right elbow on the desk with the right arm bent and the right hand holding a black marker. Each localisation movement started and ended from this position.
3. The participants were then asked to mark on the sheet of paper the point where they perceived their left index finger to be, keeping the left hand still. Each black dot on the sheet corresponded to one localisation. A total of 12 localisations were performed for each condition. The rhythm was self-paced, but the participants were asked to avoid self-correction movements during the localisation task.

4. After removing the sheet with the localisation dots, the blindfold was removed and the PC monitor re-placed on the table. The participants were asked to place their right hand on the shelf under the desk, parallel to their left hand, and to watch the monitor. Each time the finger on the monitor touched the hand on the monitor (HS and HA conditions) or just stopped in the same position of a blank space where no hand was showed (NH condition), a vibrotactile stimulation was delivered at the corresponding location on the participant's left hand. The participants undertaking the HS condition received the tactile stimulation and viewed the picture of the hand being touched at the same time. The participants undertaking the HA condition, received the two stimulation asynchronously, such that they saw the touch on the picture of the hand and, 500 ms later, they received the vibrotactile stimulus on their hand. Finally, the participants undertaking the No Hand condition received the stimulation when the finger stopped, but without seeing any other object displayed on the monitor. The finger movement was exactly the same for the three conditions: both the trajectory (from left to right) and the point where it stopped were kept constant (i.e. in the NH condition the picture of the hand was simply removed from the monitor).
5. After the visuotactile stimulation, the blindfolded participants were asked to perform again 12 localisations, using the same procedure as explained above. Then the blindfold was removed. To verify if we captured the usual effect of the RHI using our modified design with the picture on the monitor, participants performing the HS and HA conditions completed the RHI questionnaire (Botvinick & Cohen, 1998).

Each experimental session included 264 visuo-tactile stimuli (i.e all the participants received 264 tactile stimuli, while watching to 264 finger movements – synchronously or not, directed to the picture of the hand or not) and lasted approximately 30 minutes in total.

Data Analysis

The proprioceptive drift, which was the primary outcome, was defined as the mean distance along the X and Y axes, between the true location of the participant's left index finger and its perceived location, as indicated by the dots drawn by the participant on the sheet of paper. This outcome was computed separately for each participant.

In order to compare proprioceptive drift between tasks, we used an analysis of variance (ANOVA) with the within subjects factors of Time (two levels: T1 vs. T2) and Axis (X vs. Y) and the between subjects factor of Condition (HS vs. HA vs. NH). Questionnaire data verified whether or not the proprioceptive drift, resulting from our experimental manipulation, was associated with changes in body ownership (consistent with those known to be evoked by the RHI; See supplementary Table S1 for full questionnaire data).

3. Results

The three-factor Mixed ANOVA showed a main effect of the factor Time [F(1,39)=20.09, p<0.01] and of the factor Axis [F(1,39)=58.05, p<0.01]. In particular, the main effect of Time showed a significant drift towards the spatial position where the finger shown on the monitor stopped after the visuo-tactile stimulation (asynchronous stimulation). The main effect of Axis showed larger scores on the X as compared to the Y axis. This represents the participants' tendency to perceive their left arm shifted rightward and downward from its actual position (scores above 0 on the X axis and scores below 0 on the Y axis). There was no main effect of the Condition [F(2,39)=0.77, p=0.46], which suggests that neither the synchronicity, nor the nature of visual information regarding the presence/absence of a fake body part, play a role in the mislocalisation of one's own arm.

We also found a significant interaction between Time and Axis [F(1, 39)=8.53, p<0.01]. A LSD Fischer post hoc test showed a significant difference between T1 and

T2 in X scores (p<0.01), but not in Y scores (p=0.19) regardless of the Condition. That is, the participants perceived their left arm significantly more shifted towards the right side of space than downward in the asynchronous condition. Interestingly, the monitor showing the image of the hand was aligned to the participants body midline, thus to the right of their real left hand (See Fig. 2). The analysis did not revealed additional significant interactions (Time x Axis: F(1, 39)=0.17, p=0.84; Axis x Condition: F(1,39)=0.19, p=0.82).

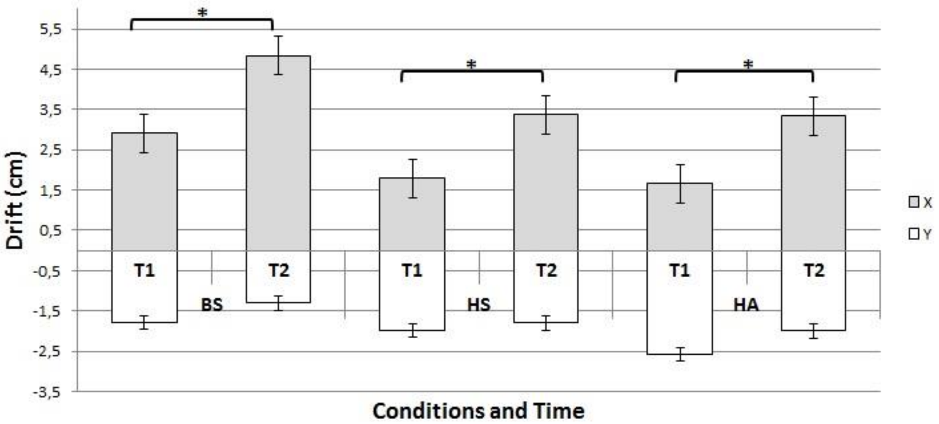


Figure 11 - Results.
On the horizontal axis is represented the proprioceptive drift under the different conditions (HS, Hand Synchronous; HA, Hand Asynchronous; BS, Blank Screen) and before (T1) and after (T2) the visuo-tactile stimulation. On the vertical axis is shown the amount of drift (in cm) both towards the participants' body (i.e., along the Y axis) and towards the point where the finger on the monitor stopped (i.e., along the X axis). A three-factor Mixed ANOVA was performed, showing two main effects: (a) Main effect of Time (F(1,39)=20.09, p<0.01): significant drift towards the spatial position where the finger shown on the monitor stopped after the visuo-tactile stimulation. (b) Main effect of Axis: larger scores on the X as compared to the Y axis. No main effect of the Condition (F(2,39)=0.77, p=0.46): neither the synchronicity, nor the presence/absence of a body-like part, played a role in the mislocalisation of one's own arm.

4. Discussion

We hypothesised that a similar mislocalisation of the body is present and equally strong, regardless of the fact that the participant exposed to a visuo-tactile stimulation could see or not an object located in the space being touched on a PC screen, and also regardless the presence of a rubber hand illusion. Indeed, according to our hypothesis, the proprioceptive drift, traditionally thought to represent the strength of the RHI (Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005; Tsakiris, Hesse, Boy, Haggard, & Fink, 2007), was found to be driven by a 'visual capture of touch' and therefore should be rather considered a visuo-tactile example of the ventriloquist effect. Our results clearly confirm our hypothesis.

In the extant literature on bodily illusion, the proprioceptive drift has often been considered a reliable measure of shift of ownership occurring during the RHI (Botvinick & Cohen, 1998; Makin et al., 2008; Tsakiris & Haggard, 2005). However, a number of studies have shown that a mislocalisation of one’s own arm can also occur when no changes in the sense of body ownership are involved (Desmurget, Vindras, Gréa, Viviani, & Grafton, 2000; Smeets, van den Dobbelsteen, de Grave, van Beers, & Brenner, 2006). Despite the latter observation, the proprioceptive drift is still used in research on bodily illusions as a valid “biomarker”’ of the shift in body ownership. Notably, shifts of ownership are generally not found for visuo-tactile asynchronous stimulation (Aimola Davies & White, 2012; Thakkar, Nichols, McIntosh, & Park, 2011; Zopf, Savage, & Williams, 2010). In the present experiment, two separate groups of healthy participants performed a hand localisation task before and after the presentation of a video showing a virtual finger touching a hand depicted on the monitor. A tactile stimulus was delivered synchronously (in Hand Synchronous condition) or asynchronously (in the Hand Asynchronous condition) to the touch seen on the monitor. Mislocalisation of the real hand involved in the visuo-tactile procedure was similar in both conditions. That is, the participant’s judgement of the location of their own hand, was shifted towards the location of the hand seen on the monitor. Critically, a comparable magnitude of proprioceptive drift was also found when no images of a hand were presented on the monitor (namely, in the NH condition). That is, the presence of a “virtual hand” on the screen made no difference to the proprioceptive drift.

We contend that, taken together, these results support our interpretation of the proprioceptive drift in terms of visuo-tactile ventriloquism. The term ‘ventriloquist effect’ was first adopted by Bertelson and colleagues (Bertelson, 1998) to describe the fact that an auditory event can be mislocalised towards a visual event under certain conditions of stimulus presentation. That is, one can genuinely perceive a sound originating from a certain location in space when a visual stimulus is concurrently presented from that location (regardless of the real position of the sound). An everyday example of this effect is hearing a lecturer’s voice as coming from the lecturer, even though the sound is coming from acoustic speakers that are located elsewhere. As far as visuo-tactile stimuli are concerned, a similar effect, named ‘visual capture of touch’, has been described by Pavani, Spence, and Driver (2000). In this case, the participants were asked to localise the position of a tactile stimulus presented on the thumb or index finger of their hands. They found that the localisation of the stimulus was affected by a synchronously-presented visual stimulus (e.g., a red LED). Pavani and colleagues (2000) suggested that vision plays a crucial role in determining tactile localisation.

In our study, the participants were not asked to localise a tactile stimulus, instead they had to localise their own hidden left hand. Thus, we can hypothesise that the participants started to perceive the touch delivered on their left hand as originating from the point on the monitor where they saw the touch to occur (for example, the virtual finger touching in turn a point in the space or a left hand). This shift in the perception of touch triggered a proprioceptive drift of the entire hidden left hand towards the point touched by the finger on the monitor. This occurred regardless of whether a body part was displayed on the monitor or not, and resulted in a mislocalisation of the hand itself.

Some researchers working on tactile perception in the last decade have suggested that the conscious perception of touch is not actually localized on the skin but on positions in external space (Gallace & Spence, 2005; Hohwy & Paton, 2010; Kitazawa, 2002; Soto-Faraco, Ronald, & Spence, 2004). Moreover, it has even been suggested that spatial coordinates (based on external space) play a more important role than somatosensory coordinates (based on the physical body) in supporting a dynamic representation of our body (Moseley, Gallace, & Spence, 2012). This development has clear implications for clinical conditions that in which bodily ownership and tactile processing both appear to be disrupted, for example those with chronic back, arm or leg pain (Wand et al., 2012; Stanton et al., 2013; Moseley, 2009; Moseley, 2012a; Moseley, 2012b; Bray, 2011) (see Wand et al., 2011; Moseley, 2012 for reviews). The results of our study would seem to support the importance of spatial coordinates, by showing that even without the presence of visual information regarding a body-like structure, participants mislocalise the position of their own body towards the position where they perceive tactile stimulation to originate (even if this perception is biased by the presentation of visual signals). As far as the presence of a rubber hand-like illusion is concerned, we were not able to find any differences in the amount of proprioceptive drift between the HS and HA conditions.

Several aspects of this experiment should be clarified in future works. First of all, the presence of an illusion of ownership within this new version of the RHI should be investigated also using other concurring measures. There is emerging evidence that biomarkers of illusory ownership may exist. For example, there is a limb-specific cooling effect of the hand involved in the illusion that occurs during synchronous stroking of the rubber hand and the real hand, but not during a range of control conditions (Hohwy & Paton, 2010; Moseley et al., 2008) and there is an increased reactivity to histamine that is also limb-specific and not observed during asynchronous stroking (Barnsley et al., 2011). That is, while the questionnaire might fail to detect the presence of shift in the sense of ownership towards the fake hand, such biomarkers might be more successful.

In summary, we found that proprioceptive drift occurs regardless of changes of body ownership and regardless of the presence of body-like images. That is, participants mislocate the position of their own body towards the position of “space” where they “see” the tactile stimuli to occur, irrespectively of the presence of their body (or of a fake counterpart of it) there. The results of the present study clearly show that the proprioceptive drift is not necessarily related to the presence of an artificial limb (e.g. a rubber hand or a virtual hand), but is rather the consequence of the visual capture of tactile sensations towards certain spatial positions. This work brings an important contribution to the comprehension of the body schema in the context of the bodily illusions, by suggesting that the “visuo-tactile” ventriloquist effect alone can have important consequence on the perception of where (and perhaps what) is our body.

CHAPTER III

STUDY II

Abbreviations used in this chapter:

CNS, Central Nervous System; DHT, Disappearing Hand Trick; EC, Eyes Closed condition; EO, Eyes Open condition; MLE, Maximum Likelihood Estimation theory

Study 2: Untangling visual and proprioceptive contributions to body localization

Study 2 has been conducted in collaboration with Helen R. Gilpin (University of South Australia), Tasha R. Stanton (University of South Australia and Neuroscience Research Australia), Roger Newport (University of Nottingham), Alberto Gallace (University of Milano-Bicocca and NeuroMI) and G. Lorimer Moseley (University of South Australia, Neuroscience Research Australia and PainAdelaide).

1. Introduction

The perception of owning our body and the ability to locate it in three dimensional space are two fundamental requirements for self-consciousness to develop. While the majority of us take these functions for granted, there are some pathological conditions in which these mechanisms are disrupted. For example, in *autotopagnosia* (a condition arising from brain damage to posterior parietal cortices) (Guariglia et al. 2002; Pick, 1922; Semenza & Goodglass, 1985) the ability to localise one's own body parts is affected. Although this condition is usually described in association with other comorbidities, it has been investigated as a single symptom by several authors (Ogden, 1985; Semenza, 1988; Sirigu et al. 1991) and it has been proposed that it may be the result of selective damage to an independent system, responsible for the ability to locate one's own body parts (Buxbaum & Coslett 2001; Sirigu et al. 1991). Furthermore chronic pain patients have a distorted body image, leading to difficulties not only in self-representing the correct size of their affected limb (Moseley, 2005), but also its position in space (Lotze & Moseley, 2007). This close relationship between the position of our body in space and processing of sensory input is further supported by evidence that the processing of tactile stimuli to the hands is impaired when the hands are crossed over the body midline (Aglioti et al., 1999; Azañón & Soto-Faraco, 2008; Eimer et al., 2003; Yamamoto & Kitazawa, 2001). This *crossed-*

hands deficit has been interpreted as a result of the mismatch between somatotopical and space-based frames of reference in determining the position of the external stimuli (e.g. when the right hand occupies the left hand of space and vice versa). Interestingly, the deficit also includes the intensity of the sensation, such that tactile or noxious stimuli to the hands are perceived as less intense if the hands are crossed than if they are not (Gallace et al., 2011; Sambo et al., 2013; Torta et al., 2013).

Generally speaking, knowing where our body is allows us to navigate our environment efficiently, avoid obstacles and perform our daily activities. In the healthy population, the central nervous system (CNS) integrates the range of internal and external cues, with ongoing motor commands (e.g. “efferent copy”, Holst & Mittelstaedt, 1950; Sperry, 1950) to generate a unique, coherent, multisensory experience. That is, I know when I am holding my arm above my head because I am receiving real-time visual and proprioceptive feedback about its location and because I am controlling it to be there (for a comprehensive review on non-visual contributions to body position sense, see Proske & Gandevia 2012). Although the CNS typically integrates multiple cues coming from different senses, it is still possible to locate one’s own body if the full suite of sensory cues is not available, for example when vision is occluded. Indeed, neurologically intact people are quite accurate in reaching for one hand with the other while keeping their eyes closed. This ability becomes fundamental for certain kinds of expertise (e.g. the speleologists frequently need to perform complex movement in almost total darkness). Furthermore, when information about position is available from both visual and proprioceptive modalities, it has been shown that the perceived location of the limb more closely aligns with the visual information about its location than with the proprioceptive information about its location (van Beers et al., 1999). Studies that have interrogated this issue have selectively distorted visual information, e.g. via prism glasses (Rossetti et al., 1998), or proprioceptive information, e.g. via tendon vibration (Lackner, 1988).

Thus, what is the relative role of vision and proprioception in correctly locating one’s own body part? Several studies have investigated this issue (Ernst & Banks, 2002; Ernst & Bülthoff, 2004; Smeets et al., 2006; van Beers et al., 1999, 1998; van Beers et al., 2002) and most of them support the idea that the CNS optimises the estimated position by integrating visual and proprioceptive signals. These studies have also shown that humans are less accurate in judging the position of their hand when they cannot directly see it, which suggests a relevant role of visual information. A consistent finding is that, when vision is occluded, the perceived location of the hand drifts towards the body (Paillard & Brouchon, 1968; Craske & Crawshaw, 1975; Wann & Ibrahim, 1992) . This drifting effect, however, does not occur immediately after vision is occluded, suggesting that the visually encoded body position maintains an influence on the localisation of one’s own body. It has been proposed that this influence reduces as the visually encoded position decays, and then proprioception takes over (Desmurget et al. 2000).

Critically, the observed drift occurs not only along the sagittal axis, but also the transverse axis. During visual occlusion, estimates of hand location decrease in accuracy, leading healthy participants to judge their left hand as more leftward and their right hand as more rightward during both reaching estimation (i.e. localisation by pointing with the seen hand; Crowe et al., 1987; Ghilardi et al., 1995; Haggard et al.. 2000)and proprioceptive estimation (i.e. no movement of the seen hand; Jones et al., 2010). This directional bias is explained in terms of a misperception of the hand location relative to the body midline (Jones et al., 2010) and confirms again the predominant role of vision in localising one’s own hands (Newport et al., 2001).

Despite the increasing evidence for the importance of vision in localising the hands, the time course of the interaction between vision and proprioception during visual occlusion remains unclear. We suggest that with one hand hidden from view, participants will initially rely more on vision, locating the hidden hand where they last saw it, on the basis of its visually encoded position. Over time, this visual trace will decay, such that the estimation of location will become more dependent on proprioceptive inputs (Chapman et al., 2000). Our hypothesis would be in line with the Maximum Likelihood Estimation rule (Ernst & Banks, 2002). This theory states that in order to create a unified perception of a stimulus by means of different senses, the nervous system combines the information coming from the different sensory modalities in a statistically optimal fashion. This would suggest that the sensory modality that carries less variance dominates in determining the final percept. Further, the variance is direction-specific and sense-specific. In fact, research has demonstrated that proprioception-based localisations are more precise in the radial direction (reference shoulder; thus carrying less variance in the azimuthal direction), while vision-based localisations are more precise in the azimuthal direction (reference cyclopean eye; thus, carrying less variance in the radial direction) (van Beers et al., 1999).

In the present study we investigated the interaction between vision and proprioception in localising one’s own hidden hand over time in a bodily visual illusion that alters the sense of where one’s hand is. That is, the hand appears to be located where it is not. In order to test our hypothesis, we used a new illusion based on the Disappearing Hand Trick (DHT), previously tested using the MIRAGE system (Newport & Gilpin, 2011). Our illusion allowed us to manipulate the relationship between the seen and felt location of the right hand.

We hypothesised that when making hand localization judgements, participants would initially rely primarily on the visually encoded position of the hand, ignoring its proprioceptive position. However, we expected that over time there would be a shift to rely more heavily on proprioception, as the visually encoded position decays. As such, we hypothesised that, following an illusory condition in which the visually encoded (perceived) position of the hand is rendered incongruent with its proprioceptively encoded (physical) position, we would observe a faster and larger drift towards the hidden right hand than in a non-illusory condition where the visually and proprioceptively encoded positions are congruent . However, a drift towards the right for the right hand is expected in any condition, but according to our hypothesis, its nature would not be the same. In particular, in congruent conditions, when the visually encoded position of the hand is not manipulated (i.e. it is congruent with the proprioceptively encoded position), we predict that the participants will localise their hidden hand as more rightwards, in line with previous research reported above. In the incongruent condition, where the visually encoded position of the hand has been manipulated (i.e. only the proprioceptively encoded position of the hand is correct) instead, we predict that we will find a summation between the directional bias towards right and a reliance on proprioception, that would lead to a larger and faster drift towards right than in the congruent condition.

Additionally, in order to better clarify the role of vision in hand localization, we manipulated the rate of decay of the visually encoded position by asking participants, after their right hand was occluded, to either close their eyes (during which that decay of the visually encoded position will be accelerated; Chapman et al., 2000) or to continue to look at the blank space. Furthermore, an increase in the amount of visual exposure to an incorrect visual trace has been found to decrease the reliance on proprioception during a reaching task (Holmes & Spence, 2005). As a consequence, a faster decay of the visual trace might accelerate the reliance on proprioception and thus provide a larger and faster drift towards the right when eyes are closed prior to localization judgements.

2. Experiment 1

2.1. Materials and methods

Participants

16 healthy volunteers (8 males, mean age: 31±11years) participated in this study. All participants had normal or corrected to normal visual acuity and were right handed (self-reported). They had no current or past neurological impairment and

no current pain or history of a significant pain disorder. They were also naïve about the purpose of the study. All the participants gave written consent prior to their participation to the experiment. The study was performed in accordance with the ethical standards laid down in the 1991 Declaration of Helsinki and was approved by the Human Research Ethics Committee of the University of South Australia.

Apparatus and experimental setup

Participants viewed a real time video image of their hands in first person perspective using the MIRAGE system (Newport et al., 2009). A combination of mirrors and camera allowed participants to view their hands in an identical spatial location and from the same perspective as if directly viewing their real hands (Newport et al., 2010). The seen position of the participants' right hand could be manipulated and presented in real time via customised in-house software. In particular, the participants' right hand could appear to them in its true location, where vision and proprioception offered congruent input (i.e. control congruent conditions) or in an alternative location in which vision and proprioception were incongruent.

Procedure

In all conditions participants were seated at a table with their hands resting inside the MIRAGE system (Fig.1). In this position they could see an online image of their hands. A fabric, opaque bib was secured around participants' necks and the bottom edge was attached to the MIRAGE to conceal the position of their elbows and thus remove any additional visual cues to hand location. The height of the chair was adjusted such that participants were able to look inside the MIRAGE and to comfortably raise their hands and forearms above the surface of the table.

Figure 1 – Experimental setup. The participants were seated at a table with their hands resting inside the MIRAGE system. A fabric bib was attached to prevent the participants of seeing the position of their elbows. The chair was adjusted for each participant in order to have a comfortable position during the experiment. The pictures on the right also show that participants perspective while watching their hands moving between the blue bars inside the Mirage.

Before starting the experiment participants underwent a training procedure to familiarize with the localisation task. During the training task, participants practised hand localisation by stopping a visual arrow (that was presented via MIRAGE software, directly above their actual hand location) when the arrow reached the middle finger of their hidden right hand. The main goals of the training procedure were: (1) fixating on a spot within a blank space without being distracted by the movement of the arrow moving and (2) being able to stop the arrow accurately, even with time constraints. The training involved three stages, for a total of 22 practise localisations. The participants were allowed to practice until they felt they were totally confident with the task and also with the timing. Then, the experimental conditions commenced (see Appendix 1 for an extensive explanation of the practice trials).

In all experimental conditions (see Appendix 1, Fig. S1), participants underwent an adaptation procedure in which they were asked to hold their hands approximately 5 cm above the table surface and maintain the position of their hands between two moving blue bars either side of their hands. In all the conditions, both hands were initially positioned approximately 13 cm laterally from the body midline. During the adaptation procedure, the positions of the blue bars were manipulated laterally, so that the positions of the hands could be gradually shifted relative to their seen position by independently moving the seen image of the hands relative to their real locations. The position of the right hand was varied across 3 conditions (Incongruent, Congruent Outer, Congruent Inner). In the Incongruent condition, the seen image of the right hand moved inwards at approximately 25 mm/s. Thus, in order to maintain the appearance of their right hand remaining stationary, participants were (unknowingly) required to move their right hand outwards at the same rate. This adaptation yielded to a visuo-proprioceptive discrepancy between the seen and real positions of the hand. In this illusory condition, the adaptation procedure resulted in the actual position of the participants' right hand being 11 cm further to the right (20 cm from midline) than the seen position (9 cm from midline). Conversely, in the Congruent control conditions the movement of the visual image was identical to the real movement of the right hand. There were two Congruent conditions based on final hand position: the Congruent Outer condition (right hand moves from 13 cm to 20 cm from the midline) and the Congruent Inner condition (right hand moves from 13 cm to 9 cm from midline). These two conditions were designed in order to control for both the seen position of the hand (9 cm from midline) and the real position of the hand (20 cm from midline) in the Incongruent condition. The final true location of the right hand was identical between the Incongruent and the Congruent Outer conditions and the final seen location of the right hand was identical between the Incongruent and the Congruent Inward condition. The movement of the left hand seen on the screen was congruent with the participant's real hand movement in all the conditions, such that its final position was 9 cm from the body midline (4 cm more inwards than the initial position). Immediately after the adaptation procedure, the experimenter placed the participant's hands on the table (maintaining their position between the blue bars) and participants kept both hands still. They were instructed to fixate on their right hand. In all conditions the right hand was then occluded from view (i.e.

disappeared from the screen). The participants were then either asked to close their eyes for 20s (Eyes Closed, EC) or to fixate on the space in which they had seen their right hand (Eyes Open, EO). Thus each of the three conditions (Incongruent, Congruent Outer and Congruent Inner) was repeated twice – once with the eyes open and once with the eyes closed. In the EC condition, once the eyes were open again, participants were instructed to fixate on the location where they felt their hand to be. Then the localisation task commenced (Appendix 1, Fig. S1, see description below). In order to avoid any reaching error bias due to mislocalisation of the non-experimental hand we used a localisation task that did not require any hand movement (i.e. a moving arrow as used in the training task). Participants performed the six conditions in a randomised, counterbalanced order: Congruent Inner, EO and EC; Congruent Outer, EO and EC; Incongruent, EO and EC (see Appendix 1, Table S1).

Following each condition, participants verbally responded to a questionnaire (see Appendix 1, Table 2), giving a number from 0 to 10 in accordance with their agreement with each sentence, in order to check whether they were aware of the visual illusion performed in the Incongruent conditions. The questionnaire was a shortened version of that used in the original DHT experiment (Newport & Gilpin, 2011). At the very end of the experimental session, the experimenters briefly interviewed the participants. The participants were told that in one or more conditions the seen position of their hands was not their actual position, because a visual illusion was elicited. They were then asked if they were aware of it and whether they could try to report in which condition (or conditions) this illusion had been performed.

Localisation task.

The localisation task did not require any movement of either hand. Reaching tasks are typically used to localise one’s own body part and require reach planning. Such tasks have been shown to utilise proprioceptive information, rely on an accurate localisation of the non-experimental hand (Jones et al., 2010) and incorporate effort and motor command components (Proske and Gandevia, 2012). As mentioned above, participants fixated on the point of the screen corresponding to their perceived location of the middle finger of their hidden right hand. An arrow (controlled by the experimenter) was displayed centrally in the upper part of the screen, pointing towards the participants. The arrow moved at a constant speed (2.65 cm/s) horizontally in the direction of the right hand (i.e. outwards from midline). Participants were instructed to say ‘stop’ when they judged the arrow to be aligned vertically with the tip of their hidden right middle finger. This gave the experimenter a numerical value corresponding to the position of the arrow on the screen. This value was recorded for each localisation. It was not possible to blind the experimenters to the conditions, so the experimenter who was controlling the arrow looked away from the screen during the localisation task in order to minimize any possible interference due to expectation about the localisation outcome. The same experimenter also visually monitored the participants’ gaze direction. The arrow was displayed 20s after the right hand had disappeared from view during which the participants either kept looking at the spot where they felt their right hand to be (EO conditions) or they had their eyes closed (EC conditions). The arrow returned to the starting point in the centre of the screen immediately after each localisation. Participants performed the localisation task every 15s for a total of 13 localisation values. A second experimenter recorded each value before the arrow was returned to the starting point by the first experimenter. Following the localisation task, participants remained with their hands in position inside the MIRAGE but viewed a blank screen, allowing the experimenters to record the numerical value of the real position of the participant’s right hand without revealing this to the participant. This was done exactly with the same procedure used in the localisation task, so recording the numerical value of the arrow when it was placed exactly on the participants' fingertip.

Data analysis

For each participant, and for each condition, the localisation error (in cm) was calculated (i.e. the difference score between the participants' judged location and the true location of their hidden hand). The true hand location was set at 0, such that overestimations (i.e. mislocalisation to the right of the hidden hand) were represented by positive values and underestimations (i.e. mislocalisation to the left of the hidden hand) by negative values. One outlier was identified and was removed from the analysis. Because the data did not satisfy the assumptions of a conventional ANOVA, we undertook a Random Effect Analysis of variance in order to analyse the error values. Based on the graphical plot of the data and on the Wald Z Test, the factor Participants was considered as a random factor and the factors Congruency (Congruent Outer, Congruent Inner, Incongruent), Sight (Eyes Open, EO; Eyes Closed, EC), Time (13 points over 3 minutes), and their interactions (Congruency*Sight, Congruency*Time, Time*Sight) as fixed factors. Different models were taken into account based on the Schwarz's Bayesian criterion (BIC) and the model with the best fit including a random intercept (Participants) and random slopes (Condition, Sight, Time) was identified.

2.2. Results

There was a significant effect on error values of Congruency [F(2,36.31)=105.63, *p*<.001; *r*=-.661] (Fig.1a) and of Time [F(1,15.03)=11.64, *p*<.005; *r*=.102]. No main effect of Sight [F(1,18.69)=0.072, *p*=.791] was detected. This indicates that both the Congruency and Time modulated the perceived location of the participants' hidden hand. We observed a significant interaction between Congruency and Sight [F(2,1162.68)=9.60, *p*<.001] and Congruency and Time

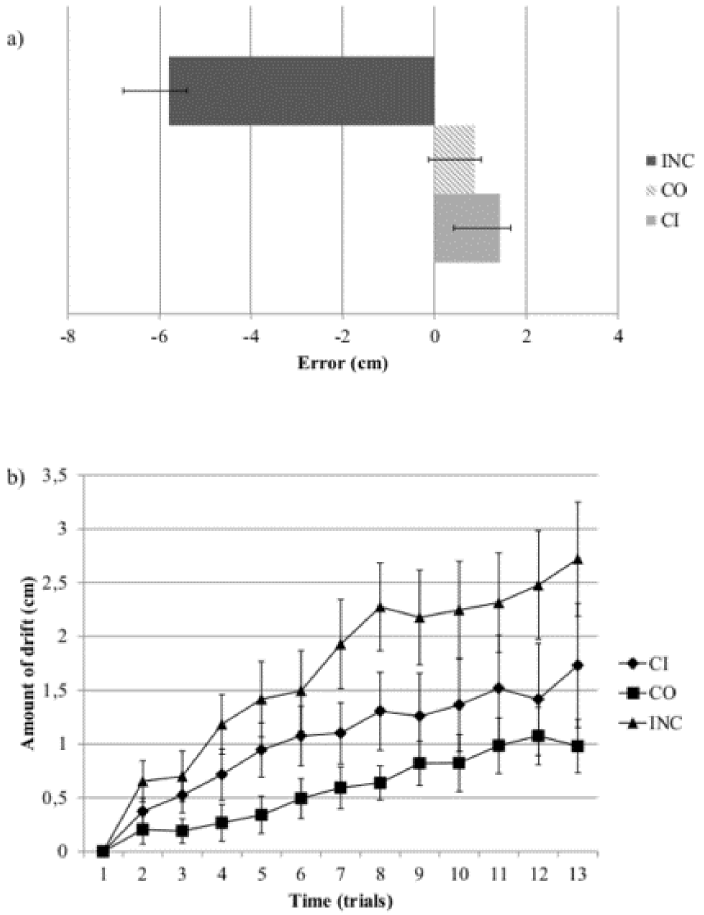


Figure 1 – Results. For the factor Congruency (a), in the Incongruent conditions the error values were significantly different to those found in the Congruent Inner (*p* < .001) or Congruent Outer (*p* < .001) conditions, in which mean error values were both positive. In Fig. 1b we set to 0 the very first localisation (and, consequently, we recalculated the other error points), in order to highlight the increase of error over time and the fact that the significant interaction between Congruency and Time (*p*<.001) showed a larger and quicker drift towards the right in the Incongruent conditions than in either of the Congruent conditions.

[F(2,1162.68)=9.72, *p*<.001] (Fig.1b). No other interactions were found to be significant. For the factor Congruency (Fig.1a), in the Incongruent conditions participants error values across all localisations were negative (i.e. left of the actual location of the hand) and were significantly different to those found in the Congruent Inner [t(60.24) = 9.766, *p*<.001] or Congruent Outer [t(60.24) = 9.006, *p*<.001] conditions, in which mean error values were both positive (i.e. right of the actual location of the hand). Thus, the fact that the error values were positive (i.e. drifted more towards the right with respect to the real hand position) in the control conditions suggests an overestimation of the hand position to the right of the real location of the hand. This is in line with previous studies that showed a drift towards right when the occluded hand was the right one (Jones et al., 2010). Conversely, the fact that the error values in the incongruent conditions were negative suggests an underestimation of hand position, that is, to the left of the real location of the hand. Of interest, in the Incongruent condition, we found a mislocalisation towards left, that is, in the opposite direction of the drift found in the congruent conditions. Since the last seen position was actually more leftwards than the real position of the hand, this findings supports that the initial localisation judgements were captured by the visual trace of the hand.

The Congruency by Time interaction showed that the change in error values over time was larger in the Incongruent condition than it was in the Congruent Inner condition [b=-.99, t(1162.68)=-1.98, *p*=.048] or the Congruent Outer condition [b=-1.44, t(1162.68)=-2.85, *p*=.004] (Fig.1b). In the Incongruent condition, this change was from larger negative error values to smaller negative error values – i.e. moving towards the correct hand position. In the Congruent conditions, this change in error values was from smaller positive error values to larger error values – i.e. moving away from the correct hand position. This result suggests a greater amount of drift over time in the Incongruent condition than in the control conditions. This drift was consistently in a rightwards direction as in the Congruent conditions, but since this significant difference, we can hypothesise that the localisations in the Incongruent conditions are not just rightwards, but they are also towards the real location of the hidden hand.

Finally, the Congruency by Sight interaction showed that in the Incongruent conditions, the difference between EO trials (mean=-6.53 cm, 90% CI -7.56 to -5.50) and EC trials (mean=-5.62 cm, 90% CI -6.66 to -4.59) was larger than it was during either the Congruent Inner conditions (EO mean=1.48 cm, 90% CI 0.45 to 2.51; EC mean=1.00 cm, 90% CI -0.03 to 2.03) or the Congruent Outer conditions (EO mean=0.86 cm, 90% CI -0.17 to 1.89; EC mean=0.17 cm, 90% CI -0.86 to 1.20). The smaller error values for the EC trials in the Incongruent condition suggest that closing the eyes for 20s before starting the localisation task might lead to an advantage in locating the hidden hand in conditions in which the physical and perceived position of the hand are incongruent.

In order to investigate overall differences in error values between conditions (i.e. participants' accuracy), all error scores were normalised to the first localisation judgement, and a 2 (EO, EC) x 3 (Congruent Outer, Congruent Inward, Incongruent) repeated measures ANOVA compared error across conditions. Since Mauchly's test for sphericity was significant, a Greenhouse-Geisser correction was applied. This analysis revealed a significant effect of Congruency [Wilks' Lambda=0.390, F(2,14)=10.958, $p<0.001$], but no effect of Sight [Wilks' Lambda=.970, F(1,15)=.460, $p=.508$] and no interaction effect [Wilks' Lambda=.861, F(2,14)=1.126, $p=.139$]. Bonferroni corrected pairwise comparisons ($\alpha=.0167$) revealed that accuracy was significantly lower in the Incongruent condition than in both the Congruent Inner ($p=.001$) and Congruent Outer ($p=.007$) conditions. No significant difference was found between the two Congruent conditions. That the participants were much less accurate during the incongruent conditions suggests that they were not only *uncertain* but also *unaware* of the true location of their hand (in fact, *uncertainty* about the position of the hand was present in all the conditions, given that the hand was out of view. However, just in the Incongruent condition the participants were also *unaware* of their hand position). We interpreted this result as confirmation that the position of the right hand was actually deceived and that this deception lasted over time. Alternatively, one may argue that the mislocalisation of the right hand during the Incongruent condition could be simply explained as a visual capture of hand position (Pavani et al., 2000). Thus, in order to check that the participants were indeed unaware of the difference between the Congruent and Incongruent conditions and so to rule out the possibility that the effect that we found was merely due to a visual capture, we analysed the questionnaire ratings. Of specific relevance was the question, *I couldn't tell where my right hand was*, as higher ratings for this question in the Incongruent condition (vs Congruent conditions) would suggest that participants were aware of the deception and thus were unsure of their actual hand position. We performed a one-way repeated measure ANOVA to compare the participants' rating scores across conditions (Congruent Outer, Congruent Inward, Incongruent) for each of the seven questionnaire items. Since the Mauchly's test for sphericity was significant, a Greenhouse-Geisser correction was applied. There was no effect of Congruency for any of the questionnaire items (see Appendix 1, Table 2). This result supports the fact that the participants were naïve to the experimental manipulations. The lack of awareness regarding the experimental manipulations is also supported by the participants' final self-report. In fact, none of the participants claimed to be aware of the illusion and when asked to try to identify the condition(s) in which the illusion was performed, they reported to be guessing. None of the participants correctly identified both of the incongruent conditions.

3. Experiment 2

In order to rule out the possibility that the shift towards right was merely an effect of the arrow movement direction used in the localisation task, we designed a second experiment, in which we simply varied this direction. The participants performed two conditions (both incongruent) that differed only for the starting point and direction of the arrow.

3.1. Materials and Methods

Participants

18 healthy volunteers (10 males, mean age: 33±9 years) participated. The conditions were randomized and counterbalanced across participants. All participants had normal or corrected to normal vision and were right handed (self-

reported). They had no current or past neurological impairment and no current pain or history of significant pain disorder. They were also naïve to the aims of the study. All the participants gave written consent prior to their participation to the experiment. The study was performed in accordance with the ethical standards laid down in the 1991 Declaration of Helsinki and was approved by the Human Research Ethics Committee of the University of South Australia.

Procedures

The participants underwent the original DHT (Newport & Gilpin, 2011) twice. Note that this illusion differed from the illusion used for Experiment 1 just for the fact that both hands were actually moving. However, we know from pilot data that this difference does not modulate the effects of the arrow direction on the localisation responses. During the localisation task, in one condition the arrow was starting from the centre of the screen and moving rightwards (as in Experiment 1), while in the other condition the arrow was moving at the same velocity but from the right hand side of the screen towards left. The task was exactly the same as that described above.

3.2. Results

We performed a 2(Arrow Direction: Centre to Right, Right to Centre) by 2(Time: T0, T12) repeated measures ANOVA. A main effect of Time [η^2=0.52, F(1,17)=18.38, $p<.001$] showed that localisation error scores were more accurate (i.e. less negative) on the last judgment (T12 mean=-9.23 cm, SE=0.86, 95% CI -11.05 to -7.40) than they were on the first (T0 mean=-11.64 cm, SE=0.46, 95% CI -12.61 to -10.58). There was no main effect of Arrow Direction [F(1,17)=3.17, p=.093] nor a significant interaction between the Arrow Direction and Time [F(1,17)=2.06, p=.170]. Thus, in line with the Experiment 1, participants became more accurate over time, but the direction of the arrow did not influence the extent of rightward drift.

4. Discussion

Our results support our prediction that, when the perceived hand position is different from the physical hand position (due to a visual illusion), in the 3 minutes following visual occlusion of the hand, participants rely less on vision and more on proprioception, such that hand localisation judgements become more accurate (i.e. closer to the physical position of the hand) over time. Conversely, we hypothesised that providing participants with a congruent physical and perceived location of the hand would result in more accurate hand localisation judgements than when a visuo-proprioceptive incongruency was introduced. In order to control for the role of vision, we also hypothesised that accelerating the decay of the visual trace (by closing the eyes immediately after hand occlusion) would similarly lead to an earlier reliance on proprioception. In line with this hypothesis, we expected the participants to be increasingly more accurate over time in localising their hidden hand when the visuo-proprioceptive incongruency was introduced or when participants closed their eyes after visual occlusion. Our data support also this hypothesis. In fact, when the participants were forced to rely more on proprioception (i.e. the physical position of the hand was different from its perceived position) the switch to proprioception occurred earlier when they closed their eyes before the localisation task that when they kept them open.

Our hypothesis that when the physical and the perceived position of the hand are congruent, the accuracy in the localisation task would decrease over time after the visual occlusion of the hand was supported, as evidenced by the increase in error values detected over the three minutes following the hand occlusion. That is, when the visually encoded (perceived) hand position was the same as the proprioceptively encoded (physical) position, the localisation judgements diverged from the physical position of the hand over time accordingly to the directional bias. Also, our hypothesis that a visuo-proprioceptive incongruence (yielded by the illusion) would increase the use of proprioception to localise the hand was confirmed by our finding of an acceleration of the drift towards the real position of the hand in the condition in which the illusion was performed. This result is consistent with the Maximum Likelihood Estimation theory of multisensory integration (Ernst & Banks, 2002), suggesting that the sensory modality that dominates over the others in a given situation is the one that carries the lower level of variance. In the Incongruent condition, the increased accuracy in time since the last visual confirmation of hand position would suggest that remembered visual information has more variance (due to decay of the visually encoded position) than proprioceptive information that continues to come from the hand (in fact, even in stationary sitting, there are continual perturbations incurred by breathing, cardiac rhythm and postural sway, that are sufficient to activate low threshold proprioceptive organs (see Proske and Gandevia, 2012). This idea seems supported by the finding that acceleration of the visual trace decay, by closing the eyes, results in better performance in hand localisation for only the incongruent condition when visual information is inaccurate. While we did not predict that the effect of closing the eyes would be specific for the Incongruent condition, this suggestion is not unreasonable. In fact, we hypothesized that vision would interfere with the correct localisation only when the visual trace is inaccurate. We hypothesised that, when this occurs (i.e. in the Incongruent condition) the participants would rely more on proprioception, leading to an increase in the accuracy of hand localization. Thus, an earlier decay of the visual trace could quicken the onset of the switch from vision to proprioception. Our results support this idea - closing the eyes only matters when an inaccurate visual trace is provided and this leads to more accurate localisations compared with keeping the eyes open.

One might argue that the effect we found might be due to a spontaneous return towards the real position. However, once the illusion is in place, the hands are still and there would not be any reason for updating their position. In Newport and Gilpin’s study (2011), after the right hand disappeared from view, the participants were required to reach across with their left hand to touch their right hand. All the participants failed in touching their disappeared hand, showing that the real position of the hands was not updated yet. We can argue that, in our experiment, until otherwise proved, the visually encoded position of the hands is maintained. However, our results show that, even though there is no actual or potential motor requirement, the location of the hand is updated on the basis of the available data, in this case proprioceptive input (i.e. visual input is no longer available). One would predict that, if there is a biological advantage to *be ready* for movement even though none is expected, then this constant updating or recalibration would be helpful. Importantly, the shift in weighting given to proprioception is not immediate and complete, but rather occurs gradually over time.

Alternatively, during the adaptation procedure of the Incongruent condition it is possible that a recalibration of the felt position of the hand with the seen position of the hand occurred, such that the relationship between proprioceptive and visual information was updated, to the detriment of proprioception. A decay of this recalibration between proprioception and visual information may be another possibility for the increased accuracy over time of hand localisation judgements in the Incongruent condition. Previous work using prism adaptation, in which the seen position of the hand is manipulated, suggests that the participants, under certain conditions, might start to use new visuospatial coordinates for their limb (Rossetti et al. 1998). Importantly, when the adaptation is removed, this re-calibration spontaneously decays (Newport and Schenk 2012). It may be that our data are a corollary of this spontaneous decay seen in prism adaptation. Again, that the decay occurred quicker when visual information was removed would support this idea. Our data are in line with both the MLE and the recalibration hypothesis; however, it was not our intent to differentially interrogate those theories.

Early prioritization of vision

In line with our hypothesis, in all conditions, participants first localised their hidden right hand at a point located towards the last seen location of the hand. This was true both for the Congruent conditions (where the last seen location matched the true location of the hand) and for the Incongruent condition (where the last seen location did not match the true location of the hand). In the Incongruent condition, localisation scores were significantly leftwards (i.e. towards the last seen location) and less accurate than those in the two control conditions, which supports the dominant role of vision in localisation of our hands. Our data confirm and extend the previous findings that relate the amount of visual exposure (in terms of time) with the reliance on proprioception (Holmes and Spence 2005). In fact, Holmes and Spence found that the longer the participants were allowed to look at the (incorrect) position of their right hand the less they relied on proprioception, tending rather to rely on vision. We found that also the opposite holds, by showing that with time, when the decay of the visually encoded position is accelerated (by closing eyes), the relative weighting and reliance on incoming sensory information switches sooner to proprioception, to the detriment of vision.

The directional bias and the proprioceptively encoded position of the hand

Regardless of the Congruency, a rightward drift was found in all the experimental conditions. A number of studies have shown that a mislocalisation of one’s own arm and hand occurs when vision is occluded (Paillard & Brouchon, 1968; Craske & Crawshaw, 1975; Desmurget et al., 2000; Smeets et al., 2006; Wann & Ibrahim, 1992). It is well established that when healthy participants are asked to locate their own hidden hand in space, there is a directional bias towards the attended side of space (i.e. the right hand is overestimated as being more rightwards, while the left hand as more leftwards) (Crowe et al., 1987; Ghilardi et al., 1995; Haggard et al,. 2000; Jones et al., 2010; van Beers et al., 1998). Thus, the significant rightward shift in localisations over time in all conditions in our study confirms and extends previous findings regarding a directional bias for hand localisation. Not only did we observe the same drift (in this case towards right) in all conditions, but we also found that this drift increased over time. We propose that this directional bias is driven by the portion of the space in which the entire experiment occurred. Due to the well-established decay of the visually encoded position after hand occlusion over time (Chapman et al., 2000), the influence of this bias, although present since the first localisation, seems to become prevalent, leading to localisations that are increasingly shifted towards the side to which the participants were performing the localisation task (i.e. to the right in our experiment). Thus, over time, the ability to localise one's own limb in space becomes less accurate due to the reliance on a rapidly fading visually encoded position. However, if the fading visually encoded position were the only reason for less accurate localisations, the localisation judgements would be randomly distributed around the real hand location, to both the right and to the left of the real hand position. Instead a specific trend towards the right, beyond the true (or last seen) location, was found. The question addressed here is why, when the participants start to become less accurate in localising their hidden right hand, do they systematically localise it increasingly towards the right? Our hypothesis accounts for this peculiar trend, suggesting that while the visual trace decays, a bias towards the space in which the experiment is occurring seems to guide the localisations. We can also exclude that this directional bias was simply the product of the arrow shifting, as clearly showed by the results from Experiment 2.

One might argue that the shift towards right is simply due to a cumulative error effect (i.e. the successive summation of the error produced by each consecutive response in a task) (Bock & Arnold, 1993; Dijkerman & de Haan, 2007) caused by the repeated measures. However, the cumulative error effects have been found, and related to, motor tasks. For example, in Bock and Arnold's study (1993) the cumulation errors were directly related to the motor component of the task. Also, Jones and colleagues (2010), on the basis of Dijkerman and de Haan's work (2007), noted that reaching tasks might lead to kinematic errors that cannot be disentangled by localisation errors. Our protocol did not involve repeated movements, but repeated judgements of an independently moved arrow. Moreover, in the Incongruent condition our protocol did not show accumulating error, but accumulating accuracy. However, even if the drift reflected an accumulating error, relative to the visually encoded location of the hand, then it would be consistent across conditions, which it is was not.

Importantly, the drift towards the right side was significantly different between the Congruent and the Incongruent conditions. We interpreted this significant difference as evidence of the contribution of proprioception when there is a visuo-proprioceptive incongruence (i.e. the physical and perceived position of the hand are different), but not when it is just faded away (i.e. when the hand is simply hidden from view). In fact, equal accuracy in the localisation task across the three conditions would have suggested reliance primarily on proprioception (i.e. in the incongruent conditions, no matter where the perceived position was, the participants correctly would localise the position of the hidden hand). We contend that the greater rightwards drift when vision was occluded confirms that an updated proprioceptive input drives the rightward shift over and above any generic directional bias. On the other hand, a similar amount of drift towards the right side across all the conditions would have suggested that the localisations were mainly guided by the directional bias. Our findings clearly confirm that vision is prioritised over proprioception even when the visual input is inaccurate, but over time, in turn, proprioception is prioritised over the directional bias.

The results reported here clearly support our initial hypothesis that the incongruence between the perceived (visually encoded) and physical (proprioceptively encoded) position of the hand would increase reliance on proprioception and improve localisation accuracy over time. Moreover, according to our hypothesis, in the Incongruent conditions after the visual trace decayed, the participants' perceptive system switched to rely more heavily on proprioception leading to a stronger and quicker drift towards the right (the physical location of the hidden hand). Our hypothesis does not exclude that a proprioceptive component was also present in the two control conditions. However, it does suggest that this component is stronger when vision is unreliable. Importantly, the adaptation procedure used in the Incongruent conditions resulted in participants being unaware of any difference between the control conditions and the illusion, as reported after the experiment and confirmed by the responses to the questionnaire. Crucially, this indicates that the switch from a visually to a proprioceptively encoded location of the hidden hand occurred entirely outside of participants' awareness. Furthermore, some participants verbally reported the sensation that their hand was shifting towards the right as well as the urge to move their hidden finger during the Incongruent conditions' localisations. This perhaps indicates the efforts of the participants' perceptual system to determine the true location of their hidden hand. Furthermore, we predicted that closing the eyes immediately after hand occlusion would augment the decay of the visually encoded position of the hand (Chapman et al., 2000), leading to an earlier reliance on proprioception. We found this effect in the Incongruent condition, but no effect was found in the Congruent conditions. This result seems to be in line with our hypothesis, since a reliance on proprioception was present (or just stronger) when the visual trace was inaccurate.

The results reported in this paper clearly show a complex interaction between visual, proprioceptive (and task-related) factors in self-localisation of one's own hand. In particular, we shed light on the relative roles of vision and proprioception over time, concluding that sighted, neurologically-healthy participants tend to rely heavily on vision even when the visually encoded position of their hidden hand has decayed and made unreliable, which in turn seems to result in a strong directional bias due to the task itself. In addition to this, our findings also underlined the important contribution of proprioception when vision is unreliable. In fact, although in most cases the physical (proprioceptively encoded) position of the hand is ignored (or perhaps just underestimated), there are some circumstances in which proprioception can be utilized effectively in accurately locating one's own body part. Vision gives us distal information about the external world, allowing us to make prediction without directly contacting a potentially dangerous stimulus (Gregory 1997). It seems then an evolutionary advantageous choice to adopt a heavy reliance on visual information in a number of situations. However, there are cases in which proprioception becomes not just useful but essential. In particular, people who are blind or partially blind and who are in a condition similar to the one described here should choose to rely on proprioception (in fact, the occluded hand is inserted into a box-like system, making other strategies, such as echolocation highly unlikely). Gaining knowledge about the relative weighting of sensory inputs for self-localisation is also of importance for a variety of disorders in which proprioception is known to be damaged. In cerebral palsy, for example, a deficit to visual-proprioceptive system has been observed (e.g. Wann, 1991). In addition, patients whose sense of touch is severely damaged (as in case of deafferentation) are also unable to locate their body in space and navigate in the environment. In order to successfully execute a movement, these patients need to visually monitor their limbs during the execution (Cole & Paillard, 1995). Also, it is well-known that chronic pain involves disturbances in the motor system (e.g. Moseley 2004) and body image (e.g. Moseley, 2005) that may also disrupt proprioception (see Lotze & Moseley, 2007 for review). Besides, recent research has pointed out the relationship between the mechanisms underlying the processing of body location and nociception (Gallace et al., 2011; Sambo et al., 2013) (see also Moseley et al., 2012, for a review).

In conclusion, by introducing incongruence between the seen, felt and veridical locations of the right hand, we demonstrate a shift from vision towards proprioceptive information, experimentally reversing the seemingly usual dominance of vision in localising the body. In addition to this, we showed that when visual information becomes less reliable and, possibly, when proprioception starts to be more stable, the participants switch from a visual-based localisation strategy to a proprioceptive-based one. Last, we show new evidence supporting the claim that the brain updates limb location, even when there is no conscious need to do so (Haggard &Wolpert, 2001).

CHAPTER IV

STUDY III

Abbreviations used in this chapter:

CNS, Central Nervous System; DHT, Disappearing Hand Trick; MLE, Maximum Likelihood Estimation; SCR, Skin Conductance Response; RHI, Rubber Hand Illusion

Study 3: Attention is not responsible for the rightward shift in the DHT, but reaching movement is

Study 3 has been conducted in collaboration with Helen R. Gilpin (University of South Australia), Tasha R. Stanton (University of South Australia and Neuroscience Research Australia), Roger Newport (University of Nottingham), Alberto Gallace (University of Milano-Bicocca and NeuroMI) and G. Lorimer Moseley (University of South Australia, Neuroscience Research Australia and PainAdelaide).

1. Introduction

Proprioception refers to the processes by which the brain monitors the position and alignment of the body and it plays a crucial role in everyday life. Contrary to Aristotle’s teaching about the existence of strictly five senses, Bell (1826) suggested the need for defining an additional sixth sense that he called ‘muscle sense’. He argued that the contraction of muscles under electrical impulses is not only fundamental to movement, but also provides important information about the position of a particular body part in space. Nowadays, the common view among neurophysiologists is broadly consistent with that of Bell - the principal (although, importantly, not the only) proprioceptors are the muscle spindles (Proske & Gandevia, 2012), which detect changes in muscle length, triggering a signal to the brain about a change in body alignment. Such proprioceptive cues are not sufficient however, for self-localisation (i.e. being aware of where one's body is in space). Rather, self-localisation is a multisensory experience that involves proprioception, vision, touch and higher order functions such as attention. The crucial role of vision has been demonstrated by several studies showing a decreased accuracy in localising one's own body part when vision is occluded (Paillard & Brouchon, 1968; Craske & Crawshaw, 1975; Wann & Ibrahim, 1992). In line with this multisensory approach, it has been proposed that an optimal statistical evaluation of the information coming from different senses is likely to generate the most accurate estimation of the position of a body part (van Beers, Sittig, & Denier van der Gon, 1998, 1999; van Beers, Wolpert, & Haggard, 2002; Ernst & Bülthoff, 2004; Smeets, van den Dobbelsteen, de Grave, van Beers, & Brenner, 2006). According to the Maximum Likelihood Estimation (MLE) theory (Ernst & Banks, 2002), the Central Nervous System (CNS) can utilise such a statistical evaluation to generate an estimate of body position that relies most heavily on the sense judged to be the most stable. In this way, we predict that, when vision is occluded or inaccurate, the CNS will automatically switch to rely more heavily on other sensory inputs, such as proprioception.

In line with the MLE theory, in Study 2 (see Chapter III) has been found that, when asked to localise their own hidden hand, healthy participants initially based their localisation judgements primarily on the last available visual trace of the stimulus (i.e. where they saw their hand to be the moment before it was occluded from vision). However, if this last visual input is experimentally manipulated in order to provide an inaccurate representation of real hand position (without the participant's awareness), estimations of hand position become more accurate over time. That study suggested two mechanisms are at play. First, fallibility of vision increases reliance on proprioception. Second, a generic drift occurred such that estimations of hand position gradually move laterally from the last place in which the hand visually appeared to be located. We proposed that this lateral drift reflects judgements being drawn towards the portion of the space to which the participant is attending.

Study 2 highlighted a potentially important role of attention within the context of body localization. That attention is often reflected in visual orientation is given and intuitively sensible, but attention can also be shifted independently of visual orientation (Eriksen & Hoffman, 1973; Klein, 1979; Posner, Nissen, & Ogden, 1978; Shaw, 1978; Von Voorhis & Hillyard, 1977; Wurtz & Mohler, 1976). It is of vital evolutionary advantage to direct attention to new objects in the environment, especially those that are moving or emitting sounds, in order to protect our body against potential threat (e.g. Solokov, 1963). Indeed, new events (Jonides & Yantis, 1988; Yantis & Hillstrom, 1994), especially those that involve dynamic (Franconeri & Simons, 2003) and coloured (Folk, Remington, & Johnston, 1992) elements, can easily capture attention. These issues highlight the importance of clarifying the relative contribution of spatial attention and proprioception to the shift in perceived position of the body when vision is occluded. This issue is seldom considered in investigations of proprioception, perhaps because it has been methodologically challenging to interrogate it.

We differentiated proprioception from spatial attention using an experimental set-up that allows us to manipulate the congruence between the seen and actual locations of one hand – the so-called Disappearing Hand Trick (Newport and Gilpin, 2012). We manipulated spatial attention using brief tones that were emitted at either the left or right side of the participant, immediately before they made a judgement about the location of each hand. This kind of auditory cue would interfere with spatial attention (Haas & Edworthy, 2006; Vu, Minakata, & Ngo, 2013), but should leave intact that portion of the lateral drift in hand localisation that is driven by proprioception. We aimed to determine the effect of the auditory cues on how quickly hand localisations shifted from the original seen location of the hand, and the actual location of the hand. We hypothesised that the drift in localisation judgements would be modulated by the location of the auditory cues, thus reflecting a contribution of spatial attention to the drift.

The second aim of the present work was to investigate the role of contradictory sensory feedback in hand localisation accuracy, when real and perceived hand positions differ. After playing the Disappearing Hand Trick (Newport & Gilpin, 2012), where the last seen location of the hand does not match its true location, the participant reached over with their opposite hand to touch the area where they perceive their right hand to be. That they feel only the table surface evokes a powerful realisation that they hand is clearly not where it was felt to be – it has been “mislaid”. In line with the MLE theory, we would predict that this manoeuver would rapidly increase the weighting placed on proprioception because visual information has been unequivocally proven to be inaccurate. Such an outcome would also show that MLE theory applies whether the cues involve implicit or explicit processing, an issue that is so far unaddressed. We hypothesised that this type of frank contradictory feedback would induce more accurate localisations than those observed without the reaching component.

To iterate, we had two primary aims. First, to detect whether the spatial attention (investigated via space attended) contribute to the drift. Second, to investigate if the contradictory feedback (due to the reaching movement towards the hidden hand) speeds up the prioritisation of proprioception, in line with the MLE.

2. Materials and Methods

Participants

Eighteen healthy volunteers (10 males, mean age: 33±9 years, range: 21-45) participated in the study. All took part in Experiment 1, half (Group I, n=9) took part in Experiment 2, and the other half (Group II, n=9) took part in Experiment 3 (see Table 1). Each participant completed two experimental sessions. The two different experimental sessions were comparable in terms of duration and number of conditions performed. Within each experiment, the conditions were randomized and counterbalanced across participants. All participants had normal or corrected to normal vision and were right handed (self-reported). They had no current or past neurological impairment involving the upper limbs, and no current pain or history of significant pain disorder. They were also naïve to the aims of the study.

All participants gave written consent prior to participating in the study. The study was performed in accordance with the ethical standards laid down in the 1991 Declaration of Helsinki and was approved by the Human Research Ethics Committee of the University of South Australia.

a)

All (n=18)	
A B C	
Group I (n=9)	**Group II (n=9)**
D E	F G

b)

Conditions labels	**Condition names**
A	No Reach, Tone Left
B	No Reach,Tone Right
C*	No Reach, No Tone*
D	Reach, Tone Left
E	Reach, Tone Right
F*	No Reach, No Tone*
G	Reach, No Tone

Table 1 - We performed 3 different experiments, each of them including the same number of conditions. (a) One experimental session included two experiments. All the participants performed the 3 conditions (A, B and C) included in the Experiment 1. In addition, the participants assigned to the Group I performed the conditions C and D, while the participants assigned to the Group II performed conditions F and G. (b) In the Experiment 1 spatial attention alone was manipulated. In the Experiment 2 the spatial attention together with the contradictory feedback were investigated. In Experiment 3 the contradictory feedback alone was explored.

*conditions C and F practically were exactly the same, but since they served different aims, they were considered and analysed separately.

General procedure

For each condition, participants first underwent an adaptation procedure using the equipment described below and, then, performed a localisation task. At the end of the experimental session, the participants' comments and spontaneous feedback about the illusion were collected using open-ended questions.

Apparatus and experimental setup

The participants viewed a real time video image of their hands in first person perspective using the MIRAGE system (Newport, Preston, Pearce, & Holton, 2009). A combination of mirrors, computer monitor and a camera allowed participants to view their hands in exactly the same spatial location and from the same perspective as if they were directly viewing their real hands (Newport, Pearce, & Preston, 2010). The seen position of the participants' hands was then manipulated (without the participant's awareness) using customised in-house Labview software, and presented in real time video. In this way, the seen position of the participants' right hand was inconsistent with real hand position, such that vision and proprioception were incongruent, but the participant is naïve to this incongruence (see Newport & Gilpin, 2011).

Adaptation procedure and training trials

In all experimental conditions, participants were seated at a table with their hands resting palm down inside the MIRAGE system. A fabric bib was attached around their neck to conceal the position of their arms/elbows. The height of the chair was adjusted such that they were able to look inside the MIRAGE to the mirror and to comfortably raise their hands and forearms above the surface of the table. During the training trials, participants practised stopping a moving visual arrow presented on the screen (and reflected in the mirror that they viewed), by using vocal commands. That is, they were required to say "stop" so that the arrow was aligned directly with the middle finger of their hidden right hand, while attending to the blank space where their right hand was located (for full details about the training procedure see Study 2 and Appendix 1). When participants felt confident with the task, the adaptation procedure for the first condition started. Participants held their hands approximately 5 cm above the table surface and were instructed to maintain the position of their hands between two blue bars that were moving inwards around their hands. During the adaptation procedure, the video of the hands was manipulated online so that while the participant saw their hands in a consistent position, in reality their hands were gradually moving outwards. The participant was naïve to this manipulation, which resulted in a discrepancy between the final seen location of the hand and its real location, such that each hand was actually positioned further from the body midline than the participant thought (for a fully detailed description, see Newport & Gilpin, 2011). Following the adaptation procedure, the experimenter placed the participant's hands on the table (maintaining their position between the two blue bars) and participants kept both hands still while fixating on their right hand. In all conditions, the right hand was then occluded from view using customised Labview software. Participants continued to fixate on the location where they felt their right hand to be and the localisation task was commenced.

Localisation task

The localisation task was the same across all experiments and did not require any movement of either hand.

Participants fixated on the point of the screen corresponding to the perceived location of their hidden right middle finger. A red arrow (controlled by the experimenter) was displayed in the upper part of the screen, pointing towards the participants in a position approximately along the body midline. The arrow moved laterally from the centre of the screen along the x-axis at a constant speed towards right (i.e. in the direction of the hidden right hand). Participants were instructed to say ‘stop’ when they judged the red arrow to be aligned vertically with their right middle fingertip. The experimenter recorded this position for each localisation as a numerical value (expressed in number of pixels) that corresponded to the position of the arrow on the screen. The arrow returned to the starting point immediately after each localisation. Participants performed the localisation task every 15 seconds for a period of 3 minutes, making a total of 13 localisation judgements. Following the localisation task, participants remained with their hands in position inside the MIRAGE but viewed a blank screen. This allowed the experimenters to record the numerical value of the real position of the participant’s right middle finger without revealing this information to the participant (for fully detailed description of the task, see Study 2 and Appendix 1).

Data analysis

For each participant and for each condition, localisation error scores were calculated (i.e. the difference between the participants’ judged location and the true location of their hidden hand). Localisation error scores were adjusted so that true hand location was set at 0, and mislocalisations to the left of the hidden hand were represented by negative values. Thus as negative values approached zero, this indicated an increase in accuracy (i.e. a rightward shift).

In order to investigate the role of Time, we took into account the first localisation (T0; measured immediately after the right hand disappeared from view) and the last localisation (T12; measured 3 minutes after). All other localisations were included in the protocol to avoid distraction or lack of attention by participants between T0 and T12, but were not analysed.

The experiments performed in this study aimed to investigate a number of different issues, such that three different comparisons were made using statistical analysis (see Table 2).

Comparisons	Conditions labels[1]	Factors		Conditions' name	Experiment number	Issue investigated
		Reach	Beep			
1	A	No	Left	Tone Left	1	Tone alone (left, right, none)
	B	No	Right	Tone Right	1	
	C*	No	None	Silent	1	
2	D	Yes	Left	Tone Left Reach	2	Reaching (yes, no) + Tone (left, right)
	E	Yes	Right	Tone Right Reach	2	
	A	No	Left	Tone Left No Reach	1	
	B	No	Right	Tone Right No Reach	1	
3	F	No	None	Reach	3	Reaching alone (yes, no)
	G*	Yes	None	No Reach	3	

Table 2 – [1] the very same labels have been employed in the text

In this study we aimed to investigate three different issues.

First, we aimed to clarify the role of spatial attention (“tone”) in the localisation task (conditions A, B and C from Experiment 1, all performed by both Group I and II). In order to do this we performed a 2 (Time: T0 vs. T12) by 3 (Tone: Right vs. Left vs. Silent) repeated measure Anova on the error scores calculated for each condition.

Second, we explored the possible interaction between the spatial attention (“tone”) and the contradictory feedback (“reaching”). We compared two conditions in which both “tone” and “reaching” were manipulated with two conditions in which only “tone” was (i.e. the error scores performed by Group I in conditions A and B from Experiment 1 and the error scores in conditions C and D from Experiment 2, performed only by Group I). Spatial attention was manipulated in an identical manner in C and D (Experiment 2) and A and B (Experiment 1). In order to explore this interaction, we performed a 2 (Tone: Right vs. Left) by 2 (Time: T0 vs. T2) by 2 (Reaching: Reaching vs. no Reaching) repeated measure Anova on the error scores calculated for each condition.

Third, we investigated the influence of the contradictory feedback by itself (“reaching”), in which we compared a condition in which contradictory feedback was provided with a condition in which it was not (i.e. condition E and F from Experiment 3, both performed by Group II). In order to do this we performed a 2 (Time: T0 vs. T12) by 2 (Reaching: Reaching vs. No Reaching) repeated measure Anova on the error scores calculated for each condition.

Below we provide the specific details for each experiment, as well as, separately, the results and discussion.

Thus, Group I performed the conditions A, B, C, D and E in a randomised counterbalanced order. Group II performed two different blocks: in the first block they performed conditions A, B, C and in the second block conditions F and G. The order of the conditions was randomised and counterbalanced within each block.

3. Experiment 1

All participants (i.e. Group I and II) took part in Experiment 1 in which we investigated whether the manipulation of spatial attention via an auditory cue affects localisation judgments. Therefore, there were three different conditions - tone coming from the right (“tone right”), tone coming from the left (“tone left”) or no tone at all (“silent”). The conditions were randomised and counterbalanced across participants.

3.1. Procedure

The characteristics of the adaptation procedure and localisation task were identical to those described above in the general procedural section, in all cases resulting in an incongruence between the seen and real hand position. The arrow started at the participant's midline and travelled to the right edge of the screen, travelling at a constant speed horizontally in the direction of the right hand. In the conditions in which the auditory cue was played (i.e. conditions A and B) each time that the arrow started moving, a 44.1 kHz tone (duration 0.1 sec, downloaded from www.soundjay.com/button/sounds/beep-08a.mp3) was played. The tones originated from a loudspeaker placed on the left ('tone left') or on the right ('tone right') side of the MIRAGE system, approximately 70 cm away from the participant's chest, with the loudspeaker position standardised between participants. The loudspeaker was hidden behind the machine, such that it was not visible to the participants.

3.1. Results

A three (Tone: TL vs.TR vs. silent, S) by two (Time: T0 vs. T12) ANOVA again revealed a main effect of Time [F(1, 17)=17.49, p=0.001], but no effect of Tone [F(2, 34)=1.14, p=0.331] and no Time by Tone interaction [F(2, 34)=1.13, p=0.334] (Fig.1).

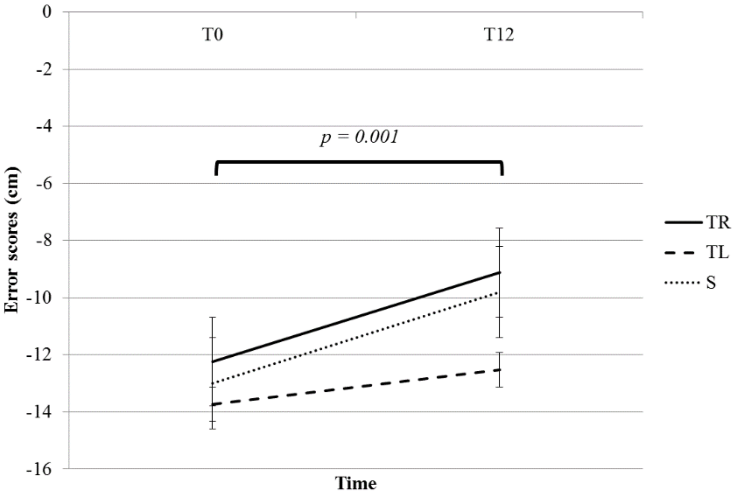


Figure 12 - The 3 (Tone: from the left, L vs. from the right, R vs. silent, S) by 2 (Time: T0 vs. T12) ANOVA performed on the error scores confirmed a significant main effect of Time (p=0.001) while nor the presence or the spatial location of the tone seemed to influence the localisation accuracy (p=0.331).

That is, the last localisation (T12: mean=-9.71 cm, SE=-0.95, 95% CI= -11.71 to -

7.71) was more accurate (i.e., less negative) than the first one (T0: mean=-12.52 cm, SE=0.44, 95% CI= -13.46 to -11.58)

4. Experiment 2

In the original DHT described in Newport and Gilpin (2011), the participants were asked to reach across with their left hand to touch their hidden right hand. In contrast, in Experiment 1 of the current study, participants were not allowed to move either hand following the adaptation procedure. Despite this, participants performed differently when the seen and actual hand positions were incongruent than when they were congruent, revealing an unconscious knowledge of the real right hand position. So, the question we addressed here is: can the reaching procedure modulate the perceived position of the hidden right hand by means of a conscious knowledge that the hand is “lost”? And if so, how?

We were also interested in whether spatial attention might have an additive effect when combined with relevant sensory feedback that provides information that the visual trace was inaccurate. Thus auditory cues identical to those used in Experiment 1 were added to the new conditions (reaching) in Experiment 2. In this way, the two new conditions were identical to the two conditions previously performed in Experiment 1, with only the reaching movement (versus no reach) manipulated. Since the reaching procedure reveals the presence of the illusion to the participants, it was necessary that Experiment 2 was always performed after Experiment 1.

Overall, the participants who took part in Experiment 2 performed two new conditions: “reach and tone left” and “reach and tone right”. The localisation judgements during these conditions were compared to the judgements during the conditions already performed in Experiment 1 and here labelled as “no reach tone left” (labelled “tone left” in Experiment 1) and “no reach tone right” (“tone right” in Experiment 1). The conditions were randomised and counterbalanced between participants.

4.1. Participants

Nine participants (4 female, mean age 29 ±8) took part in this experiment, all of whom had already participated in Experiment 1.

4.2. Procedure

The participants underwent two conditions in which we included both the auditory cue (i.e. the same used in Experiment 1) and the reaching movement. In the ‘reach’ trials, after completion of the adaptation procedure and once the right hand had been removed from view, participants were asked to perform a single direct reaching movement towards the position that they perceived their hidden right hand to be, before immediately returning their left hand to its original position. The experimenter gently guided the participants’ left hand back immediately after the reaching, to ensure the left hand was returned to the same position it was prior to reaching. After their left hand was again in its initial position, the localisation task commenced. The task localisation was the same as described in Experiment 1, that is, each time the arrow started moving from the centre of the screen towards the right an auditory cue was played (from the left or from the right). The two ‘reaching’ conditions were compared with the other two ‘tone’ conditions already performed in the Experiment 1.

4.3. Results

We analysed the error scores by means of a two (Reach: reach vs. no reach) by two (Time: T0 vs. T12) by two (Tone: right vs. left) repeated measure ANOVA .

The ANOVA detected main effects of Reach [η_p^2=0.631, F(1,8)=13.67, p=.006] and of Time [η_p^2=0.791, F(1,8)=30.19, p=.001], but no main effect of Tone [F(1,8)=.051, p=.828] (Fig. 2). There were no interactions (Reach x Time [F(1,8)=.484, p=.506], Reach x Tone [F(1,8)=.246, p=.633], Time x Tone [F(1,8)=.454, p=.519], and Reach x Time x Tone [F(1,8)=1.08, p=.329]). In analysing the effect of Reach, we found that the participants tended to be more accurate (i.e. less negative scores) when they reached for their right hand just prior to making the first localisation judgement

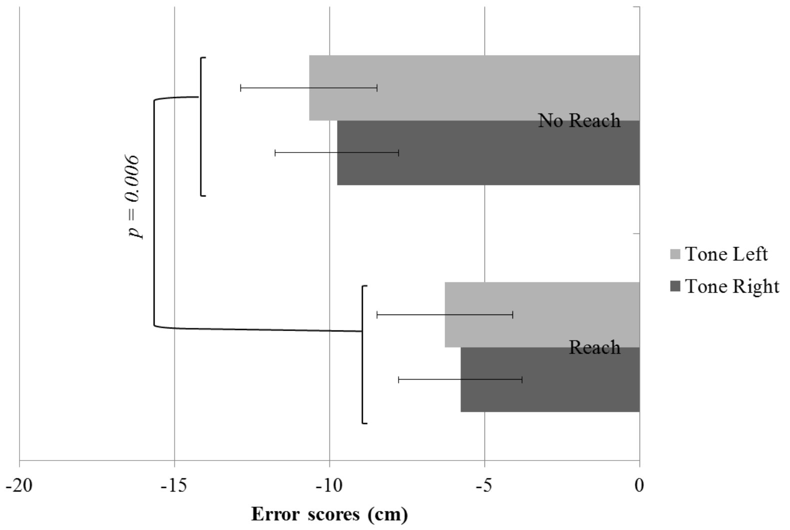


Figure 2 - The 2 levels (Reach, No Reach) by 2 (Time: T0, T12) by 2 (Tone: Right, Left) Anova detected significant main effects of Reach (p=.006), while the source position of the Tone did not resulted significant (p=0.828). Less negative scores are when participants were provided with the reaching movement (mean=-6.62 cm, SE=1.08, 95% CI= -9.12 to -4.12) than when they were not (mean=-1.11 cm, SE=1.11, 95% CI= -13.03 to -7.80).

(mean=-6.62 cm, SE=1.08, 95% CI= -9.12 to -4.12) than when they did not (mean=-1.11 cm, SE=1.11, 95% CI= -13.03 to -7.80).

The factor Time, in line with Experiment 1, did play a major role in localisation accuracy. Error scores were less negative for the final localisation (mean= -7.05 cm, SE=1.09, 95% CI: -9.56 to -4.53) than they were for the first localisation (mean= -10.04 cm, SE=0.91, 95% CI: -12.14 to -7.93), suggesting an increase in accuracy over time.

5. Experiment 3

One possible confounder of Experiment 2 relates to the order of conditions. We predicted that the reaching task would confound subsequent non-reaching tasks because participants would have conscious knowledge of the illusory trick we were playing. However, by always doing this condition second, we raise the possibility that the effect of reaching is in fact an effect of order. To clarify this possibility, in Experiment 3 participants underwent two randomised and counterbalanced conditions, in which we varied the presence of a reaching movement. In this way, even if a learning effect was present (as Experiment 3 was always performed after Experiment 1), it would bias both the Reach and No Reach conditions in the same way because they were performed in a randomised order. We expected to replicate the results of Experiment 2 and hypothesised that the reaching movement would cause an overall increase in localisation accuracy.

5.1. Participants

Nine healthy volunteers (4 female, mean age 37±8 years) participated. All had participated in Experiment 1 but not Experiment 2.

5.2. Procedure

Identical adaptation procedures occurred as per both Experiment 1 and 2. Immediately after the right hand disappeared from view, participants were either told to keep both of their hands perfectly still (i.e., the ‘no reach’ condition), or to reach across with their left hand to touch their hidden right hand (i.e. the ‘reach’ condition). This reaching movement was identical to that described in Experiment 2, except in this Experiment no auditory cues were present in either condition. The localisation task (same as in Experiment 1 and 2) commenced immediately after the left hand had returned to its original position following the reach (“reach”) or immediately after the right hand had disappeared from view (“no reach”).

5.3. Results

Experiment 3 replicated the results of Experiment 2. That is, a two (Reach: reach vs. no reach) by two (Time: T0 vs. T12) repeated measures ANOVA was performed on the error scores. Our data show significant main effects of Reach [η_p^2=0.531, F(1, 8)=9.048, p=0.017] and Time [η_p^2=0.478, F(1, 8)=7.33, p=0.027] (Fig. 3), but no significant interaction between the two factors [F(1, 8)=0.18, p=.896]. Mean error in the “reach” condition was -9.12 cm (SE=0.82, 95% CI= -11.02 to -7.21) and mean error in the ‘no reach’ condition was -11.74 cm (SE=0.85, 95% CI= -13.70 to -9.78). In line with our previous findings, our analysis also detected a significant change in accuracy due to the factor Time. Specifically, the amount of error in the final

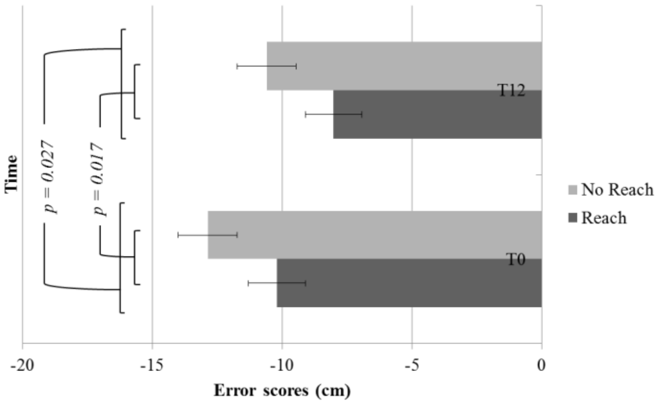


Figure 3 - The 2 (Reach: reach, no reach) by 2 (Time: T0, T12) ANOVA showed again a significant effect of Time (p=0.027) over the error scores. Besides, the reaching movement as well seems to significantly affect the localisation accuracy (p=0.017).

localisation (i.e., T12: mean=-9.32 cm, SE=1.01, 95% CI= -11.65 to -7.01) was smaller than in the first localisation (i.e., T0: mean=-11.54 cm, SE=0.58, 95% CI= -12.88 to -10.20). Thus, there was an increase in accuracy over time. However, that there was no significant interaction between Reach and Time suggests that updated sensory information (provided by Reach) has the greatest effect immediately after it is received.

6. Discussion

With the present study we wanted to clarify the relationship between attention and proprioception and their specific roles in locating one's own hidden arm when the visual trace is inaccurate. Furthermore, we wanted to investigate the role of awareness in self-localisation. In order to investigate this, we designed three separate experiments in which we manipulated visual and auditory-cued spatial attention as well as the participants' awareness of the presence of the illusion. Our findings clearly exclude an artefact of the localisation task as contributing to the results and also show that the manipulation of spatial attention does not interfere with accuracy in the localisation task. Conversely but consistent with MLE theory, receiving feedback that the visual trace was inaccurate did result in a heavier reliance on proprioception during localisation judgements, even though most participants were not consciously aware of where their hidden right hand might be.

Our hypotheses that spatial attention would not significantly alter the accuracy of hand localisation judgements, were supported, as evidenced by no effect of changing arrow direction (Experiment 1), or preceding the judgement with an auditory cue from one side or the other (Experiment 1 and 2), on localisation accuracy. Our results also replicated our previous observation (see Study 2) and strengthen the proposal that proprioception plays a powerful role in localising the body when vision is or suddenly becomes unreliable.

Furthermore, we wanted to investigate the hypothesis that a reaching movement towards the hidden right hand (when seen and real hand positions were incongruent) would increase localisation accuracy (Experiment 2 and 3). Our data confirm this hypothesis, revealing more accurate localisations when the reaching movement was performed than when it was not. In the original DHT paradigm (Newport & Gilpin, 2011) the procedure included the reaching movement, that is, reaching across with the left hand to touch the hidden right hand. Failure to find one's own hidden hand led to sensations of disownership over the hidden limb. We previously compared localisation accuracy when the illusion was present and when it was not, but participants did not perform this reaching movement (Study 2). When informed of the illusion after the experiment, participants reported that they were completely unaware this illusion had taken place. In particular our hypothesis was that participants, following the reaching movement, would realise the real position of their hand and rapidly shift their localisations rightwards (i.e. towards their hidden hand). Our results supported this hypothesis, revealing more accurate localisations following the reaching movement. At the end of the experimental session, we interviewed the participants asking them where they thought their hand was in the moment that it 'disappeared' and they could not touch it. Surprisingly, only a few participants realised that the hand was located further to the right, reporting the sensation that they "did not reach far enough". The majority (12 out of 18) of participants stated that they were unsure about hand location, and others felt that the hand was closer to the midline (i.e. further left) than the spot they actually touched. Two participants also stated that the hand was actually more central than where they touched, such that they crossed over the arms. One participant reported that the hidden hand was moved by the experimenter to another level or compartment inside MIRAGE, such that the spot she touched was correct on the horizontal plane, but not on the vertical. Crucially, regardless of beliefs about actual hand position, participants consistently located the hand more rightwards following the reach than when no reach was made. This finding suggests that while participants in fact remained unaware that any deception taken place, some unconscious process led them to shift their localisations to the right. That is, a top down process in which participants attempted to find a cognitive explanation for the trick is not sufficient to explain their performance. Previous studies using illusions to deceive hand position or features of the body part using tendon vibrations (Ehrsson, Kito, Sadato, Passingham, & Naito, 2005; Lackner, 1988; Longo, Kammers, Gomi, Tsakiris, & Haggard, 2009) have found that after inducing a new proprioceptive input, participants are able to rapidly readjust their body representation and position accordingly. For example, Lackner (1988) showed that it is possible to modify the perceived orientation of the entire body just by vibrating the biceps tendon. This suggests that proprioceptive information alone has the ability to significantly alter body localisation and provides support for our findings.

It should also be considered that the sensory motor system offers information about the position of different body parts in relation to each other (e.g., Dijkerman & de Haan, 2007). When the left hand performs the reaching movement, the sensory motor system is required to update the current position of the body because the right hand is not located where it was last seen. This recalibration of body position could, in turn, initiate the reliance on proprioception in making hand localisation judgements. However, these two explanations are not necessary mutually exclusive. It could be argued that two different kind of awareness are involved: participants are crucially guided by a ‘bottom up’ driven awareness, triggered by the movement itself of the participants left hand, that causes the sensory motor system to update the current body position and to shift localisations towards the correct position of the hidden hand. In addition to this, a ‘top down’ driven awareness (see, for example Varraine, Bonnard, & Pailhous, 2002) occurs when participants consciously realise that they have been deceived. Investigating the mechanism underlying the increased accuracy following the reaching movement was beyond the scope of this experiment, but it would be an interesting avenue to pursue in future research. If the bottom up recalibration theory were true, we would expect an increase in accuracy not only after a movement specifically directed to the hidden hand but also after any generic reaching movement, either active or passive, as this would still be sufficient to induce the sensory motor system to update information about body position.

Our results confirm and extend what was previously found by Newport and Gilpin in the original description of the illusion (2011). These authors investigated the presence of disownership towards the hidden hand following the illusion. Interestingly, the participants felt as the hand was actually disappeared when they reached across and failed to touch it. None of the participants were able to accurately identify the position of the hidden hand at the end of the experiment and as assessed by negligible skin conductance responses (SCR) of the hidden hand elicited during illusory stabbing of its true and last seen location), physiological signs of disownership were present.

In line with their results, we also found that the reaching movement towards the hidden hand represents the core factor of the entire illusion, given the increase in accuracy in the trials when the reaching movement was performed compared to when it was not. However, Newport and Gilpin’s experiment also showed that there is no physiological evidence that the participants – consciously or not – actually locate their own hand in a certain spot (e.g. where they last saw it) instead of another (e.g. where is actually located), showing similar SCRs when the two spots were threatened. In the present work, though, we suggested that when participants’ sensory motor system is explicitly updated (by mean of the reaching movement), being somehow aware of the real position of their right hand, they start to rely on proprioception , being more accurate. This might suggest a dissociation between the physiological and the sensory motor response to the same task, at least earlier after the reaching movement. In fact, our findings show that the sensorimotor recalibration due to the reaching movement occurs early in time, as supported by the lack of interaction between the factors Time and Reach. It might be that a physiological response simply requires more time to readapt. Furthermore, when the position of one's own limb is unknown, one cannot be sure if (and where) a response to a threatening stimulus is needed. In other words, as in Newport and Gilpin's study, in the present experiment the participants felt unsure about the real position of their hand, despite their localisation responses and the fact of knowing that an illusion was performed. Thus, we propose that the 'disappeared' hand is not actually disowned, as initially hypothesised. Rather, the participants might simply not show any SC response because they did not know where their hand was, and so, whether the stimulus was actually threatening their hand or not. After inducing the RHI a cooling effect of the hand involved in the illusion correlated with the strength of the illusion was detected (Moseley et al., 2008). The authors interpreted this as a consequence of taking ownership of the artificial limb and a consequent disownership of the real limb. This means also that is possible separate the sensations of owing a limb from knowing where that limb is. This simulates some pathological conditions in which the patients' sense of ownership over their affected body part is intact (e.g. in case of deafferentation, see Cole & Paillard, 1998), but they need visual monitoring in order to accurately localise it and their sense of touch is disrupted as well. This is certainly related with the body matrix concept, according to which one own's body is rather represented as a dynamic space where the body can be (Moseley, Gallace, Spence, 2012).

The MLE theory (Ernst & Banks, 2002) can provide a convincing explanation for the observed effects. It has been widely demonstrated that vision plays a crucial role in self-localisation, with deafferented patients reporting that they need to visually monitor their limb in order to know its position in space (Cole & Paillard, 1998). Vision is typically a reliable source of information, and thus most of the time it is prioritized over all the other senses. However, when vision becomes less stable, such as in a dark room, one rapidly takes into account this loss of reliability and switches the CNS to prioritise a more stable sense, for example proprioception. Blind individuals might also learn to use sounds in order to navigate through space by means of the echolocation (for a recent overview see Kolarik, Cirstea, Pardhan, & Moore, 2014). In this case, hearing is prioritized over the other senses, as vision is not available. Interestingly, in the case of people that are both deaf and blind, who cannot rely on hearing to locate objects in space, a technique involving touch has also been developed since early 1970s (see Bach-y-Rita, 2004 for a review)

An increasing body of research suggests that the information processing occurring within the CNS can be manipulated in multiple ways. For example, in the rubber hand illusion (RHI, Botvinick & Cohen, 1998) the sense of ownership over one's own limb is transferred to a fake hand, and the perceived position of the real limb is thought to be shifted towards that of the fake limb (i.e. proprioceptive drift, see for example also Makin, Holmes, & Ehrsson, 2008; Tsakiris & Haggard, 2005). Similarly, in the DHT, the CNS is deceived via multisensory illusion to miscalculate hand position. The current study extends these findings, demonstrating that the CNS is capable of adjusting its estimation over time, according to the MLE, to create a more accurate estimation of body position using the most reliable sensory information. Van Beers et al.'s model of the integration between proprioceptive and visual position information, even underlining the fact that the weights are assigned based on the precision of each modality (assigning more weight to the most precise one), does not exclude the possibility that attention can still influence how these weights are used (van Beers, 1999). Our results, indeed, confirm that attention is included in the process of hand localisation. Furthermore, our findings highlight the alternation between the role of vision and proprioception and show that the CNS is able to re-calculate the position of the hidden hand on the base of new information (after the reaching movement), re-distributing the weights and assigning more to proprioception than to vision.

Taken together, our results support our hypothesis that when the visual trace is inaccurate participants tend to rely more heavily on proprioception than when vision is accurate. The role of attention in localising a body part is only marginal and appears to be driven by the portion of the space attended rather than specific visual or auditory cues.

CHAPTER V

STUDY IV

Abbreviations used in this chapter:

EMG, Electromyography

Study 4: No telescoping effect with dual tendon vibration.

Study 4 has been conducted in collaboration with Sarah B. Wallwork (University of South Australia), Tasha R. Stanton (University of South Australia and Neuroscience Research Australia), Alberto Gallace (University of Milano-Bicocca and NeuroMI) and G. Lorimer Moseley (University of South Australia, Neuroscience Research Australia and PainAdelaide).

1. Introduction

Various studies have investigated the effect of visually resizing one’s own body part on the processing of information regarding that body part. For example, it has been shown that the tactile threshold measured on the arm is improved when the image of that arm is magnified (Kennett, Taylor-Clarke, & Haggard, 2001). Furthermore, in people with pathological limb pain, less pain is evoked by movement when their affected arm appears to be smaller (and more pain is evoked when it appears to be larger) than its normal size (Moseley, Gallace, & Spence, 2012; Moseley, Parsons, & Spence, 2008). In healthy controls, visual distortion of body size has an analgesic effect whether the distortion shrinks or magnifies the visual appearance of the limb (Mancini, Longo, Kammers, & Haggard, 2011).

Research has also demonstrated that the perceived orientation of limbs can be modulated by vibrating the tendons that act on the limb (Lackner, 1988). For example at the elbow, vibrating the flexor biceps tendon while keeping the arm still (i.e. strapped in place), induces the perceptual illusion of elbow extension. Conversely, if the extensor triceps tendon is vibrated, the opposite, illusory elbow flexion, occurs (Eklund, 1972; Goodwin, McCloskey, & Matthews, 1972). These illusions can also induce physiologically impossible perceptions. For example, in the so-called “Pinocchio illusion”, vibrating biceps tendon while holding one’s nose can induce the illusion of one’s nose lengthening as the hand is perceived moving away from one’s own head (Lackner, 1988). Similarly, holding one's own finger, while the biceps tendon of the opposite arm is vibrated, induces both illusory extension of the vibrated elbow and an impossible stretching of the finger being held (de Vignemont, Ehrsson, & Haggard, 2005; Lackner, 1988). Finally, such illusions penetrate tactile judgements, with tactile distances measured on the finger being perceived as longer during the finger stretching illusion than under control conditions (de Vignemont et al., 2005). How then might the brain interpret vibration-induced input arriving simultaneously from the flexors and extensors of the same joint? This question was investigated almost thirty years ago by simultaneous vibration of the biceps and triceps tendons of one elbow (Gilhodes et al., 1986). Gilhodes and colleagues reported no illusory movement and no associated muscle activity. However, the issue was revisited recently to an apparently contrasting result - a "telescoping" illusion of the forearm shrinking towards the elbow (Longo et al., 2009). Those authors attributed their result to the inconsistent nature of proprioceptive cues induced by simultaneous vibration of the agonistic tendons and a consequent readjustment of the cortical representation of limb alignment.

We see this as a very interesting development, not least because of its clear relevance to the perplexing observation of telescoping phantom limbs reported by some amputees (Flor, 2002), a link clearly made by Longo et al.(2009). That the original study (Gilhodes et al., 1986) evaluated perceived shifts in only the transverse plane left open the possibility that the results were confounded by a sideward drift in perceived hand location, a drift that might be unrelated to tendon manipulations (see Study 2 and 3). Thus, we sought to interrogate this phenomenon in the sagittal plane by also clarifying aspects not made clear by previous work. For example, Longo et al. (2009) assessed on the horizontal axis the effects of biceps vibration, dual tendon vibration (i.e. biceps and triceps) and no vibration, but did not also assess the effects of triceps vibration. Further, they assessed the perceived position of the limb on the horizontal axis by means of one task (i.e. a pointing task) and on the vertical axis by means of another task (i.e. a matching task). However, by not including a triceps vibration condition, only considering results coming from a pointing task and basing their conclusions on only the findings on the horizontal axis, we contend that the Longo et al. (2009) study leaves open the possibility that localisation errors during dual vibration simply reflect a sensation of stabilised position and, therefore, a more accurate perception, as declared by Gilhodes et al. (1986). On the grounds that our perceived bodily alignments concur with biomechanical constraints (Moseley & Brugger, 2009), we contend that both vertical (Y) and horizontal (X) coordinates would be required to evaluate shifts in perceived location and to differentiate telescoping from illusory joint rotation.

We compared the X and Y coordinates of perceived location of the hand during four different conditions - biceps vibration, triceps vibration, dual vibration and no vibration. We hypothesised, first, that the perceived location of the hand would align with predictions from previous literature – as though the elbow had extended during biceps tendon vibration and as though it had flexed during triceps tendon vibration. The key hypothesis however, was that dual vibration would induce a shift in perceived location of the hand along the X-axis but not the Y-axis – a telescoping effect – as reported by Longo et al. (2009).

2. Materials and Methods

Our main aim was to verify the presence of a telescoping effect induced by a dual tendon stimulation. To do this we introduced new elements to the original experiment by Longo et al. (2009). In particular, we applied changes to the sample (size and composition), the task employed for the localization of the vibrated arm, and analysed measurements on both X and Y axis for each localization. Finally, we also evaluated a condition where the triceps tendon alone was vibrated. These changes are fully described in Table S1 (Appendix 2).

Participants

Thirteen participants (5 female, mean ± SD age = 34 ± 10, range 21-51) volunteered for this repeated measures randomised experiment. Sample size was calculated a priori according to detecting with 95% confidence an effect size comparable to that reported previously (Gilhodes et al., 1986; Lackner, 1988; Longo et al., 2009). All participants had normal, or corrected to normal, visual acuity and were right handed (self-reported). They had no current or past neurological impairment involving the upper limbs, and no current pain or history of a significant pain disorder. They were naïve about the purpose of the study.

All the participants gave written informed consent prior to participation. The study was performed in accordance with the ethical standards laid down in the 1991 Declaration of Helsinki and was approved by the institutional Human Research Ethics Committee.

Apparatus and experimental setup

The participants were comfortably seated on a stool, facing the vertical edge of a panel that was aligned with their body midline. They were asked to place their right hand on the right vertical surface of the panel, in a way that the tip of their right index finger (i.e. the “target finger”) made contact with a push pin inserted into the panel about 30 cm away from the edge. The participants’ right arm and hand were then placed into a looped piece of fabric that was pinned on the panel, such that their elbow formed a ~150o angle (Fig. 1a).

In this way the participant’s right hand and arm were kept in position and slightly supported by the piece of fabric, leaving the elbow to protrude from the panel. The position of the stool was adjusted for each participant, according to their height and to the length of their arms, in order to standardise these parameters between participants. On the left surface of the panel (Fig. 1b), two perpendicular 40 cm axis were drawn such that their origin corresponded with the position of the participant’s target finger on the other side of the panel.

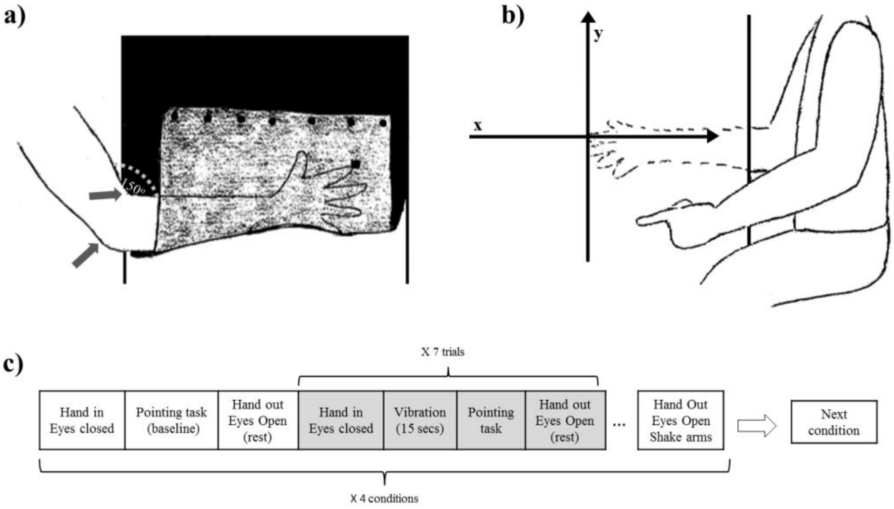


Figure 1 - (a) The participant's right hand was placed on the right surface of a panel, in a way that the left fingertip made contact with a pin inserted on the panel itself. The arm and hand were then wrapped with a piece of fabric so that the position was kept constant and the participant's right elbow made a ~150º angle. Vibration was applied at two locations indicated by the arrows: the biceps tendons and the triceps tendon. A trained physiotherapist identified the two locations and delivered the stimuli. (b) On the left surface of the panel, two axis were drawn such that their intersection corresponded to the position of their left index fingertip on the other side of the panel. During the localisation task, participants were asked to point with their left index finger where they felt their right index fingertip to be.
(c) A timeline indicating the progression of each condition.

The ~40Hz vibration stimuli were delivered over the tendon, between its insertion and the musculotendinous junction, of the prime elbow flexor (biceps brachii ulnar attachment) and the elbow extensor (triceps brachii) of the right arm. Stimuli were delivered by a trained physiotherapist, using commercially available General Purpose Massagers (www.drgraeme.com).

Procedure

The participants underwent four different conditions - one control (No vibration) and three experimental (Biceps, Triceps and Dual vibration). Each condition included an initial baseline measure of the target finger position, followed by seven trials. For each trial a trained physiotherapist applied a 15 second vibratory stimulation to either the triceps, biceps or both tendons simultaneously. Then the participants were then asked to point at the target right index finger with the left index finger (on the left surface of the panel) with the eyes closed (the same procedure was employed to acquire the baseline measure). The vibration lasted until the participant completed the pointing task (on average approximately 18 seconds). An experimenter then recorded the X and Y axis coordinates and thus the finger position indicated by the participants. After the measures were recorded, the participants were asked to open their eyes, take the arm out of the sling and rest both arms on their lap for a few seconds before the next trial. Between each pair of conditions, the participants were asked to open their eyes and to "shake" both their arms before engaging in the next condition.

The participants, thus, underwent four different blocks (one condition per block), in counterbalanced randomised order. The conditions adopted were: vibratory stimulation on the biceps tendon (Biceps vibration condition); vibratory stimulation of the triceps tendon (Triceps vibration condition); synchronous vibratory stimulation of both tendons (Dual vibration condition); no vibration control (No vibration condition). Although no vibration was applied, the participants kept the left hand and arm inside the sling and their eyes closed, as they did for the other conditions.

Data analysis

Each pointing response was measured as a shift from the origin (i.e. correct position of the target finger) such that, for each localisation, errors reflected both X and Y coordinates. We conducted two repeated measures ANOVAs that compared the error values on the X axis and on the Y axis across the four conditions (Factor Condition: Biceps vibration, Triceps vibration, Dual vibration, No vibration).

3. Results

For the X axis, we found a significant main effect of Vibration [$F(3,36)=46.9$, $p<0.001$, $\eta 2=.796$]. All the error values were positive and significantly different from zero (see Fig.2) (in particular Dual vibration: M= 1.82 cm, SE=0.55, 95% CI 0.62 to 3.03), meaning that in all the conditions the target finger's actual position was significantly mislocalised towards the body. Furthermore, a pairwise planned comparison revealed significantly larger errors for the Triceps vibration than for the Biceps vibration ($p=0.002$, 95% CI 0.769 to 2.621); than for the Dual vibration (p<0.001, 95% CI 3.33 to 5.51); and No vibration (p<0.001, 95% CI 2.72 to 4.71). In turn, the participants showed significantly larger errors for the Biceps vibration than for the Dual vibration (p<0.001, 95% CI 2.02 to 3.43) and No vibration (p<0.001, 95% CI 1.14 to 2.90) (Fig. 2). No significant difference in the amount of error on the X axis (i.e. towards the body) was found between the Dual vibration and No vibration conditions (p=0.067, 95% CI -1.48 to 0.06).

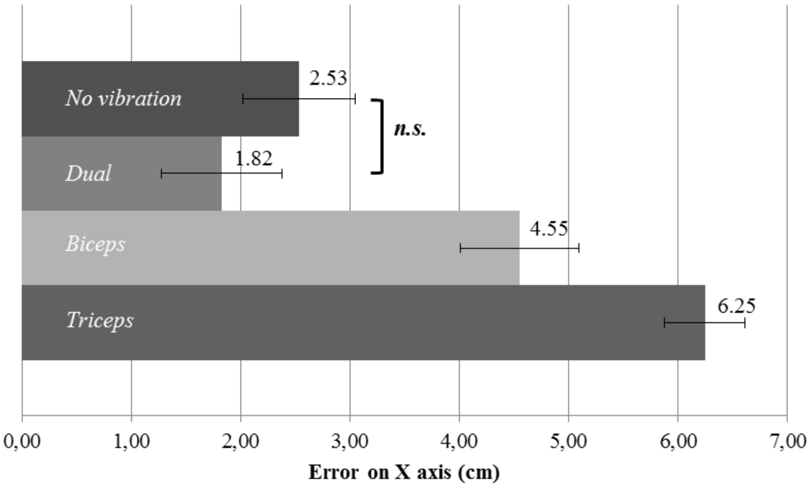


Figure 2 – “0” represents the origin of the axis and the position of the right index fingertip. The scores represent the mean error during the pointing task. In particular, higher scores describe larger error towards the elbow, such that the Triceps stimulation condition lead to the largest shift towards the body on the X axis (i.e. in this condition the left fingertip was perceived farthest from its real position) compared to the Biceps (p=0.002), the Dual (p<0.001) and the No vibration (p<0.001) conditions. All the other comparisons resulted significant, except Dual vs. No vibration (p=0.067). (Triceps: M=6.24 cm, SE=0.37, 95% CI 5.44 to 7.05; Biceps: M= 4.55 cm, SE=0.54, 95% CI 3.37 to 5.74; Dual: M= 1.82 cm, SE=0.55, 95% CI 0.62 to 3.03; No vibration M= 1.82 cm, SE=0.51, 95% CI 1.41 to 3.65). The Dual stimulation, thus, seems to produce the smallest error and is not significantly different from the condition where no stimulation was applied at all. The bars represent the standard error and the top of each histogram bar the mean is displayed.

As would be predicted, the Triceps vibration induced the largest mislocalisation of the target finger towards the body along the X axis. A significant shift in the same direction, although smaller, was also induced by the Biceps vibration. Conversely, during the Dual vibration the target finger was not perceived significantly more shifted towards the body than in the control (No vibration) condition, not supporting

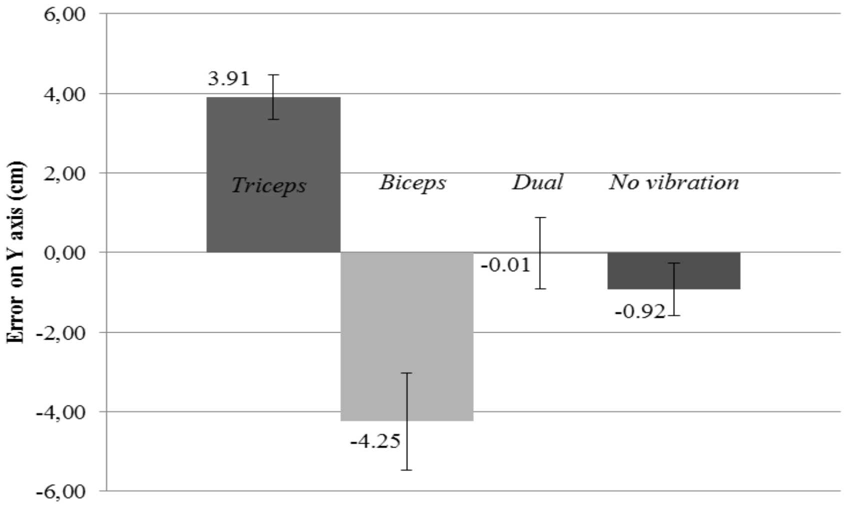


Figure 3 – ‘0’ represents the position of the target finger on the right surface of the panel. The scores represent the mean error of the pointing task on the Y axis. There is a clear and significant upward bias induced by the stimulation of the triceps tendon and a significant downward bias induced by the stimulation of the biceps tendon. All the comparison resulted significant. (Triceps: M=3.91 cm, SE=0.56, 95% CI 2.69 to 5.13; Biceps: M= -4.25 cm, SE=1.22, 95% CI -6.91 to -1.59) (Dual: M=-0.014 cm, SE=0.89, 95% CI -1.95 to 1.93; None: M= -0.92 cm, SE=0.67, 95% CI -2.38 to 0.53). In particular, the Dual stimulation seemed to produce the smaller error on the Y axis. The mean errors in the Dual and No vibration conditions are not significantly different from 0. The bars represent the standard error and for each histogram bar the mean is displayed.

our experimental hypothesis regarding telescoping (Longo et al., 2009). To re-iterate, under all conditions the hand was mislocalised towards the body.

On the Y axis there was also a significant effect of Vibration [F(3,36)=33.5, p<.001, η2=.736]. The error values for the Triceps vibration and Biceps vibration conditions were significantly different from zero, while in both the Dual vibration and No vibration conditions they were not (Dual vibration: M=-0.014 cm, SE=0.89, 95% CI -1.95 to 1.93; No vibration: M= -0.92 cm, SE=0.67, 95% CI -2.38 to 0.53). Furthermore, a pairwise planned comparison showed that the error values in the Triceps vibration condition were larger (i.e. more positive error values) than the error values in the Biceps vibration (p<0.001, 95% CI 5.53 to 10.78), Dual vibration (p<0.001, 95% CI 2.16 to 5.69), and No vibration conditions (p<0.001, 95% CI 3.26 to 6.41). We also found that the error scores in the Biceps vibration condition were larger (i.e. more negative error values) than the Dual vibration (p<0.001, 95% CI -5.88 to -2.85) and the No vibration (p=0.002, 95% CI -5.15 to -1.49).

The error scores in the Dual vibration condition were larger (i.e. more positive) than the error scores in the No vibration condition (p=0.025, 95% CI 0.133 to 1.69) (Fig. 3). Finally, in order to compare the amount of error between the Triceps vibration and Biceps vibration conditions, we conducted a paired sample t-test on the absolute values of the error for each condition. There was no difference in the amount of error between the Triceps vibration (M=3.91, SD=2.02) and Biceps vibration (M=5.32, SD=2.87) conditions on the Y axis [t(12)=-1.307, p=0.216]. This result clearly shows that the stimulation of the biceps and triceps tendons did not vary for the absolute amount of error, but only for the direction of the error (i.e. upward for the triceps and downward for the biceps). The amount of error was in fact similar in both the conditions.

Our data univocally show that the single vibration of the brachial tendons induces an equal and opposite mislocalisation of the target finger. In particular, triceps tendon induces a large upward shift (i.e. illusory flexion) while the biceps tendon a downward shift (i.e. illusory extension). In the Dual vibration and No vibration conditions the participants did not perceived the target finger as shifted from its real position, but they were more accurate in the Dual vibration than they were in the No vibration conditions. The pattern of results across conditions is presented graphically in Fig. 4: the triceps vibration induces the sensation of elbow flexion, leading the index finger to be perceived upward and closer to the body; the biceps vibration induces the sensation of elbow extension, with the index finger being perceived downward and again closer to the body; the most accurate perception is the one induced by the vibration of both tendons simultaneously.

4. Discussion

We hypothesised that, in line with Longo and colleagues' findings (Longo et al., 2009), a simultaneous vibration of the triceps and biceps brachial tendons would induce an illusion of the arm shrinking towards the elbow - the so-called 'telescoping effect'. Furthermore, we hypothesised that the vibration of the biceps brachial tendon would produce the illusion of arm extension, while vibration of the triceps brachial tendon an illusion of arm flexion. Our results show that the way the body is perceived does not change during dual tendon stimulation, but it seems to result in a more accurate perception of the limb position, as compared to single stimulations. To our knowledge, only two studies (Longo et al., 2009; Gilhodes et al., 1986) have previously observed the effects of the dual tendon vibrations on the perception of one's own limb. In particular, Gilhodes and colleagues (1986) demonstrated that during the dual vibration there is no EMG activity in the muscles involved. In contrast, muscular activity can be recorded on the antagonist muscle when the agonist muscle tendon is vibrated (i.e. activity of the biceps when the triceps tendon was vibrated and vice versa). We did not investigate muscle activation. However, from a perceptual perspective, our results appear more in line with those of Gilhodes et al. (1986) than with those of Longo et al. (2009). That is, when both tendons were vibrated at the same frequency, participants in our study did not perceive any illusory movement. Gilhodes et al. (1986) interpreted this lack of effect as reflecting a perception of stable position induced by having to balance the incoherent cues coming from the muscle spindles. Longo et al. (2009) reported a contrasting effect and had an opposite interpretation - that the dual vibration induces an error that manifests as telescoping, similar to that observed for the phantom limb by some amputees (Flor, 2002).

Gravity would normally cause a resting forearm to extend downwards. In this study, the participant's arm was probably not completely at rest because it was suspended in the sagittal plane by means of a piece of fabric pinned at the panel, with the simple aim of keeping the right index finger in place (as also used by Longo et al., 2009). We suspect that the participants probably had some level of biceps activity in order to avoid an excessive burden on the piece of fabric, although neither we, nor Longo et al. (2009) verified this. This may have been a problem because it has been shown that sustained flexion of the biceps muscle produces changes in perceived limb position in the opposite direction (i.e. downward errors) (Proske & Gandevia, 2012; Winter, Allen, & Proske, 2005). However, this possibility actually adds weight to our main finding because localisation was more accurate during the dual stimulation condition than when it was simply resting – perhaps the dual vibration overrides the sustained flexor activity effect.

On the X axis, localisation responses were more accurate for the Dual vibration conditions than they were for the other experimental conditions (Biceps and Triceps vibration) and similar to the control condition (No vibration). Furthermore, the displacement along the X axis was slightly but significantly larger for the triceps than for the biceps stimulation. Perhaps this difference occurs because the triceps is the only elbow extensor. In contrast, biceps also has an aponeurotic attachment to the forearm and even then is not the only flexor. The brachioradialis muscle is an important flexor when the forearm is in pronation (Murray, Delp, & Buchanan, 1995) as it was for our study and that of Longo et al. (2009). That the brain does not have confirmatory proprioceptive input from brachioradialis during this illusion might dilute the effects on perceived alignment of the elbow. Even so, this explanation does not account for the fact that, on the Y axis, error scores produced by the biceps and triceps tendons vibration were symmetrical and not significantly different in absolute terms. Further investigations are needed to clarify this discrepancy. Our findings also suggest a general trend toward participants perceiving the target finger as being closer to the body than it really is. In line with this, previous research showed the perception of one’s own limb during visual occlusion tends naturally to drift towards the body (Wann & Ibrahim, 1992). Interestingly, the simultaneous stimulation of the biceps and triceps tendons produced the smallest drift on the X axis, confirming a more balanced and accurate localisation under this condition.

Our results seem to be in line with Gilhodes et al.’s results and they do not support the existence of a shrinking effect caused by the dual stimulation of the brachial tendons.

In fact, our sample did not show any telescoping effect of the forearm under the dual vibration condition, as measured with a pointing task. Our data actually appear opposite, with the farthest localisation judgement from the body and most accurate localisation response during the dual condition. Why might our results differ from those of Longo et al. (2009)? As stated earlier, we think the most obvious reason probably relates to our analysis of both Y axis and X axis data for the pointing task as well as standardising assessments across all vibration conditions. We contend that, to interpret X axis shifts as telescoping without verifying Y axis coordinates, requires the assumption that there is indeed no Y axis shift. One possible contributor to the contrasting results also relates to the choice of participants. Longo et al. (2009) had only female participants, whereas we had both females and males. Although a gender-specific effect is unlikely, recent data (Adamo, Scotland, & Martin, 2012), showing that women seem to be more likely than men to report illusions after vibratory stimulation of the tendons, means that we cannot completely exclude that an exclusively female sample might represent a bias in the outcome. Evaluating a gender-based influence on results was beyond the scope, and power, of this experiment.

We propose a new interpretation for the Dual tendon vibration illusion. When our data

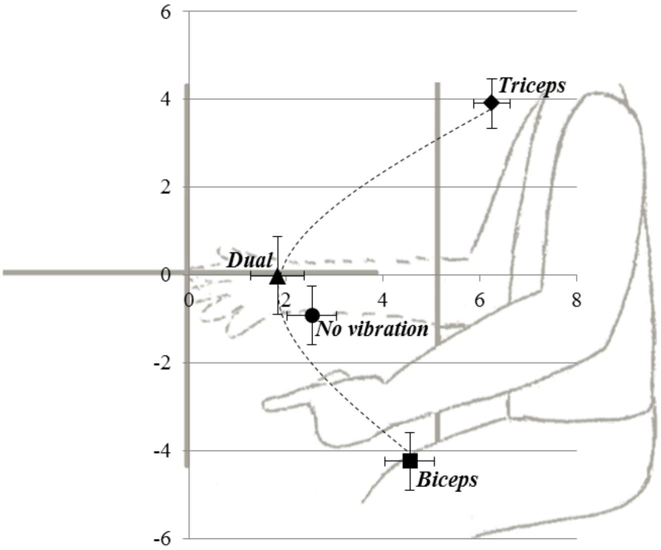


Figure 4 – The errors measured on the X and Y axis are plotted together on a Cartesian system. It appears clear that in our sample, the single tendon vibration induced an illusion extension (Biceps vibration) and flexion (Triceps vibration) of the arm. Stimulating both the tendons simultaneously (Dual vibration) leads to the best estimation of the arm position, supporting the idea that this potentially incoherent stimulation is resolved as a balanced position of the arm.

are plotted on a Cartesian plane (i.e. with the mean of the errors on the X and on the Y axis merged together), as in Fig. 4, it appears quite clear that the triceps stimulation creates the illusory sensation of flexing the arm, with the index finger being perceived upward and closer to the body. This explains why the vibration of the biceps and triceps tendons alone led to a larger amount of error on the X axis. In fact, both the flexion and the extension of the arm require the arm itself to move towards the body, even though in the opposite direction.

Thus, our results are in line with the findings that when both tendons are vibrated at the same time and at the same intensity, no sensation of movement is perceived and, presumably, the muscles remain inactive (Gilhodes et al., 1986). The arm would then be in balance, in a position that is half way through the extreme upward (full flexion of the arm and triceps stimulation) and the extreme downward (full extension of the arm and biceps stimulation) positions. We can conclude that the contrasting information coming from the arm muscle spindles is reinterpreted as a static balanced situation, in which there is actually no need to readjust the body representation. Thus, in the general population, equal and opposite information coming from two antagonist muscles is resolved as a balance in the body location. Perhaps this suggests that the brain does not use absolute information coming from each tendon, but instead integrates different pieces of information coming for different tendons (and more in general information coming from the limb) and, on the basis of this computation, determines the arm position.

CHAPTER VI

A PILOT STUDY

Abbreviations used in this chapter:

CNS, Central Nervous System; RHI, Rubber Hand Illusion; EAT, Eating Attitude Test; BUT, Body Uneasiness Test

A pilot study: Evaluating the effect of seeing human body images on people's ability to estimate their own body size and on body satisfaction

1. Introduction

The studies presented in this thesis clearly support the advantage of using bodily illusions as an effective tool to investigate the "self" and the body representation. One of the most relevant conclusion arising from the study reported so far is that vision plays a crucial role in the way in which people perceive themselves, both in terms of where their body parts are (i.e. self-localisation) and which body parts belong to them (i.e. body ownership). Thus, it does not sound hyperbolic to affirm that "we believe to be what (i.e., the body) we see", primarily. Extending this view to our social life, one should not fail to notice that people tend to take as models those bodies that the society suggests to be the most appropriate ones.

The idea underpinning this project is to try to explore the feasibility of a series of experiment in which visual images are used to induce changes in a participant's body image. More specifically, we would like to understand how implicit can be a manipulation in order to induce a modification in body representation. Can we measure this modification by using a virtual scale model? Are there other variables that need to be taken into account?

2. Theoretical background

The Central Nervous System (CNS) plays a key role in building and updating a representation of one's body by integrating information from different senses. During a person's lifetime the body continuously changes shape, size, aspect (especially during adolescence) and position (Gallace & Spence, 2014). For this very reason, our body representation must be extremely malleable and ready to adapt quickly. Nevertheless, this plasticity may also lead to pathological consequences (e.g. phantom limb pain).

Interestingly, one of the easiest way to rapidly and temporarily manipulate the body representation is through illusions (see also Chapters III, IV and V). In general, there are illusions, where the position of a stimulus is perceived to be far from its physical origin. For example, ventriloquists fool the audience in thinking that a puppet is speaking when the voice actually comes from the puppet master. The audience interpretation of the reality is thus guided in this case by the visual cues (and, to a lesser extent, by auditory cues). Other forms of illusions, confirm the predominant role of vision in the interpretation of the surrounding world (e.g. Wang, Miletich, Ramsey, & Samson, 2014). Crucially, most of the bodily illusions (such as the RHI, for example) are based on this concept: we believe what our eyes tell us to believe. A full review of the bodily illusions used in research and in clinical setting is beyond the purpose of this work, instead we will focus on the manipulations of the size of one's own body. This has been previously done by showing to participants a body part that is enlarged or shrunk by means of lenses (Moseley, Parsons, & Spence, 2008) or by means of virtual reality devices (e.g. Banakou, Groten, & Slater, 2013). The results of these studies have shown that, even when the participants were not supposed to "embody" the new larger or smaller limb, their response to tactile stimuli delivered on that limb was influenced by its new size (Moseley et al., 2008). This means that vision alone is often sufficient to manipulate the way one's own body is perceived and the way in which bodily stimuli are processed. The question is then "how quickly and how easily" this can occur?

One area in which the possible effect of visual manipulation of bodies might have important implications is that related to the influence of the media in our everyday life. Interestingly, several studies in the last couple of decades have explored the impact of the media on people's body perception and body satisfaction, in particular in women (Crouch & Degelman, 1998; Dohnt & Tiggemann, 2006; Ogden & Mundray, 1996; Shaw, 1995), but not only (see Andersen & DiDomenico, 1992; Leit, Pope, & Gray, 2001; Nemeroff, Stein, Diehl, & Smilack, 1994; Spitzer, Henderson, & Zivian, 1999). These studies have clearly showed that there is a close relationship between the stereotyped ideal shape of the body, as portrayed by television, magazine and the movie industry, and the development of an inaccurate representation of one's own body – that, in turn, has been related to eating disorders (Tovée, Benson, Emery, Mason, & Cohen-Tovée, 2003). A number of studies reported that women that spend more time reading magazines, visualising friends' photos and uploading photos of themselves on social networks (Meier & Gray, 2013) have, on average, a lower body satisfaction. Importantly, these findings cannot be used to establish a role of causality between the images seen and the individual body satisfaction. In fact, other authors showed that people with a poor body image are more keen than others to resort to media to find thin ideal images (Thomsen, McCoy, Gustafson, & Williams, 2002). However, this mutual interaction can be better explained by the Objectivation Theory (Fredrickson & Roberts, 1997). According to Fredrickson and Roberts, "objectivation" occurs when an individual is conceived as an object, thus dehumanised. This entails a fragmentation of the human body into pieces with different aims and functions. In particular, the most dangerous characteristic of the objectivation is the instrumental role that the body may play (e.g. the sexual objectivation: the individual is evaluated not as a person, but as group of different characteristics that serve or not the sexual attraction, see Bartky, 1990). Women raised in the Western society seem to have internalised these unrealistic and sexualised models (auto-objectivation) and have learnt to think about themselves in these terms. Higher self-objectivation scores have been reported to correlate with the presence of eating disorders (also related to feeling ashamed towards one's own body because too far from the current culturally-expected idea of beauty; Noll & Fredrickson, 1998). According to Meier and Gray's study (2013), then, social networks (such as Facebook) confirm and strengthen this trend, as the individuals' value is perceived to be quantified by the number of "likes" and to the comments to self-uploaded body photos.

Unsurprisingly, young females (less than 19 years old) with a high body dissatisfaction (Groesz, Levine & Murnen, 2002) seem to be more exposed than males to this kind of body image manipulation, even though recent studies would seem to suggest that also young men might be not totally immune from this new trend. However, the media impact seems to be less severe in men, compared to women (Arbour & Martin Ginis, 2006; Hausenblas, Janelle, Gardner, & Hagan, 2003; Humphreys & Paxton, 2004).

What remains unclear in the extant literature is whether viewing unrealistic, but stereotypical, bodies can actually shift the perception of one's own body size. Interestingly, this would be a clear extension of those work that used illusions to change how one's whole body feels (e.g. Banakou et al., 2013; Ehrsson, Kito, Sadato, Passingham, & Naito, 2005; Groenegress, Thomsen, & Slater, 2009). Previous research on bodily illusions manipulated the physical appearance of participants in order to understand if this could also affect bodily sensations and behaviour (by exploiting the fact that the brain is likely to process more quickly and effectively congruent multisensory inputs). In some cases, it has been shown that even bodily illusions can influence a participant's implicit associations regarding race, according to the age or race of an avatar that is assigned to him/her. For example, a study showed that white people are less prone to show an implicit racial bias, when they identify themselves with a black avatar (Peck, Seinfeld, Aglioti, & Slater, 2013). Also, another study highlighted that when people identify themselves with a child avatar, their implicit behaviour changes accordingly (Banakou et al., 2013). In all these cases, though, the participants identified themselves with an avatar, probably updating their "original" body representation with the avatar's features, in terms of both appearance and size. Interestingly, the society, mainly through the media, has the important (and often educational) role to provide models. People, then, are naturally lead to self-identify with these models and to adapt to them. However, what happens when these models are too extreme and impossible to reach, such as unrealistic standard of thinness and beauty? According to the Bayesian theory, the evaluation of a stimulus (being it an object or a body) relies on previous experiences learnt from the environment, in order to provide the best possible estimation (Chater, Oaksford, Hahn, & Heit, 2010). If the body shape and size that the society provides as models are internalised, can this fallacious cue result into an inaccurate estimation of one's own body?

Here we report the results of a pilot study performed, separately on a female and male sample, in order to understand if the vision of other people bodies can affect the perception of one's own body parts. In particular, this study should clarify if watching "media-created perfect bodies" or more "natural" bodies can affect the participants' estimation of body parts, as well as their sense of body satisfaction.

3. Female sample

3.1. Materials and methods

Participants

Twenty healthy volunteers (all females, mean age: 22±4 years, range 19-27) took part in Experiment 1. Participants were all students at University of Milano-Bicocca (Milan, Italy) and received course credits for taking part in the experiment. From each participant the Body Mass Index (BMI = weight/height^2) was calculated, based on self-reported height and weight (see Appendix 3). All participants had normal or corrected to normal vision and were naïve about the purpose of the study. They all gave written consent prior to their participation to the experiment. The study was performed in accordance with the ethical standards laid down in the 1991 Declaration of Helsinki and was approved by the local Human Research Ethics Committee.

Procedure

All the participants were invited to report their height and weight. They were also asked to estimate how many hours on average they spend every day in visualising or uploading pictures on the social media "Instagram", and how many hours they spend in reading fashion and/or wellness magazines.

Then, they were asked to fill in two different questionnaires. The Eating Attitude Test (EAT-26, Italian version) (Dotti & Lazzari, 2014; Garner, Olmsted, Bhor, &

Garfinkel, 1982) (see Appendix 3) measures symptoms and concerns commonly found in people diagnosed with eating disorders. Twenty-six statements about attitude towards food and physical shape are addressed. For each statement the participants are asked to rate how often that situation occurred in their life, giving a number ranging between 0 and 5 (0 = never, 1 = rarely, 2 = sometimes, 3 = often, 4 = usually, 5 = always). Total scores above 20 indicate a significative risk of developing eating disorders or the presence of an underway eating disorder. This questionnaire has been validated with anorexic patients and in non-clinical samples as well (Thompson & Schwartz, 1982).

The Body Uneasiness Test (BUT) (Cuzzolaro, Vetrone, Marano, & Garfinkel, 2006) investigates the cognitive-affective attitude towards one's own body (see Appendix 3). This 71-item test includes two parts: BUT1 explores fears to gain weight, concerns about one's own body image, avoidance behaviours, compulsive restraints, feelings of detachment and depersonalisation. BUT2 focuses on concerns regarding specific body parts. The validity of this questionnaire has been proven both in female and male samples (Cuzzolaro et al., 2006).

After the completion of both questionnaires, the participants were presented with a computerised virtual scale model representing a female body (http://www.makehuman.org/) (Fig. 1). The size of the scale model's waist and thighs could be manipulated by the participants via a customised in-house software by using the up and down arrows on the keyboard. The participants were asked to adjust the size of the virtual model's thighs and waist of in order to match their own thighs and waist . The measures chosen by each participants for each body part were registered by the software. For each body part the participants were able to choose between ten possible sizes (waist: from 62 cm to

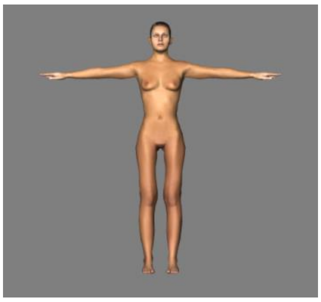


Figure 1 – Virtual female body scale. The participants were asked to manipulate this virtual body's thighs and waist sizes in order to match their own.

85 cm, 2.6 cm interval in between; thighs: from 42 cm to 60 cm, 2 cm interval in between).

The participants were asked to watch 36 images (each image was displayed for 5 seconds, for a total of 3 minutes) showing either thin or curvaceous female bodies. All the images were selected through a web search from fashion events or photo shoots. The participants were randomly assigned to one kind of presentation or the other. One group ("thin bodies") watched images of thin female bodies, while another group ("curvaceous bodies") watched images of curvaceous female bodies.

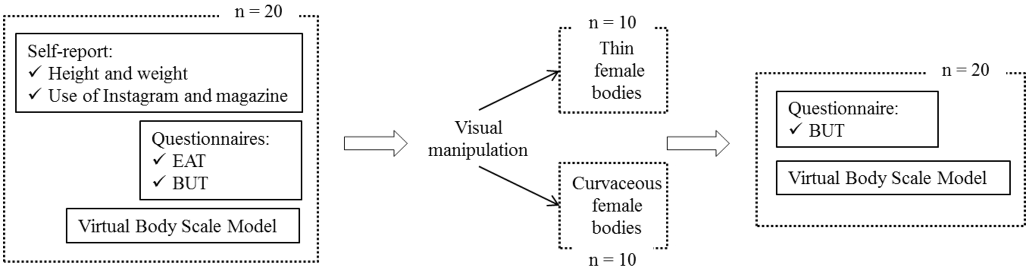


Figure 213 – Experimental procedure. All the participants reported their height and weight and their use of Instagram and fashion and wellness magazines, then they filled in two questionnaires about their attitude towards the food and their own bodies. Finally they modified the measures of thighs and waist of a virtual body scale in order to match their own thighs and waist size. Then they were assigned to two groups – one watched images of thin bodies while the other one curvaceous bodies. At the end one of the questionnaires and the perceived size of their body were reassessed.

After the vision of the images (i.e. "visual manipulation"), the perceived size of the participants' body (through the scale model) and their level of body satisfaction (through the BUT questionnaire) were reassessed. The experimental procedure's steps are summarised in Fig. 2.

Data Analysis

The difference in body satisfaction (as measured by the BUT questionnaire) and the difference in body size perception (as measured by the body scale model) before and after two different visual manipulations (i.e. thin vs. curvaceous model's bodies) were taken into account. As far as the perceived body size is concerned, two repeated measures 2 (between factor "image": "thin" vs. "curvaceous") by 2 (within factor "time": "pre" vs. "post" visual manipulation) Anova were performed on the visual body scale model scores regarding the waist and the thighs, respectively. Furthermore, the effect of watching the body images on the level of body satisfaction was examined, by means of three repeated measure mixed 2 (between factor "image": "thin" vs. "curvaceous") by 2 (within factor "time": "pre" vs. "post") Anova on the total scores of the BUT questionnaire, and, separately, on the partial scores of the BUT1 and BUT2.

3.2. Results

Body size perception

As far as the change in the waist size perception is concerned the factor Time did not result significant [F (1,18) = 1.49, p = 0.237] and so did the factor Image [F (1, 18) = 2.16, p = 0.159)]. The interaction between Time and Image [F (1, 18) = 0.59, p = 0.452)] also did not result to be significant. Thus, viewing models' bodies, did not influenced the perceived size of the participants' waist.

The analysis of the perceived size of the thighs, showed a main effect of Time [F (1, 18) = 5.153, p = 0.036] but no significant effect of Image [F (1, 18) =1.33, p = 0.264], while, the interaction between the two factors reached a significant level [F (1, 18) =6.618, p = 0.019] (see Fig. 3). The main effect of Time indicates that after the visual manipulation, the participants perceived their thighs as smaller than before (pre: visual manipulation: mean = 51.4 cm, SE = 0.92, 95% CI 49.47 to 53.33; post visual manipulation: mean = 49.9 cm, SE = 1.17, 95% CI 47.45 to 52.35). A Duncan post hoc analysis on the interaction between Time and Image revealed that the perceived size of the thighs was significantly smaller after watching curvaceous female bodies (p = 0.003; pre: mean = 53.4 cm, SE = 1.30, 95% CI 50.66 to 56.13; post: mean = 50.2 cm, SE = 1.65, 95% CI 46.73 to 53.67) but not after watching thin female bodies (p = 0.83; pre: mean = 49.4 cm, SE = 1.30, 95% CI 46.66 to 52.13; post: mean = 49.6 cm, SE = 1.65, 95% CI 46.13 to 53.07). The participants estimated their thighs as smaller than the baseline after watching images of curvaceous women, while watching thin bodies did not have any effect on the thighs size perception.

The table below summarise the mean estimation of the thighs and waist before (pre) and after (post) the visual manipulation for each experimental group (the one who watched thin models and the one who watched curvaceous models). It is possible to see a reduction of the estimation of thighs size for the group that watched curvaceous model but an increase of the perceived size of the waist. The group that watched thin models, instead, experienced an increase in the estimation of both waist and thighs.

	Thighs			Waist		
	pre (cm)	post (cm)	change (cm)	pre (cm)	post (cm)	change (cm)
Thin	49.4±15.62	49.6±15.68	0.2 ↑	69.65±22.02	70.94±22.43	1.3 ↑
Curvaceous	53.4±2.84	50.2±5.12	-3.2 ↓	72.84±3.26	73.13±3.26	0.3 ↑

Body satisfaction

For total scores at the BUT questionnaire the factor Time did not result significant [F (1, 18) =4.05, p = 0.059], and so did the factor Image [F (1, 18) =3.47, p = 0.079] and the interaction between these two factors [F (1, 18) =0.28, p = 0.869]. Interestingly, for the scores at the BUT1, the factor Time resulted to be significant [F (1, 18) =4.95, p = 0.039], while the factor of Image [F (1, 18) =1.903, p =0.185] or the interaction between the two factors did not [F (1, 18) =0.129, p =0.724]. Thus, the general attitude towards one's own body seems to become more positive after watching the images of the female bodies (pre: mean score 50.6, SE 6.73, 95% CI 36.46 to 64.74; post: mean score 47.5, SE 7.31, 95% CI 32.13 to 62.87).

For the BUT2 scores, instead, the factor Time was not significant [F (1, 18) =1.48, p = 0.239], but a significant effect of Image [F (1, 18) =5.51, p = 0.030] was found. The interaction between the two factors did not result to be significant [F (1, 18) =0.005, p = 0.944]. In particular, the group of participants who watched the curvaceous female bodies was generally less satisfied about their body shape than the group that watched the skinny bodies (skinny: mean score 29.8, SE 7.74, 95% CI 13.54 to 46.06; curvy: mean score 55.5, SE 7.74, 95% CI 39.24 to 71.76).

The table below show the participants' response (mean ± standard deviation) to the BUT questionnaire. The general level of body satisfaction increased in all cases after the visual manipulation (i.e. lower scores at the Body Uneasiness Test).

	BUT 1			BUT 2			BUT total		
	pre	post	change	pre	post	change	pre	post	change
Thin	41.2±21.76	37.6±24.71	-3.6 ↓	30.6±17.66	29±21.12	-1.6 ↓	71.8±37.32	66.6±43.38	-5.2 ↓
Curvaceous	60±36.58	57.4±39.13	-2.6 ↓	56.4±29.57	54.6±28.32	-1.8 ↓	116.4±64.66	112±65.74	-4.4 ↓

Eating Attitude Test questionnaire, use of Instagram and magazines consumption

The tables below show the response to the EAT questionnaire, the number of hour per day spent using Instagram and reading wellness or fashion magazines. Each line represent a single participant, separately for the group that watched thin models (Thin) and the group that watched curvaceous models (Curvaceous). The scores are displayed in ascending order for each group.

EAT	
Thin	Curvaceous
0	1
0	1
0	1
0	1
1	2
1	2
7	5
8	7
8	12
8	29

Instagram	
Thin	Curvaceous
0	0
0	0
0	1
0	2
0	2
0	4
2	4
2	4
4	4
5	5

Magazines	
Thin	Curvaceous
0	0
0	1
0	1
1	1
1	1
1	2
2	2
2	2
2	3
4	4

4. Male sample

4.1. Materials and methods

Participants

Twenty healthy volunteers (all males, mean age: 23±2 years, range 19-28) took part in Experiment 2. Participants were all students at the University of Milano-Bicocca (Milan, Italy) and received course credits for taking part in the experiment. From each participant the Body Mass Index (BMI = weight/height^2) was calculated, based on self-reported height and weight (see Appendix 3). All participants had normal or corrected to normal vision and were naïve about the purpose of the study. They all gave written consent prior to their participation to the experiment. The study was performed in accordance with the ethical standards laid down in the 1991 Declaration of Helsinki and was approved by the local Human Research Ethics Committee.

Procedure

The procedure was in the same as that of Experiment 1, with the following exceptions. Participants reported their weight and height (in order to calculate their BMI, see Appendix 3). In addition, they were asked if they generally attend a gym club (and, if so, for how many hours per week), if they practised a sport (and, if so, for how many hours per week). Then, they were asked to fill in the BUT and the EAT questionnaires (see Appendix 3). Finally, the participants were presented with the computerised virtual scale model, this time representing a male body (http://www.makehuman.org/)). As in Experiment 1, the participants were asked to adjust the virtual model's size, but in Experiment 2 the body part to be modified were the chest and the waist. The procedure was the same as that described in Experiment 1. For each body part the participants were able to choose between nine possible sizes (waist: from 72 cm to 89 cm, 2 cm interval in between; chest: from 32 cm to 36.8 cm, 0.6 cm interval in between).

The participants were asked to watch 36 images (5 seconds per image, for a total of 3 minutes) displaying either muscular or average build male bodies. All the images were selected through a web search from fashion events or photo shoots. The participants were randomly assigned to one kind of presentation of the other. One group ("muscular") watched images of muscular male bodies, while another group ("average") watched images of average build male bodies.

After the vision of the images (i.e. the visual manipulation), the perceived size of the participants' body (through the scale model) and their level of body satisfaction (through the BUT questionnaire) were reassessed. The experimental procedure's steps were the same showed for Experiment 1 in Fig. 2.

Data Analysis

Whether the perception of one's own body size was influenced by watching different kinds of bodies was investigated. In particular, variation in body satisfaction level (as measured by the BUT questionnaire) and, separately, in body size perception (as measured by the body scale model) due to different visual manipulations (i.e. muscular vs. average build male bodies) were analysed. As far as the perceived body size is concerned, two repeated measures 2 (between factor "image": "muscular" vs. "average") by 2 (within factor "time": "pre" vs. "post" visual manipulation) Anovas on the visual body scale model scores of waist and the chest, separately were performed. Furthermore, the effect on the level of body satisfaction was examined by performing three further repeated measure mixed 2 (between factor "image": "muscular" vs. "average") by 2 (within factor "time": "pre" vs. "post") Anovas: one on the total scores of BUT questionnaire, and, separately, on the partial scores of each BUT1 and BUT2.

4.2. Results

Body size perception

The perceived size of the chest did not significantly change over Time [F(1,18)=0.109, p=0.745] nor as effect of the Images viewed [F(1,18)=0.58, p=0.812]. The interaction between the two factors did not result significant as well [F(1,18)=1.574, p=0.226]. The perceived size of the waist was not significantly affected by the factor Time [F(1,18)=0.14, p=0.907] nor by the factor Image [F(1,18)=0.004, p=0.949] and the interaction between these two factors did not reach a significant level[F(1,18)=2.36, p=0.142].

The table below summarise the mean estimation of the waist and chest before (pre) and after (post) the visual manipulation for the group that watched muscular men

(Muscular) and the group that watched average build men (Average). The group that watched muscular men perceived their shoulder as smaller and their chest as bigger after the visual manipulation. The group that watched average build men, instead, experienced the opposite pattern after the visual manipulation (i.e. bigger shoulder and smaller chest).

	Waist			Chest		
	pre (cm)	post (cm)	change (cm)	pre (cm)	post (cm)	change (cm)
Muscular	77.8±3.91	76.6±3.62	-1.2 ↓	35.16±1.30	35.45±1.07	0.3 ↑
Average	76.4±3.40	77.8±4.73	1.4 ↑	35.64±0.96	34.95±1.27	-0.5 ↓

<u>Body satisfaction</u>

As far as the scores at the BUT questionnaire, we found a main effect of Time [F(1,18)=5.407, p=0.032], while the factor Image [F(1,18)=2.71, p=0.117] or the interaction between the two factors resulted to be significant [F(1,18)=2.954, p=0.103]. As far as the factor of Time is concerned, the visual manipulation in our sample increased the level of body satisfaction (i.e. lower scores at the BUT) (pre: mean score = 47.5, SE = 5.209, 95% CI 36.56 to 58.44; post: mean score = 40.6, SE = 5.92, 95% CI 28.16 to 53.04).

When the two parts of the questionnaire were analysed separately, we found for the BUT1 a trend towards a significant effect of Time [F(1,18)=4.23, p=0.054], but the Image [F(1,18)=2.748, p=0.115] and the interaction between Image and Time did not result to be significant [F(1,18)=0.973, p=0.337]. Just ss for the BUT total scores, the scores at the BUT1 decreased after the visual manipulation, indicating an increase in the body satisfaction (pre; mean score = 28.1, SE = 3.39, 95% CI 20.97 to 35.23; post: mean score = 24.45, SE = 4.06, 95% CI 15.92 to 32.98).

The results for the BUT2 confirmed and extended the previous results, showing a trend towards significance for the factor of Time [F(1,18)=4.295, p=0.053] and a significant interaction between Time and Image [F(1,18)= 4.564, p=0.047], even though the factor Image did not reach a significant level [F(1,18)=1.319, p=0.266]. The interaction between Time and Image was analysed by means of a Duncan post hoc test. The participants scores to the BUT 2 were significantly lower after viewing muscular bodies (p=0.008, pre: mean score = 23.9, SE 3.613, 95% CI 13.31 to 31.49; post: mean score = 17.3, SE 3.69, 95% CI 9.55 to 25.05) than after viewing average build bodies.

The table below show the participants' response (mean ± standard deviation) to the BUT questionnaire. The general level of body satisfaction was increased in all cases after the visual manipulation (i.e. lower scores at the Body Uneasiness Test).

	BUT 1			BUT 2			BUT total		
	pre	post	change	pre	post	change	pre	post	change
Muscular	35±19.40	29.6±23.05	-5.4 ↓	23.9±14.12	17.3±12.67	-6.6 ↓	58.9±29.55	46.9±33.06	-12 ↓
Average	21.2±9.16	19.3±11.31	-1.9 ↓	14.9±7.85	15±10.55	0.1 ↑	36.1±14.57	34.3±17.59	-1.8 ↓

Eating Attitude Test questionnaire, gym club and sport activity

The tables below show the response to the EAT questionnaire, the number of hour per day spent using Instagram and reading wellness or fashion magazines. Each line represent a single participants, separately for the group that watched muscular men (Muscular) and the group that watched average build men (Average). The scores are displayed in ascending order for each group.

EAT	
Muscular	Average
0	0
0	1
0	1
0	1
2	2
3	2
4	4
4	6
9	6
18	9

Gym	
Muscular	Average
0	0
0	0
0	1
0	1
0	1
0	2
2	2
2	2
4	2
5	4

Sport activity	
Muscular	Average
2	1
2	2
3	2
3	2
3	2
4	3
4	3
4	5
5	5
5	5

5. General conclusions and future directions.

In the present pilot study some hypothesis have been preliminary explored. First, the possibility that watching same-sex bodies might affect the way one's own body is perceived was investigated. Specifically, women who watch thin female bodies might perceive themselves as bigger, while women who watch curvaceous female bodies might perceive themselves as thinner. A similar effect was investigated for men (i.e. watching muscular male bodies might trigger a decrease in the perceived size of their own bodies, while watching average build men an increase). Also, possible changes in body satisfaction were investigated, by exploring whether or not a decreased body satisfaction occurs after watching ideal stereotyped bodies (i.e. thin female bodies for women and muscular male bodies for men). Finally, the general role of the amount of exposure to ideal body shapes, both in men (i.e. attendance to a gym club or practising a sport) and in women (i.e. reading fashion magazines or using social networks) was explored.

As far as the female group is concerned, we found that the participants' body size was influenced by the body shape seen, but only in the sense that seeing curvaceous women decreased the participants' perceived body size. Also, this holds true for the thighs but not for the waist. Watching thin models did not have any effect on our sample. Furthermore, all the women showed a general increase in the satisfaction level towards their own bodies after watching both thin and curvaceous models. However, the participants that were randomly assigned to watch the curvaceous models reported a general significant higher body dissatisfaction compared to the group that watched thin models, perhaps suggesting that the two groups were not well balanced satisfaction-wise. Finally, the time spent on Instagram or reading fashion and wellness magazines did not seem to affect the change in body size.

The data concerning the male sample showed that the visual manipulation had no effect in the change of body size or body satisfaction. However, it has been reported that in general men are less vulnerable to this kind of visual manipulation. Given the fact that probably the visual manipulation was not strong enough to manipulate the female samples' body size, even more so for the male sample, by itself less keen to body perception variations. However, what is interesting is that seeing muscular bodies increased the participants' body satisfaction. This findings is in line with some other researches (e.g. Humphreys & Paxton, 2004) that found that men have a different attitude towards same sex bodies compared to women. In fact, they seem to consider ideal bodies not as an unrealistic target, but as an inspiration, something they can tend to. Thus, perhaps, this inspirational attitude increased their body satisfaction, in the sense that they felt more positive about their body and their possibilities.

The present preliminary data suggest that some changes are needed for future experiments to be accomplished.

Visual manipulation

First of all, the exposure (only 3 minutes) might not be long enough for an effect to be seen. Two possible solutions (not mutually exclusive) should be taken into account: increasing the number of visual stimuli and allowing each image to last longer on the screen. Also, the participants' focus of attention need to be monitored, to ensure that they are actually paying attention to the presentation. A way to fulfil this aim is asking the participants to report some characteristics of the images afterwards to ensure they were actually processing the visual stimuli (e.g. asking to count how many people in the presentation were wearing something blue).

Furthermore, as far as the female sample is concerned, according to a recent study (Krul, Daanen, & Choi, 2011), Italian women are on average around 161 cm tall and 57 kg of weight. This means that for our sample not only the thin bodies represented an unrealistic target, but also the curvaceous models might have appeared as unrealistic as the thin models. In fact, they represent a woman type that is robust and tall, quite uncommon for the average Italian female population. Even if the two body shapes presented were actually representing two different extremes, perhaps they simply would not work for an Italian sample. A similar issue should be carefully considered for the male sample as well.

Another important issue that needs to be considered relates to the fact that the visual stimuli included a number of images depicting popular people (such as actors or famous models). This might have somehow affected the results. One possible solution might be simply to show the bodies from the neck down (i.e. avoiding the head), in order to rule out the possibility that the participants' judgement is confounded by the attractiveness of or familiarity to the face, while the focus should be on the body shape. Though, it is worth nothing that this might affect the ecological validity of the study, since people are usually exposed to both famous and unknown people. Another more ecologically-valid possibility might be to include both famous and unknown people, but balancing them between the different visual stimuli sets.

Finally another possible confounding variable that needs to be controlled and balanced in the different sets of images are clothes and accessorises worn by the models and, in case, brand names.

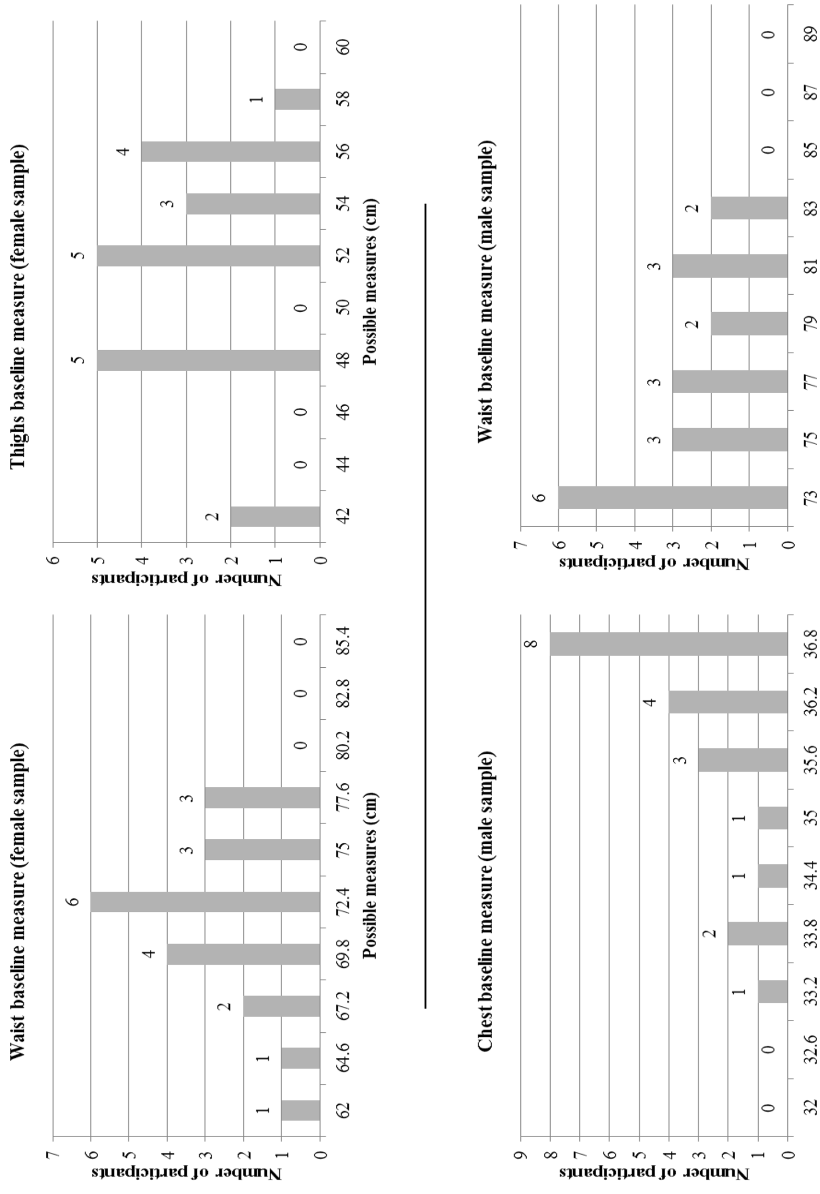
Body scale model

The virtual body scale model needs to be improved under different aspects. In fact, the scale model used for the men sample was probably not accurate enough. In particular, in the baseline judgement of the chest size 40% of the sample (8/20 participants) chose the maximum size of the virtual body scale model (i.e. 36.8 cm), while no one chose the minimum size (i.e. 32 cm). In general, 75% of the sample (15/20 participants), out of 9 possible sizes, picked one of the three largest measures (i.e. 35.6, 36.2 or 36.8 cm). Besides, as far as the baseline judgement of the waist size is concerned, none of the participants chose either of the three maximum measures (i.e. 85, 87 and 89 cm), while the 30% of the sample (6/20 participants) chose the minimum measure (i.e. 73 cm). That is, the range reachable is not sufficient, on the basis of the male average body size and given our samples' choices, to cover a large sample of the population. Moreover, the shape of the body at the end of the manipulation was probably not well proportioned and not reflecting an actual average male body.

The scale model used for the female sample, resulted to be slightly more appropriate, even if for the baseline judgement of the thighs the 65% of the sample (13/20 participants) chose between the four intermediate measures (i.e. 48, 50, 52 and 54 cm), while no one chose the maximum size (60 cm) and just the 10% (2/20 participants) chose the minimum size (42 cm). Furthermore, the 30% of the sample (6/20 participants) chose as waist baseline measure 72.4 cm, while just the 5% (1/20 participants) chose the smallest size (62 cm) and no one chose either one of the three largest sizes (80.2, 82.8 and 85.4 cm).

These data are summarised and graphically displayed in Fig.3.

Figure 3 – In the figures below, the choices of the participants as far as the virtual body scale model is concerned, are reported.



Sample

On the basis of the evaluation of the 95% confidence intervals, the effects found were quite small. An a priori sample size calculation was not possible, due to the novelty of the present study. Nonetheless, on the basis of the pilot study's results, a larger sample might improve the effect size in future experiments. Moreover, age limits should also be more carefully considered. In fact, in order to increase the chance to observe an effect, very young adults might be invited to participate in the study. Ideally, participants should be around 19 years old, as this has been shown to be this is the most vulnerable age. Our sample, for reasons related to the recruitment possibilities, included mainly university students (i.e. usually older than 18 years old). Future experiments should extend the inclusion criteria to younger volunteers.

Furthermore, all participants suffering from body disorders or at risk of developing one should be excluded (or their data analysed in a separate experiment). The present sample included 4 female participants reporting to be underweight (Body Mass Index < 18.5). In addition, one of them, according to the Eating Attitude Test, was at risk of developing or currently having some eating disorders (cut off >20). As for the male sample no participant was underweight, but one of them scored 18 at the Eating Attitude Test, with the cut off for eating disorders (at risk or current) is for scoring 20 or higher. Also other psychiatric conditions should be considered between the exclusion criteria.

Finally, weight and height should be measured directly by the experimenters, because people might not be very accurate in their report (Krul et al., 2011).

Instagram, magazines, gym attendance and sport activity

A more detailed questionnaire including all these items both for male and female need to be designed in order to be able to perform a gender comparison. For example, the use of other social media might be investigated as well as the participants' approach to them (i.e. whether they spend more time updating their own photographs, what is the content of these photographs, how much time they spend in visualising other people's photograph and, again, what is the content – e.g. people, landscapes…). Also, magazine consumption need to be investigated amongst men population as well. The same can be said for the gym attendance and the sport activity in female sample. For example, a study showed that elite female athletes might be more exposed than the controls, to the development of eating disorders (Sundgot-Borgen, 1993).

Conclusions and future developments

The preliminary data obtained with the present pilot study contribute to highlight limitations and strengths of the experimental design employed. In particular, the present experimental design offer the advantage to measure different aspects concerning the body representation in both women and men in an ecologically valid fashion. Moreover, the procedure and the tools employed are reasonably cheap in term of both economic resources and time.

Nonetheless, few crucial changes are necessary. First, a more accurate virtual body scale model is going to be developed and new visual stimuli need to be selected, according to the weaknesses emerged (and highlighted above) during the pilot study. Furthermore, a younger and larger sample needs to be recruited, considering as exclusion criteria the presence of eating disorders (already diagnosed or at risk of developing one) or other psychiatric conditions. Eventually, the influence of the media in participants with current body representation disturbances (e.g. anorexia nervosa) will need to be investigated separately, in a parallel series of experiment.

Even if with several limitations, the preliminary data obtained suggest the potential relevance of the proposed study design in exploring the possibility that the body size can be implicitly influenced by viewing other people's bodies. The present project is certainly relevant to the study of the eating disorders and how these can be related to the media impact in Western society. The data obtained by such a project might shed light on the causes of body representation disturbances and on the reason why their incidence is rapidly escalating over the past few decades (Hoek & Van Hoeken, 2003).

It is also worth mentioning that the preliminary result obtained here, showing that body size perception can be positively affected by watching curvaceous bodies in female participants, can be seen as an indirect confirmation of the positive effect of showing more natural bodies in media advertisement (a campaign started by a few multinational companies in the last few years).

CHAPTER VII

GENERAL DISCUSSION

General discussion

The present thesis mainly focuses on one of the two main aspects that describe the body representation: the perception of body position. In particular, self-localisation abilities have been investigated through bodily illusions and bodily manipulations. The findings brought about by the studies described in Chapter II, III, IV, V, and the pilot study presented in Chapter VI, suggest that it is possible to manipulate one's body representation at many different levels (e.g., both implicit and explicit, motor, perceptual, and emotional).

As mentioned above, the representation of one's own body has been quite widely explored over the last few decades, leading to profoundly diverse descriptions (e.g. de Vignemont, 2010; Head & Holmes, 1911; Melzack & Wall, 1965; Melzack, 1989, 2005; Moseley, Gallace, & Spence, 2012). Within these descriptions it is often mentioned the close relationship that exists between body neural representation and the concept of 'self'. That is, building a constant sense of 'self', and, consequently, a coherent body representation, requires the development of the sense of ownership and the ability of self-localising the body. "Ownership" refers to the (normally) undoubtable feeling that a certain body or body part belongs to me while "self-localisation" refers to the feeling of knowing exactly the position of my body or body parts in space. The present thesis investigated in particular this second aspect by means of bodily illusions.

Bodily illusions are a powerful tool with which to investigate the self and how the body is represented. In fact, they offer the possibility to temporarily (but realistically) manipulate one's own body representations, possibly mimicking some pathological conditions, in which one or more aspects of the self are disrupted. Diverse bodily illusions can influence different aspects of the body representation and different questions can be addressed.

Traditionally, illusions such as the rubber hand illusion or the mirror box, by involving both the aspect of ownership and self-localisations, led to the suggestion that these two elements cannot be fully dissociated. In addition to this, the number of studies that make use of bodily illusions has grown very rapidly in the more recent years. This is likely due to the flexibility of the paradigm adopted and to their relative low cost (i.e. for the rubber hand illusion nothing more than a rubber glove can be effectively used). However, perhaps also due to this rapid development, a number of basic issues related to the study of body perception were left partially unexplored by these paradigms. For example, it remains somehow unclear the relationship between self-localisation and the sense of body ownership. Some authors have claimed that the former (such as in the case of the proprioceptive drift) can be considered a measurable representation of the latter (e.g. Aimola Davies & White, 2012; Botvinick & Cohen, 1998; Kammers, de Vignemont, Verhagen, & Dijkerman, 2009; Preston, 2013; Wold, Limanowski, Walter, & Blankenburg, 2014). This connection has been suggested following the evidence reported by Botvinik and Cohen (1998), who reported the presence of a drift in the self-perceived position of one’s own hand after the induction of the rubber hand illusion, that positively correlated with the strength of the illusion. In other words, the stronger is the sense of ownership towards the rubber hand, the closer to the rubber hand the real hidden hand is perceived. This finding was also initially supported by the fact that arm mislocalisation is weaker during the condition of asynchronous visuo-tactile stimulation, in which a sense of ownership towards the rubber hand is not induced. However, further studies showed that this is not always the case. In particular, Pavani, Spence, and Driver showed that vision can capture tactile localisation, a phenomenon known as the “visual capture of touch” (Pavani, Spence, & Driver, 2000). Therefore, the fact that one’s own hand is mislocated towards the rubber hand might be simply due to the fact that the touch seen on the rubber hand (and synchronously provided to the real hidden hand) is captured towards such position (thus leading to a misperception of body position). Later, other studies supported the idea that self-localisation and body ownership are not as closely related as they have been thought to be. Various authors, in fact, showed that the proprioceptive drift (i.e., a shift in the perception of arm position) generally found during the rubber hand illusion can be induced not only when this illusion develops, but also in total absence of a limb to embody (e.g. Rohde, Di Luca, & Ernst, 2011; Wann & Ibrahim, 1992). The first series of experiment (Study 1, Chapter II) presented in this thesis clearly supports this idea, showing a perceptual drift in finger localization towards a point in space that was simply seen to be touched by a virtual finger. Therefore, one might wonder about what really guides self-localisation. It is well-known, now, that the sense of ownership carries (if any) just partial and very limited responsibility in this function. Vision certainly contributes to self-localisation, however an important role is also played by proprioception (Ernst & Banks, 2002; Smeets, van den Dobbelsteen, de Grave, van Beers, & Brenner, 2006; van Beers, Sittig, & Denier van der Gon, 1996, 1998, 1999; van Beers, Sittig, & van der Gon, 1999; van Beers, Sittig, & Van Der Gon, 1999; van Beers, Wolpert, & Haggard, 2002a, 2002b). In this thesis, we investigated what happens when visual and proprioceptive signals are in conflict in signalling body position, and how this conflict is resolved in time. In particular, by employing a bodily illusion, it has been shown, that, under conditions of uncertainty, when the visual and proprioceptive position of the limb have been deliberately manipulated in order to be incongruent, vision is initially predominant over proprioception, but very soon (a few seconds, according to the data presented in Study 2 and 3, see Chapter III and IV) the weighting of proprioception increases. The most innovative aspect of these findings is probably related to the fact that vision and proprioception realign just as a function of time. That is, the sensory-motor system does not need a reason to update – such as a planned movement – but updating occurs, likely in an automatic manner, over time. This is supported by Study 2 and 3’s data. In fact, in both these studies, after inducing an incongruency between the visually encoded and proprioceptively encoded position of the right hand (i.e. the disappearing hand trick), the participants were asked to localise their hidden right hand. They initially judged their hand according to the visually encoded position, but, over time, the proprioceptively encoded position was more heavily weighted, leading to a more accurate localisation of the hand. This way of functioning would seem to represent a successful strategy in evolutionary terms: an animal might rest apparently still, but its neural processor does not stop to elaborate its current position, just in case a possible menace appears. It is vital that this processing is based on the actual position of the joints (that also during rest adjust their position) and not on the visual signals regarding the position where they were last seen. Also, importantly, the body must not be, and indeed is almost certainly not, completely still. In fact, respiration and even heartbeat may generate sufficient perturbation to provide ongoing proprioceptive feedback (Proske and Gandevia, 2012). This finding not only shed light on the relationship between vision and proprioception in self-localisation, but also helps to interpret what really happens to the hidden hand when an incongruency between its “visually encoded” and “proprioceptively encoded” position is provided. In particular, when the disappearing hand trick was firstly described (Newport & Gilpin, 2011), the authors concluded that threatening the space where the hand was supposed to be (i.e. the visually encoded space) or the space where the hand actually was (i.e. the proprioceptively encoded space) did not show any difference in terms of skin conductance responses. Furthermore, these responses were comparable to the responses obtained when a space far from the body was threatened. The authors interpreted this result in term of a lack of ownership towards the disappeared hand. Nevertheless, it seems that disowning a body part without replacing it with a “new” one (such as in the case of the rubber hand illusion) breaches one of the fundamental assumption of the body representation: the tendency to maintain its integrity (see Haggard & Wolpert, 2005). The results of the present work suggest that during the disappearing hand trick the participants are simply not able to correctly locate their hand. That is, body localization and ownership should be considered as two different aspects. The real question then becomes: is it possible to protect one’s own body (by means of an arousal response) when there is no knowledge of its actual position? Further experiments will be needed to explore and clarify this hypothesis. In this thesis, the studies in which the disappearing hand trick was used suggest that vision can affect self-localisation, but that, over time, proprioception is more heavily weighted.

Interestingly, research has shown that a manipulation of proprioception not only disrupt self-localisation but also the perception of body size (Longo, Kammers, Gomi, Tsakiris, & Haggard, 2009). Specifically, Longo and his colleagues showed that when a body part receives two conflictual proprioceptive cues (the vibration of biceps and triceps tendons), that body part is perceived as being shrunk (though see Gilhodes, Roll, & Tardy-Gervet, 1986, for a different result). By means of a more rigorous experimental design, it has been here showed here (Study 4, Chapter V) that, in line with Gilhodes and colleagues (1986) and contrary to Longo et al.'s work, when a limb receives equal and opposite information about its own position, surprisingly, self-localisation becomes more accurate than when no information at all is provided. In fact, in Study 4, self-localisation was more accurate in the condition in which both the triceps and biceps tendons were synchronously vibrated, than in the condition in which no vibration was applied. This result might be interpreted in terms of an equal weighting given to opposite information coming from two antagonist muscles. So, it seems likely to hypothesise that the central nervous system rather than using absolute information coming from each tendon, integrates different cues coming from the limb, by using a ratio between these signals to determine the current position of the body.

With this last study, thus, we underlined how the vibratory stimuli might be potentially useful to enhance the self-localisation. Further studies will be needed in order to test this effect on patients whose self-localisation abilities are disrupted while their proprioception seems to be intact (i.e. Complex Regional Pain Syndrome patients).

The current thesis highlights that bodily illusions still represent an effective tool to reveal a number of unclarified aspects concerning the self. Importantly, it can be easily noted how vision represents a recurrent and crucial element for most of the illusions, meaning that most of the time, when vision is available, we tend to rely on it. Taking together the great weight assigned to vision and the malleability of the self, one might then wonder about the impact of the images that we see every day in manipulating our sense of self. In a pilot study we showed that the presentation of different body shapes taken from the visual media can change not only the level of satisfaction that we have towards our body, but also the perception of our body size. These preliminary results, might pave the way to strategies addressed at improving people's wellbeing and sense of self adequacy through media campaigns.

In conclusion, the present work has cast light on the role of different factors (visual and proprioceptive) and of the temporal dynamic of their interaction in affecting some important aspects of our sense of self, such as body localization and ownership. Moreover, this thesis clearly showed that the self-localisation should be very carefully reconsidered as a possible measure of the sense of body ownership. In fact, the two concepts seem to be more dissociable than has previously been considered. This thesis also highlighted the fact that the result of research in the field of body representation can be extended to many applied contexts. In particular, one might expect that the role of the visual images (as presented by the media) in shaping our body representations, especially in the younger population, should be further investigated, in an effort to understand the recent widespread of eating disorders and the high levels of body dissatisfaction found in our society.

References

Adamo, D. E., Scotland, S., & Martin, B. J. (2012). Upper limb kinesthetic asymmetries: gender and handedness effects. Neuroscience Letters, 516(2), 188–92. doi:10.1016/j.neulet.2012.03.077.

Aglioti, S. M., & Pazzaglia, M. (2011). Sounds and scents in (social) action. Trends in Cognitive Sciences, 15(2), 47–55. doi:10.1016/j.tics.2010.12.003.

Aglioti, S., DeSouza, J. F., & Goodale, M. a. (1995). Size-contrast illusions deceive the eye but not the hand. Current Biology : CB, 5(6), 679–85. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/7552179.

Aglioti, S., Smania, N., & Peru, a. (1999). Frames of reference for mapping tactile stimuli in brain-damaged patients. Journal of Cognitive Neuroscience, 11(1), 67–79. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9950715.

Aimola Davies, A. M., & White, R. C. (2012). A sensational illusion: Vision-touch synaesthesia and the rubber hand paradigm. Cortex; a journal devoted to the study of the nervous system and behavior, 49(3), 806–818. .

Amoruso, L., Couto, B., & Ibáñez, A. (2011). Beyond Extrastriate Body Area (EBA) and Fusiform Body Area (FBA): Context Integration in the Meaning of Actions. Frontiers in Human Neuroscience, 5(November), 124. doi:10.3389/fnhum.2011.00124.

Andersen, A. E., & DiDomenico, L. (1992). Diet vs. shape content of popular male and female magazines: A dose-response relationship to the incidence of eating disorders? International Journal of Eating Disorders, 11(3), 283–287.

Arbour, K. P., & Martin Ginis, K. A. (2006). Effects of exposure to muscular and hypermuscular media images on young men's muscularity dissatisfaction and body dissatisfaction. Body Image, 3(2), 153–161.

Armel, K. C., & Ramachandran, V. S. (2003). Projecting sensations to external objects: evidence from skin conductance response. Proceedings. Biological Sciences / The Royal Society, 270(1523), 1499–506. doi:10.1098/rspb.2003.2364.

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. Nat Neurosci, 7(5), 542–548. Retrieved from http://dx.doi.org/10.1038/nn1241.

Azañón, E., & Soto-Faraco, S. (2008). Changing reference frames during the encoding of tactile events. Current Biology : CB, 18(14), 1044–9. doi:10.1016/j.cub.2008.06.045.

Bach-y-Rita, P. (2004). Tactile sensory substitution studies. Annals of the New York Academy of Sciences, 1013, 83–91. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/15194608.

Banakou, D., Groten, R., & Slater, M. (2013). Illusory ownership of a virtual child body causes overestimation of object sizes and implicit attitude changes. doi:10.1073/pnas.1306779110/-/DCSupplemental.www.pnas.org/cgi/doi/10.1073/pnas.1306779110.

Bárány, R. (1906). Untersuchungen über den vom vestibularapparatdes ohres reflektorisch aus- gelösten rhythmischen nystagmus und seine begleiterscheinungen. Mschr. Ohrenheilk. 40, 193–297.

Bárány, R. (1967). “Some new methods for functional testing of the vestibular apparatus and the cerebellum. Nobel Lecture, September 11, 1916,” in Nobel Lectures Including Presentation of Speeches and Laureates' Biographies, Physiology or Medicine 1901–1921 (Amsterdam: Elsevier Publishing Company), 500–511.

Barnsley, N., McAuley, J. H., Mohan, R., Dey, a., Thomas, P., & Moseley, G. L. (2011). The rubber hand illusion increases histamine reactivity in the real arm. Current Biology, 21(23), R945–R946.

Bartky, S. L. (1990). Femininity and domination: Studies in the phenomenology of oppression. Psychology Press.

Belin, P., & Zatorre, R. J. (2000). ‘What’, ‘where’ and ‘how’ in auditory cortex. Nature Neuroscience, 3, 965–966.

Bell, C. (1826). On the nervous circle which connects the voluntary muscles with the brain. *Philos Trans R Soc* 115: 163-173.

Berlucchi, G., & Aglioti, S. M. (2010). The body in the brain revisited. Experimental Brain Research. Experimentelle Hirnforschung. Expérimentation Cérébrale, 200(1), 25–35. doi:10.1007/s00221-009-1970-7.

Bertelson, P. (1998). Starting from the ventriloquist : The perception of multimodal events. In M. Sabourin, F. I. M. Craik, & M. Robert (Eds.), Advances in psychological science: Vol. 2. Biological and Cognitive aspects (Psychologi., pp. 419–439). Hove, England.

Block, A.M. (1890) Expériences sur les sensations musculaires. Revue Scientifique, 45:294–301.

Blom, R. M., Hennekam, R. C., & Denys, D. (2012). Body integrity identity disorder. PloS One, 7(4), e34702. doi:10.1371/journal.pone.0034702.

Bock, O., & Arnold, K. (1993). Error accumulation and error correction in sequential pointing movements. Experimental Brain Research, 95, 111–117.

Botvinick, M., & Cohen, J. (1998). Rubber hands “feel” touch that eyes see. Nature, 391(6669), 756. doi:10.1038/35784.

Bray H., Moseley G.L. (2011). Disrupted working body schema of the trunk in people with back pain. British Journal of Sports Medicine 45(3):168-73.

Buxbaum, L. J., & Coslett, H. B. (2001). Specialised structural descriptions for human body parts: Evidence from autotopagnosia. Cognitive Neuropsychology, 18(4), 289–306. doi:10.1080/02643290126172.

Chapman, C. D., Heath, M. D., Westwood, D. a, & Roy, E. a. (2000). Memory for kinesthetically defined target location: evidence for manual asymmetries. Brain and Cognition, 46(1-2), 62–6. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11527365.

Chater, N., Oaksford, M., Hahn, U., & Heit, E. (2010). Bayesian models of cognition. Wiley Interdisciplinary Reviews: Cognitive Science, 1(6), 811–823.

Cole, J., & Paillard, J. (1995). Living without Touch and Peripheral Information about Body Position and Movement : Studies with Deafferented Subjects Cole and Jacques. In J. Bermudez (Ed.), The Body and the Self (pp. 245–266).

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 (New York, N.Y. : 1991), 18(12), 2879–90. doi:10.1093/cercor/bhn046.

Costantini, M., Galati, G., Ferretti, A., Caulo, M., Tartaro, A., Romani, G. L., & Aglioti, S. M. (2005). Neural Systems Underlying Observation of Humanly Impossible Movements: An fMRI Study. Cerebral Cortex , 15 (11), 1761–1767. doi:10.1093/cercor/bhi053.

Craig, A. (2003). Interoception: the sense of the physiological condition of the body. Current Opinion in Neurobiology, 13(4), 500–505. doi:10.1016/S0959-4388(03)00090-4.

Craig, A. D. B. (2009). How do you feel now? The anterior insula and human awareness. Nature Reviews. Neuroscience, 10(1), 59–70. doi:10.1038/nrn2555.

Craske, B., & Crawshaw, M. (1975). Shifts in kinesthesis through time and after active and passive movement. Perceptual and Motor Skills, 40(3), 755–61. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/1178361.

Critchley, H. D., Wiens, S., Rotshtein, P., Ohman, A., & Dolan, R. J. (2004). Neural systems supporting interoceptive awareness. Nature Neuroscience, 7(2), 189–95. doi:10.1038/nn1176.

Critchley, M. (1979). The divine banquet of the brain and other essays (pp. 92-105). New York: Raven Press.

Crouch, A., & Degelman, D. (1998). Influence of female body images in printed advertising on self-ratings of physical attractiveness by adolescent girls. Perceptual, 87, 585–586.

Crowe, A., Keessen, W., Kuus, W., Van Vliet, R., & Zegeling, A. (1987). Proprioceptive accuracy in two dimensions. Perceptual and Motor Skills, (64), 831–846.

Cuzzolaro, M., Vetrone, G., Marano, G., & Garfinkel, P. E. (2006). The Body Uneasiness Test (BUT): Development and validation of a new body image assessment scale. Eating and Weight Disorders - Studies on Anorexia, Bulimia and Obesity, 11(March), 1–13.

Darwin, C. (1854). A Monograph on the Sub-class Cirripedia: With Figures of All the Species: The Balanidæ (or Sessile Cirripedes); the Verrucidæ, Etc. (Vol. 2). Ray society.

De Vignemont, F. (2010). Body schema and body image--pros and cons. Neuropsychologia, 48(3), 669–80. doi:10.1016/j.neuropsychologia.2009.09.022.

De Vignemont, F. (2011). A mosquito bite against the enactive approach to bodily experiences. Journal of Philosophy, 1–23.

De Vignemont, F. (2011). Embodiment, ownership and disownership. Consciousness and Cognition, 20(1), 82–93. doi:10.1016/j.concog.2010.09.004.

De Vignemont, F., Ehrsson, H. H., & Haggard, P. (2005). Bodily illusions modulate tactile perception. Current Biology : CB, 15(14), 1286–90. doi:10.1016/j.cub.2005.06.067.

Denny-brown, D., Meyer, J. S., & Horenstein, S. (1952). the significance of perceptual rivalry resulting from parietal lesion. Brain , 75 (4), 432–471. doi:10.1093/brain/75.4.432.

Desmurget, M., Vindras, P., Gréa, H., Viviani, P., & Grafton, S. T. (2000). Proprioception does not quickly drift during visual occlusion. Experimental Brain Research, 134(3), 363–377. doi:10.1007/s002210000473.

Diagnostic and statistical manual of mental disorders: DSM-IV-TR. (4th ed.). (2000). Washington, DC: American Psychiatric Association.

Dijkerman, H. C., & de Haan, E. H. F. (2007). Somatosensory processes subserving perception and action. The Behavioral and Brain Sciences, 30(2), 189–201; discussion 201–39. doi:10.1017/S0140525X07001392.

Dohnt, H. K., & Tiggemann, M. (2006). Body Image Concerns in Young Girls: The Role of Peers and Media Prior to Adolescence. Journal of Youth and Adolescence, 35(2), 135–145. doi:10.1007/s10964-005-9020-7.

Dotti, A., & Lazzari, R. (2014). Validation and reliability of the Italian EAT-26. Eating and Weight Disorders - Studies on Anorexia, Bulimia and Obesity, 3(4), 188–194. doi:10.1007/BF03340009.

Downing, P. E., & Peelen, M. V. (2011). The role of occipitotemporal body-selective regions in person perception. Cognitive Neuroscience, 2(3-4), 186–203.

Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A Cortical Area Selective for Visual Processing of the Human Body. Science , 293 (5539), 2470–2473. doi:10.1126/science.1063414.

Ehrsson, H. H., Kito, T., Sadato, N., Passingham, R. E., & Naito, E. (2005). Neural substrate of body size: illusory feeling of shrinking of the waist. PLoS Biology, 3(12), e412. doi:10.1371/journal.pbio.0030412.

Ehrsson, H. H., Spence, C., & Passingham, R. E. (2004). That's my hand! Activity in premotor cortex reflects feeling of ownership of a limb. Science (New York, N.Y.), 305(5685), 875–7. doi:10.1126/science.1097011.

Ehrsson, H. H., Wiech, K., Weiskopf, N., Dolan, R. J., & Passingham, R. E. (2007). Threatening a rubber hand that you feel is yours elicits a cortical anxiety response. Proceedings of the National Academy of Sciences of the United States of America, 104(23), 9828–33. doi:10.1073/pnas.0610011104.

Eimer, M., Forster, B., & Van Velzen, J. (2003). Anterior and posterior attentional control systems use different spatial reference frames: ERP evidence from covert tactile-spatial orienting. Psychophysiology, 40(6), 924–933. doi:10.1111/1469-8986.00110.

Eklund, G. (1972). Position sense and state of contraction; the effects of vibration. Journal of Neurology, Neurosurgery & Psychiatry, 35(5), 606–611. doi:10.1136/jnnp.35.5.606.

Eriksen, C. W. and Hoffman, J. E. (1973). The extent of processing of noise elements during selective encoding from visual displays. Perception and Psychophysics, 14, I 55 -60.

Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. Nature, 415(6870), 429–33. doi:10.1038/415429a.

Ernst, M. O., & Bülthoff, H. H. (2004). Merging the senses into a robust percept. Trends in Cognitive Sciences, 8(4), 162–9. doi:10.1016/j.tics.2004.02.002.

Fechir, M., Klega, A., Buchholz, H. G., Pfeifer, N., Balon, S., Schlereth, T., … Schreckenberger, M. (2010). Cortical control of thermoregulatory sympathetic activation. European Journal of Neuroscience, 31(11), 2101–2111. doi:10.1111/j.1460-9568.2010.07243.x.

Flor, H. (2002). Phantom-limb pain: characteristics, causes, and treatment. The Lancet Neurology, 1(3), 182–189. doi:10.1016/S1474-4422(02)00074-1.

Flor, H. (2002). The modification of cortical reorganization and chronic pain by sensory feedback. Applied Psychophysiology and Biofeedback, 27(3), 215–27. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12206052.

Folk, C. L.,Remington, R.W., & Johnston, J.C. (1992). Involuntary covert orienting is contingent on attentional control settings. Journal of Experimental Psychology: Human Perception& Performance, 18, 1030-1044.

Franconeri, S. L., & Simons, D. J. (2003). Moving and looming stimuli capture attention. Perception & Psychophysics, 65(7), 999–1010.

Fredrickson, B. L., & Roberts, T.-A. (1997). Objectivation theory. Toward understanding womens's lived experiences and mental health risks. Psychology of Women. Quaterly, 21, 173–206.

Gallace, A., & Spence, C. (2005). Visual capture of apparent limb position influences tactile temporal order judgments. Neuroscience Letters, 379(1), 63–8. doi:10.1016/j.neulet.2004.12.052.

Gallace, A., & Spence, C. (2014). In touch with the future: the sense of touch from cognitive neuroscience to virtual reality. Oxford University Press.

Gallace, A., Torta, D. M. E., Moseley, G. L., & Iannetti, G. D. (2011). The analgesic effect of crossing the arms. Pain, 152(6), 1418–23. doi:10.1016/j.pain.2011.02.029

Gallagher S, Cole J. (1995). Body image and body schema in a deafferented subject. Journal of Mind and Behavior. 16:369–90.

Gallagher, S., & Meltzoff, A. N. (1996). The earliest sense of self and others: Merleau-Ponty and recent developmental studies. Philosophical Psychology, 9(2), 211–233. doi:10.1080/09515089608573181.

Garner, D. M., Olmsted, M. P., Bhor, Y., & Garfinkel, P. E. (1982). The Eating Attitudes Test: psychometric features and clinical correlates. Psychological Medicine, 12, 871–878.

Gerstmann, J. (1942). Problem of imperception of disease and of impaired body territories with organic lesions: relation to body scheme and its disorders. Archives of Neurology & Psychiatry, 48(6), 890–913.

Ghilardi, M. F., Gordon, J., & Ghez, C. (1995). Learning a visuomotor transformation in a local area of work space produces directional biases in other areas. Journal of Neurophysiology, 73(6), 2535–9. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/7666158.

Gilhodes, J. C., Roll, J. P., & Tardy-Gervet, M. F. (1986). Perceptual and motor effects of agonist-antagonist muscle vibration in man. Experimental Brain Research, 61, 395–402.

Goodwin, G. M., McCloskey, D. I., & Matthews, P. B. (1972). Proprioceptive illusions induced by muscle vibration: contribution by muscle spindles to perception? Science (New York, N.Y.), 175(4028), 1382–4. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/4258209.

Grant, John Charles Boileau - An atlas of anatomy, / by regions 1962.

Gregory, R. L. (1997). Eye and brain: The psychology of seeing. Princeton University press.

Groenegress, C., Thomsen, M. R., & Slater, M. (2009). Correlations between Vocal Input and Visual Response. Cyberpsychology, Behavior and Social Networking, 12(4), 429–431.

Groesz, L. M., Levine, M. P., & Murnen, S. K. (2001). The Effect of Experimental Presentation of Thin Media Images on Body Satisfaction : A Meta-Analytic Review. doi:10.1002/eat.10005.

Guariglia, C., Piccardi, L., Puglisi Allegra, M. C., & Traballesi, M. (2002). Is autotopoagnosia real? EC says yes. A case study. Neuropsychologia, 40(10), 1744–9. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11992662.

Haas, E., & Edworthy, J. (2006). An introduction to auditory warnings and alarms. In M. S. Wogalter (Ed.), Handbook of warnings (pp. 189–198). Mahwah: Erlbaum.

Haggard, P., & Wolpert, D. M. (2001). Disorders of Body Scheme. Body Image, 1–7.

Haggard, P., Newman, C., Blundell, J., & Andrew, H. (2000). The perceived position of the hand in space. Perception & Psychophysics, 62(2), 363–77. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10723215.

Hänsel, A., Lenggenhager, B., von Känel, R., Curatolo, M., & Blanke, O. (2011). Seeing and identifying with a virtual body decreases pain perception. European Journal of Pain (London, England), 15(8), 874–9. doi:10.1016/j.ejpain.2011.03.013.

Hausenblas, H. A., Janelle, C. M., Gardner, R. E., & Hagan, A. L. (2003). Affective responses of high and low body satisfied men to viewing physique slides. Eating Disorders, 11(2), 101–113.

Head, H., & Holmes, G. (1911). Sensory disturbance from cerebral lesion. Brain, 34(2-3), 102–254. doi:10.1093/brain/34.2-3.102.

Heilman, K. M., Watson, R. T., & Valenstein, E. (1993). Neglect and related disorders. Clinical Neuropsychology, 3, 279–336.

Hoek, H. W., & Van Hoeken, D. (2003). Review of the prevalence and incidence of eating disorders. International Journal of Eating Disorders, 34(4), 383–396.

Hohwy, J., & Paton, B. (2010). Explaining away the body: experiences of supernaturally caused touch and touch on non-hand objects within the rubber hand illusion. PloS one, 5(2), e9416.

Holmes, N. P., & Spence, C. (2005). Visual bias of unseen hand position with a mirror: spatial and temporal factors. Experimental Brain Research. Experimentelle Hirnforschung. Expérimentation Cérébrale, 166(3-4), 489–97. doi:10.1007/s00221-005-2389-4.

Holst, E., & Mittelstaedt, H. (1950). Das reafferenzprinzip. Naturwissenschaften, 37(20), 464–476.

Humphreys, P., & Paxton, S. J. (2004). Impact of exposure to idealised male images on adolescent boys' body image. Body Image, 1(3), 253–266.

Ionta, S., Heydrich, L., Lenggenhager, B., Mouthon, M., Fornari, E., Chapuis, D., Blanke, O. (2011). Multisensory mechanisms in temporo-parietal cortex support self-location and first-person perspective. Neuron, 70(2), 363–74. doi:10.1016/j.neuron.2011.03.009.

Iriki, A., Tanaka, M., & Iwamura, Y. (1996). Coding of modified body schema during tool use by macaque postcentral neurones. Neuroreport, 7(14), 2325–2330.

Jones, S. H., Cressman, E. K., & Henriques, D. Y. P. (2010). Proprioceptive localization of the left and right hands. Experimental Brain Research. Experimentelle Hirnforschung. Expérimentation Cérébrale, 204(3), 373–83. doi:10.1007/s00221-009-2079-8.

Jonides, J., & Yantis, S. (1988). Uniqueness of abrupt visual onset in capturing attention. Perception& Psychophysics, 43, 346-354.

Kammers, M. P. M., de Vignemont, F., Verhagen, L., & Dijkerman, H. C. (2009). The rubber hand illusion in action. Neuropsychologia, 47(1), 204–11. doi:10.1016/j.neuropsychologia.2008.07.028.

Kammers, M. P. M., Mulder, J., de Vignemont, F., & Dijkerman, H. C. (2010). The weight of representing the body: addressing the potentially indefinite number of body representations in healthy individuals. Experimental Brain Research, 204(3), 333–42. doi:10.1007/s00221-009-2009-9.

Kammers, M. P. M., Rose, K., & Haggard, P. (2011). Feeling numb: Temperature, but not thermal pain, modulates feeling of body ownership. Neuropsychologia, 49(5), 1316–1321. doi:10.1016/j.neuropsychologia.2011.02.039.

Kennett, S., Taylor-Clarke, M., & Haggard, P. (2001). Noninformative vision improves the spatial resolution of touch in humans. Current Biology : CB, 11(15), 1188–91.

Kilteni, K., Bergstrom, I., & Slater, M. (2013). Drumming in Immersive Virtual Reality: The Body Shapes the Way We Play. IEEE Transactions on Visualization and Computer Graphics, 19(4), 597–605. doi:http://doi.ieeecomputersociety.org/10.1109/TVCG.2013.29.

Kitazawa, S. (2002). Where conscious sensation takes place. Consciousness and cognition, 11(3), 475–7.

Klein, R. (1979). Does oculomotor readiness mediate cognitive control of visual attention? Attention and Performance VIII. Hillsdale, N. J.: Lawrence Erlbaum and Associates.

Kolarik, A. J., Cirstea, S., Pardhan, S., & Moore, B. C. J. (2014). A summary of research investigating echolocation abilities of blind and sighted humans. Hearing Research, 310C, 60–68. doi:10.1016/j.heares.2014.01.010.

Krul, A. J., Daanen, H. a M., & Choi, H. (2011). Self-reported and measured weight, height and body mass index (BMI) in Italy, the Netherlands and North America. European Journal of Public Health, 21(4), 414–9. doi:10.1093/eurpub/ckp228.

Lackner, J. (1988). Some proprioceptive influences on the perceptual representation of body shape and orientation. Brain, 111, 281–297.

Lacroix R, Melzack R, Smith D, Mitchell N. Multiple phantom limbs in a child. Cortex 1992; 28: 503–7.

Leit, R. A., Pope, H. G., & Gray, J. J. (2001). Cultural expectations of muscularity in men: The evolution of Playgirl centerfolds. International Journal of Eating Disorders, 29(1), 90–93.

Longo, M. R., Cardozo, S., & Haggard, P. (2008). Visual enhancement of touch and the bodily self. Consciousness and Cognition, 17(4), 1181–1191. doi:10.1016/j.concog.2008.01.001.

Longo, M. R., Kammers, M. P. M., Gomi, H., Tsakiris, M., & Haggard, P. (2009). Contraction of body representation induced by proprioceptive conflict. Current Biology : CB, 19(17), R727–8. doi:10.1016/j.cub.2009.07.024.

Longo, M. R., Kammers, M. P. M., Gomi, H., Tsakiris, M., & Haggard, P. (2009). Contraction of body representation induced by proprioceptive conflict. Current Biology : CB, 19(17), R727–8. doi:10.1016/j.cub.2009.07.024.

Longo, M. R., Schüür, F., Kammers, M. P. M., Tsakiris, M., & Haggard, P. (2008). What is embodiment? A psychometric approach. Cognition, 107(3), 978–98. doi:10.1016/j.cognition.2007.12.004.

Lotze, M., & Moseley, G. L. (2007). Role of distorted body image in pain. Current Rheumatology Reports, 9(6), 488–96. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/18177603.

Makin, T. R., Holmes, N. P., & Ehrsson, H. H. (2008). On the other hand: dummy hands and peripersonal space. Behavioural Brain Research, 191(1), 1–10. doi:10.1016/j.bbr.2008.02.041.

Mancini, F., Longo, M. R., Kammers, M. P. M., & Haggard, P. (2011). Visual distortion of body size modulates pain perception. Psychological Science, 22(3), 325–30. doi:10.1177/0956797611398496.

Marinus, J., Moseley, G. L., Birklein, F., Baron, R., Maihöfner, C., Kingery, W. S., & van Hilten, J. J. (2011). Clinical features and pathophysiology of complex regional pain syndrome. The Lancet. Neurology, 10(7), 637–48. doi:10.1016/S1474-4422(11)70106-5.

Marsh, A. A., Kozak, M. N., Wegner, D. M., Reid, M. E., Yu, H. H., & Blair, R. J. R. (2010). The neural substrates of action identification. Social Cognitive and Affective Neuroscience , 5 (4), 392–403. doi:10.1093/scan/nsq004.

Marshall, W. H., Woolsey, C. N., & Bard, P. (1937). Cortical representation of tactile sensibility as indicated by cortical potentials. Science, 85(2207), 388–390.

McCloskey, D. I. (1973). Differences between the senses of movement and position shown by the effects of loading and vibration of muscles in man. Brain Research, 61, 119–131.

Meier, E. P., & Gray, J. (2014). Facebook photo activity associated with body image disturbance in adolescent girls. Cyberpsychology, Behavior and Social Networking, 17(4), 199–206. doi:10.1089/cyber.2013.0305.

Melzack, R. (1989). Phantom limbs, the self and the brain (the D. O. Hebb Memorial Lecture). Canadian Psychology/Psychologie Canadienne, 30(1), 1–16. doi:10.1037/h0079793.

Melzack, R. (2005). Evolution of the neuromatrix theory of pain. The Prithvi Raj Lecture: presented at the third World Congress of World Institute of Pain, Barcelona 2004. Pain Practice : The Official Journal of World Institute of Pain, 5(2), 85–94. doi:10.1111/j.1533-2500.2005.05203.x.

Melzack, R., & Wall, P. D. (1965). Pain Mechanism: A New Theory.

Melzack, R., Israel, R., Lacroix, R., & Schultz, G. (1997). Phantom limbs in people with congenital limb deficiency or amputation in early childhood. Brain : A Journal of Neurology, 120 (Pt 9, 1603–20. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9313643.

Merleau-Ponty, M. (1996). Phénoménologie de la perception, Paris, Éditions Gallimard, collection « Bibliothèque des Idées », 1945, 531 pages. (Première publication en 1945 dans la collection « Bibliothèque des Idées » ; dans la collection « Tel » à partir de 1976).

Merzenich, M. M., & Kaas, J. H. (1980). Principles of organization of sensory-perceptual systems in mammals. Progress in Psychobiology and Physiological Psychology, 9, 1–42.

Milner, A. D., & Goodale, M. A. (1995). The visual brain in action. Oxford University Press.

Moro, V., Urgesi, C., Pernigo, S., Lanteri, P., Pazzaglia, M., & Aglioti, S. M. (2008). The neural basis of body form and body action agnosia. Neuron, 60(2), 235–46. doi:10.1016/j.neuron.2008.09.022.

Moseley G.L., Flor H. (2012). Targeting cortical representations in the treatment of chronic pain: a review. Neurorehabilitation and Neural Repair 26(6):646-52.

Moseley G.L., Gallagher L., Gallace A. (2012) Neglect-like tactile dysfunction in chronic back pain. Neurology 79(4):327-32.

Moseley, G. L. (2004). Why do people with complex regional pain syndrome take longer to recognize their affected hand? Neurology, 62(12), 2182–2186.

Moseley, G. L. (2005). Clinical / Scientific Notes Distorted body image in complex, 773–778.

Moseley, G. L., & Brugger, P. (2009). Interdependence of movement and anatomy persists when amputees learn a physiologically impossible. Proceedings of the National Academy of Sciences of the United States of America, 106(44), 18798–18802.

Moseley, G. L., Gallace, A., & Spence, C. (2009). Space-based, but not arm-based, shift in tactile processing in complex regional pain syndrome and its relationship to cooling of the affected limb. Brain : A Journal of Neurology, 132(Pt 11), 3142–51. doi:10.1093/brain/awp224.

Moseley, G. L., Gallace, A., & Spence, C. (2012). Bodily illusions in health and disease: physiological and clinical perspectives and the concept of a cortical “body matrix”. Neuroscience and Biobehavioral Reviews, 36(1), 34–46. doi:10.1016/j.neubiorev.2011.03.013.

Moseley, G. L., Olthof, N., Venema, A., Don, S., Wijers, M., Gallace, A., & Spence, C. (2008). Psychologically induced cooling of a specific body part caused by the illusory ownership of an artificial counterpart. Proceedings of the National Academy of Sciences of the United States of America, 105(35), 13169–73. doi:10.1073/pnas.0803768105.

Moseley, G. L., Parsons, T. J., & Spence, C. (2008). Visual distortion of a limb modulates the pain and swelling evoked by movement. Current Biology : CB, 18(22), R1047–8. doi:10.1016/j.cub.2008.09.031.

Moseley, G.L., Gallace A., Iannetti G.D. (2012) Spatially defined modulation of skin temperature and hand ownership of both hands in patients with unilateral complex regional pain syndrome. Brain 135(Pt 12):3676-86.

Moseley, G.L., Gallace, A., and Spence, C. (2009). Space-based, but not arm-based, shift in tactile processing in complex regional pain syndrome and its relationship to cooling of the affected limb. Brain 132, 3142-3151.

Murray, W. M., Delp, S. L., & Buchanan, T. S. (1995). Variation of muscle moment arms with elbow and forearm position. Journal of Biomechanics, 28(5), 513–25.

Mussap, A. J., & Salton, N. (2006). A “rubber-hand” illusion reveals a relationship between perceptual body image and unhealthy body change. Journal of Health Psychology, 11(4), 627–39. doi:10.1177/1359105306065022.

Nemeroff, C. J., Stein, R. I., Diehl, N. S., & Smilack, K. M. (1994). From the Cleavers to the Clintons: Role choices and body orientation as reflected in magazine article content. International Journal of Eating Disorders, 16(2), 167–176.

Netter, F. H., & Colacino, S. (1989). Atlas of human anatomy. Ciba-Geigy Corporation.

Newport, R., & Gilpin, H. R. (2011). Multisensory disintegration and the disappearing hand trick. Current Biology : CB, 21(19), R804–5. doi:10.1016/j.cub.2011.08.044.

Newport, R., & Schenk, T. (2012). Prisms and neglect: what have we learned? Neuropsychologia, 50(6), 1080–91. doi:10.1016/j.neuropsychologia.2012.01.023.

Newport, R., Hindle, J. V, & Jackson, S. R. (2001). Links between vision and somatosensation. Vision can improve the felt position of the unseen hand. Current Biology : CB, 11(12), 975–80. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11448775.

Newport, R., Pearce, R., & Preston, C. (2010). Fake hands in action: embodiment and control of supernumerary limbs. Experimental Brain Research. Experimentelle Hirnforschung. Expérimentation Cérébrale, 204(3), 385–95. doi:10.1007/s00221-009-2104-y.

Newport, R., Preston, C., Pearce, R., & Holton, R. (2009). Eye rotation does not contribute to shifts in subjective straight ahead: implications for prism adaptation and neglect. Neuropsychologia, 47(8-9), 2008–12. doi:10.1016/j.neuropsychologia.2009.02.017.

Noll, S. M., & Fredrickson, B. L. (1998). A mediational model linking self-objectification, body shame, and disordered eating. Psychology of Women Quarterly, 22(4), 623–636.

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(4), 1009–1022. doi:10.1093/brain/108.4.1009.

Ogden, J. E., & Mundray, K. (1996). The effect of the media on body satisfaction: The role of gender and size. European Eating Disorders Review, 4(3), 171–182.

Owen, R., 1843. Lectures on Comparative Anatomy and Physiology of the Invertebrate Animals. Longmans, Brown, Green and Longmans, London.

Paillard, J. (1991). Knowing where and knowing how to get there. Paillard, Jacques (Ed), (1991). Brain and space, (pp. 461-481), New York, NY, US: Oxford University Press, xi, 499 pp.

Paillard, J. (1999). Body schema and body image: a double dissociation in deafferented patients. Motor control, today and tomorrow, 197.

Paillard, J., Brouchon, M. (1968). Active and passive movements in the calibration of position sense. In: S.J., Freedman (Ed.), The neuropsychology of spatially oriented behaviour (pp 35–56). Illinois: Dorsey Press.

Paillard, J., Michel, F., & Stelmach, G. (1983). Localization without content: A tactile analogue of'blind sight'. Archives of neurology, 40(9), 548-551.

Pavani, F., Spence, C., & Driver, J. (2000). Visual Capture of Touch: Out-of-the-Body Experiences With Rubber Gloves. Psychological Science, 11(5), 353–359.

Peck, T. C., Seinfeld, S., Aglioti, S. M., & Slater, M. (2013). Putting yourself in the skin of a black avatar reduces implicit racial bias. Consciousness and Cognition, 22(3), 779–787. doi:10.1016/j.concog.2013.04.016.

Peelen, M. V., & Downing, P. E. (2005). Selectivity for the human body in the fusiform gyrus. *Journal of neurophysiology*, *93*(1), 603-608.

Penfield, W., & Boldrey, E. (1937). Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. Brain, 60(4), 389–443. doi:10.1093/brain/60.4.389.

Penfield, W., & Rasmussen, T. (1950). The cerebral cortex of man; a clinical study of localization of function. Rasmussen, Theodore (Eds), Oxford, England: Macmillan. (1950). xv 248 pp.

Perez-Marcos, D., Slater, M., & Sanchez-Vives, M. V. (2009). Inducing a virtual hand ownership illusion through a brain–computer interface. NeuroReport, 20(6), 589–594. doi:10.1097/WNR.0b013e32832a0a2a.

Petkova, V. I., & Ehrsson, H. H. (2008). If I were you: perceptual illusion of body swapping. *PloS One*, *3*(12), e3832. doi:10.1371/journal.pone.0003832.

Petkova, V. I., Björnsdotter, M., Gentile, G., Jonsson, T., Li, T.-Q., & Ehrsson, H. H. (2011). From part- to whole-body ownership in the multisensory brain. Current Biology : CB, 21(13), 1118–22. doi:10.1016/j.cub.2011.05.022.

Pick, A. (1922). Störung der Orientierung am eigenen Körper. Psychologische Forschung, 1(1), 303–318. doi:10.1007/BF00410392.

Pitcher, D., Charles, L., Devlin, J. T., Walsh, V., & Duchaine, B. (2009). Triple dissociation of faces, bodies, and objects in extrastriate cortex. Current Biology : CB, 19(4), 319–24. doi:10.1016/j.cub.2009.01.007.

Poeck K. Phantoms following amputation in early childhood and in congenital absence of limbs. Cortex 1964; 1: 269–75.

Posner, M. I. (1980). Orienting of attention. Quarterly Journal of Experimental Psychology (2006), (32), 3–25.

Posner, M. I., Nissen, M. J. and Ogden, W. C. (1978). Attended and unattended processing modes: The role of set for spatial location. In Pick, H. L. and Saltzman, I. J. (Eds), Modes of Perceiving and Processing Information. Hillsdale, N.J.: Lawrence Erlbaum Associates.

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(11), 2621–5. doi:10.1016/j.neuropsychologia.2007.04.005.

Press, C., Taylor-Clarke, M., Kennett, S., & Haggard, P. (2004). Visual enhancement of touch in spatial body representation. Experimental Brain Research. Experimentelle Hirnforschung. Expérimentation Cérébrale, 154(2), 238–45. doi:10.1007/s00221-003-1651-x.

Preston, C. (2013). The role of distance from the body and distance from the real hand in ownership and disownership during the rubber hand illusion. Acta Psychologica, 142(2), 177–83. doi:10.1016/j.actpsy.2012.12.005.

Preston, C., & Newport, R. (2011). Analgesic effects of multisensory illusions in osteoarthritis. Rheumatology (Oxford, England), 50(12), 2314–5. doi:10.1093/rheumatology/ker104.

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(4), 1651–97. doi:10.1152/physrev.00048.2011.

Rade, G., Perenin, M. T., Honoré, J., & Boisson, D. (1998). Improvement of the motor deficit of neglect patients through vestibular stimulation: evidence for a motor neglect component. Cortex, 34(2), 253–261.

Ramachandran, V.S. Behavioral and magnetoencephalographic correlates of plasticity in the adult human brain. Proceedings Natural Academy of Science USA 1993; 90: 10413–20.

Ramachandran, V. S., & Rogers-Ramachandran, D. (1996). Synaesthesia in phantom limbs induced with mirrors. Proceedings. Biological Sciences / The Royal Society, 263(1369), 377–386.

Rohde, M., Di Luca, M., & Ernst, M. O. (2011). The Rubber Hand Illusion: feeling of ownership and proprioceptive drift do not go hand in hand. PloS One, 6(6), e21659. doi:10.1371/journal.pone.0021659.

Ronchi, R., & Vallar, G. (2010). Après lésion droite: somatoparaphrénie. Revue de Neuropsychologie Neurosciences Cognitives et Cliniques, 2(EPFL-ARTICLE-183227), 225–230.

Rossetti, Y., and Rode, G. (2002). “Reducing spatial neglect by visual and other sensory manipulations: noncognitive (physiological) routes to the rehabilitation of a cognitive disorder," in The Cognitive and Neural Bases of Spatial Neglect, eds H. O. Karnath, D. Milner, and G. Vallar (New York, NY: Oxford University.

Rossetti, Y., Rode, G. & Boisson, D. (2001) Numbsense: A case study and implications. In: Out of mind: Varieties of unconscious processing, ed. B. de Gelder, E.H. F.De Haan&C. A.Heywood. Oxford University Press.

Rossetti, Y., Rode, G., Pisella, L., Alessandro, F., Li, L., Boisson, D., & Perenin, M.-T. (1998). Prism adaptation to a rightward optical deviation rehabilitates left hemispatial neglect, 395(September), 8–11.

Rubens, A. B. (1985). Caloric stimulation and unilateral visual neglect. Neurology, 35(7), 1019.

Saadah ES, Melzack R. Phantom limb experiences in congenital limb-deficient adults. Cortex 1994; 30: 479–85.

Sambo, C. F., Torta, D. M., Gallace, A., Liang, M., Moseley, G. L., & Iannetti, G. D. (2013). The temporal order judgement of tactile and nociceptive stimuli is impaired by crossing the hands over the body midline. Pain, 154(2), 242–7. doi:10.1016/j.pain.2012.10.010.

Saxe, R., Jamal, N., & Powell, L. (2006). My Body or Yours? The Effect of Visual Perspective on Cortical Body Representations. Cerebral Cortex , 16 (2), 178–182. doi:10.1093/cercor/bhi095

Schilder, P. (1936). The Image and Appearance of the Human Body: Studies in the Constructive Energies of the Psyche. Psyche Monographs, No. 4. The Journal of Nervous and Mental Disease, 83 (2), 227-228.

Schilder, R. (1923). Das korperschema. Verlag J. Springer.

Schwarzlose, R. F., Baker, C. I., & Kanwisher, N. (2005). Separate Face and Body Selectivity on the Fusiform Gyrus. The Journal of Neuroscience , 25 (47), 11055–11059. doi:10.1523/JNEUROSCI.2621-05.2005.

Schwoebel, J., & Coslett, H. B. (2005). Evidence for multiple, distinct representations of the human body. Journal of Cognitive Neuroscience, 17(4), 543–53. doi:10.1162/0898929053467587.

Semenza, C. (1988). Impairment in Localization of Body Parts Following Brain Damage. Cortex, 24(3), 443–449. doi:10.1016/S0010-9452(88)80007-8.

Semenza, C., & Goodglass, H. (1985). Localization of body parts in brain injured subjects, 23(2), 161–175.

Serino, A., Alsmith, A., Costantini, M., Mandrigin, A., Tajadura-Jimenez, A., & Lopez, C. (2013). Bodily ownership and self-location: components of bodily self-consciousness. Consciousness and Cognition, 22(4), 1239–52. doi:10.1016/j.concog.2013.08.013.

Shaw, J. (1995). Effects of fashion magazines on body dissatisfaction and eating psychopathology in adolescent and adult females. European Eating Disorders Review, 3(1), 15–23.

Shaw, M. L. (1978). A capacity allocation model for reaction time. Journal of Experimental Psychology: Human Perception and Performance, 4, 586-98.

Sierra, M., & Berrios, G. E. (1998). Depersonalization: neurobiological perspectives. Biological Psychiatry, 44(9), 898–908. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9807645.

Silberpfennig, M. D. J. (1941). Contributions to the problem of eye movements. III. Disturbances of ocular movements with pseudohemianopsia in frontallobetumors. Confin. Neurol. 42, 1–13. doi: 10.1159/000106147.

Simmel, M. L. (1958). The conditions of occurrence of phantom limbs. Proceedings of the American Philosophical Society, 492-500.

Sirigu, A., Grafman, J., Bressler, K., & Sunderland, T. (1991). Multiple representations contribute to body knowledge processing: evidence from a case of autotopagnosia . Brain , 114 (1), 629–642. doi:10.1093/brain/114.1.629.

Smeets, J. B. J., van den Dobbelsteen, J. J., de Grave, D. D. J., van Beers, R. J., & Brenner, E. (2006). Sensory integration does not lead to sensory calibration. Proceedings of the National Academy of Sciences of the United States of America, 103(49), 18781–6. doi:10.1073/pnas.0607687103.

Sokolov EN (1963): Perception and the conditioned reflex. Oxford: Pergamon Press.

Soto-Faraco, S., Ronald, A., & Spence, C. (2004). Tactile selective attention and body posture: assessing the multisensory contributions of vision and proprioception. Perception & psychophysics, 66(7), 1077–94.

Sperry, R. W. (1950). Neural basis of the spontaneous optokinetic response produced by visual inversion. Journal of Comparative and Physiological Psychology, 43(6), 482.

Spitzer, B. L., Henderson, K. A., & Zivian, M. T. (1999). Gender differences in population versus media body sizes: A comparison over four decades. Sex Roles, 40(7-8), 545–565.

Stanton, T. R., Lin, C. W., Bray, H., Smeets, R. J., Taylor, D., Law, R. Y., Moseley, G. L. (2013) Tactile acuity is disrupted in osteoarthritis but is unrelated to disruptions in motor imagery performance. Rheumatology, 52(8), 1509-1519.

Steptoe, W., Steed, A., & Slater, M. (2013). Human Tails: Ownership and Control of Extended Humanoid Avatars. IEEE Transactions on Visualization and Computer Graphics, 19(4), 583–590. doi:http://doi.ieeecomputersociety.org/10.1109/TVCG.2013.32.

Stratton, G. M. (1897). Vision without inversion of the retinal image. Psychological Review, 4(4), 341.

Sundgot-Borgen, J. (1993). Prevalence of eating disorders in elite female athletes. International Journal of Sport Nutrition, 3(1), 29–40.

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), 1626–33. doi:10.1152/jn.00012.2007.

Thakkar, K. N., Nichols, H. S., McIntosh, L. G., & Park, S. (2011). Disturbances in Body Ownership in Schizophrenia: Evidence from the Rubber Hand Illusion and Case Study of a Spontaneous Out-of-Body Experience. (M. H. Herzog, Ed.)PLoS ONE, 6(10), e27089.

Thompson, E. (2005). Sensorimotor subjectivity and the enactive approach to experience, 407–427. doi:10.1007/s11097-005-9003-x.

Thompson, M. G., & Schwartz, D. M. (1982). Life adjustment of women with anorexia nervosa and anorexic-like behavior. International Journal of Eating Disorders, 1(2), 47–60.

Thomsen, S. R., McCoy, J. K., Gustafson, R., & Williams, Hm. (2002). Motivations for reading beauty and fashion magazines and anorexic risk in college-age women. Media Psychology, 4(2), 113–135.

Torta, D. M., Diano, M., Costa, T., Gallace, A., Duca, S., Geminiani, G. C., & Cauda, F. (2013). Crossing the line of pain: FMRI correlates of crossed-hands analgesia. The Journal of Pain : Official Journal of the American Pain Society, 14(9), 957–65. doi:10.1016/j.jpain.2013.03.009.

Tovée, M. J., Benson, P. J., Emery, J. L., Mason, S. M., & Cohen-Tovée, E. M. (2003). Measurement of body size and shape perception in eating-disordered and control observers using body-shape software. British Journal of Psychology (London, England : 1953), 94(Pt 4), 501–16. doi:10.1348/000712603322503060.

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. doi:10.1037/0096-1523.31.1.80.

Tsakiris, M., Hesse, M. D., Boy, C., Haggard, P., & Fink, G. R. (2007). Neural signatures of body ownership: a sensory network for bodily self-consciousness. Cerebral Cortex (New York, N.Y. : 1991), 17(10), 2235–44. doi:10.1093/cercor/bhl131.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical systems. In D. J. Ingle, M. Goodale, & R. J.W. Mansfield (Eds.), Analysis of visual behaviour (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 nonfacial body parts. Current Biology : CB, 14(23), 2130–4. doi:10.1016/j.cub.2004.11.031.

Urgesi, C., Candidi, M., Ionta, S., & Aglioti, S. M. (2007). Representation of body identity and body actions in extrastriate body area and ventral premotor cortex. Nat Neurosci, 10(1), 30–31. Retrieved from http://dx.doi.org/10.1038/nn1815.

Vallar, G., & Ronchi, R. (2009). Somatoparaphrenia: a body delusion. A review of the neuropsychological literature. Experimental Brain Research, 192(3), 533–51. doi:10.1007/s00221-008-1562-y.

Van Beers, R. J., Sittig, a C., & Denier van der Gon, J. J. (1996). How humans combine simultaneous proprioceptive and visual position information. Experimental Brain Research. Experimentelle Hirnforschung. Expérimentation Cérébrale, 111(2), 253–61. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/8891655.

Van Beers, R. J., Sittig, a C., & Denier van der Gon, J. J. (1998). The precision of proprioceptive position sense. Experimental brain research. Experimentelle Hirnforschung. Expérimentation cérébrale, 122(4), 367–77.

Van Beers, R. J., Sittig, a C., & Denier van der Gon, J. J. (1999). Localization of a seen finger is based exclusively on proprioception and on vision of the finger. Experimental Brain Research. Experimentelle Hirnforschung. Expérimentation Cérébrale, 125(1), 43–9. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10100975.

Van Beers, R. J., Sittig, A. C., & Van Der Gon, J. J. D. (1999). Integration of Proprioceptive and Visual Position-Information : An Experimentally Supported Model. Journal of Neurophysiology, 81(3), 1355–1364.

Van Beers, R. J., Wolpert, D. M., & Haggard, P. (2002). When feeling is more important than seeing in sensorimotor adaptation. Current Biology : CB, 12(10), 834–7. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12015120.

Varraine, E., Bonnard, M., & Pailhous, J. (2002). The top down and bottom up mechanisms involved in the sudden awareness of low level sensorimotor behavior. Brain Research. Cognitive Brain Research, 13(3), 357–61.

Von Voorhis, S. and Hillyard, S. A. (1977). Visual evoked potentials and selective attention to points in space. Perception and Psychophysics, 22, 54-62.

Vu, K.-P. L., Minakata, K., & Ngo, M. K. (2013). Influence of auditory and audiovisual stimuli on the right-left prevalence effect. Psychological research 78(3), 400-410.

Wand B.M., Parkitny L., O'Connell N.E., Luomajoki H., McAuley J.H., Thacker M., Moseley G.L. Cortical changes in chronic low back pain: current state of the art and implications for clinical practice. Manual Therapy 16(1):15-20.

Wand, B. M., Tulloch, V. M., George, P. J., Smith, A. J., Gouke, R., O'Connell, N. E., Moseley, G. L. (2012). Seeing it helps: movement-related back pain is reduced by visualization of the back during movement. Clinical Journal of Pain 28(7):602-8.

Wang, J. J., Miletich, D. D., Ramsey, R., & Samson, D. (2014). Adults see vision to be more informative than it is. Quarterly Journal of Experimental Psychology (2006), 67(12), 2279–92. doi:10.1080/17470218.2014.915331.

Wann, J. P. (1991). The integrity of visual-proprioceptive mapping in cerebral palsy. Neuropsychologia, 29(11), 1095–106. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/1775227.

Wann, J. P., & Ibrahim, S. F. (1992). Does limb proprioception drift? Experimental Brain Research. Experimentelle Hirnforschung. Expérimentation Cérébrale, 91(1), 162–6. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/1301369.

Weinstein, S., Sersen, E. A., & Vetter, R. J. (1964). Phantoms and somatic sensation in cases of congenital aplasia. Cortex, 1(3), 276-290.

Weinstein, S., and Sersen, E. A. (1961). Phantoms in cases of congenital absence of limbs. Neurology.

White, J. C., & Sweet, W. H. (1969). Pain and the neurosurgeon: a forty-year experience. CC Thomas Springfield.

Winter, J. a, Allen, T. J., & Proske, U. (2005). Muscle spindle signals combine with the sense of effort to indicate limb position. The Journal of Physiology, 568(Pt 3), 1035–46. doi:10.1113/jphysiol.2005.092619.

Wold, A., Limanowski, J., Walter, H., & Blankenburg, F. (2014). Proprioceptive drift in the rubber hand illusion is intensified following 1 Hz TMS of the left EBA. Frontiers in Human Neuroscience, 8(June), 1–6. doi:10.3389/fnhum.2014.00390.

Wurtz, R. H. and Mohler, C. W. (1976). Organization of monkey superior colliculus: enhanced visual response of superficial layer cells. Journal of Neurophysiology, 39, 745-765.

Yamamoto, S., & Kitazawa, S. (2001). Reversal of subjective temporal order due to arm crossing. Nature Neuroscience, 4(7), 759–65. doi:10.1038/89559.

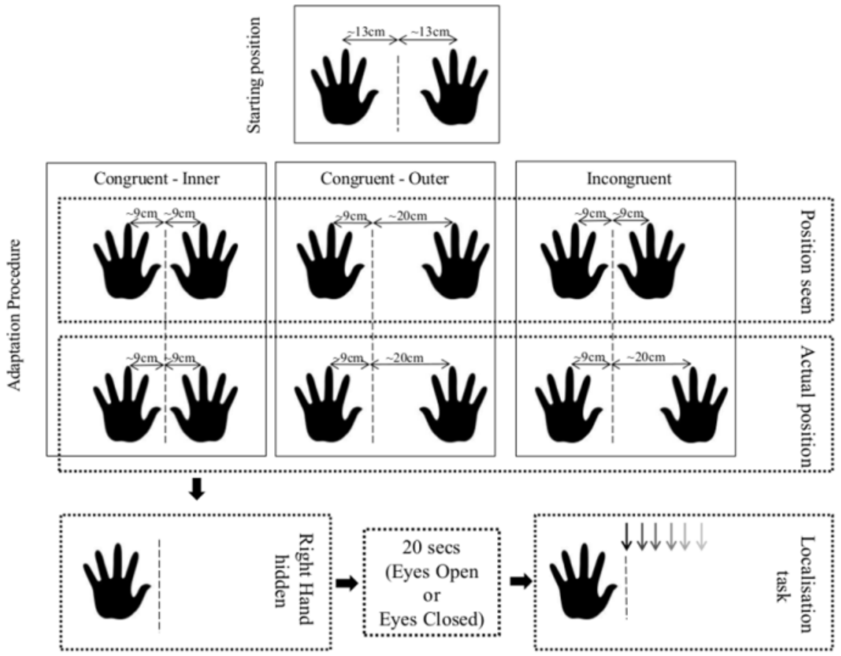
Yantis, S., & Hillstrom,A. P. (1994). Stimulus-driven attentional capture: Evidence from equiluminant visual objects. Journal of Experimental Psychology: Human Perception & Performance, 20, 95-107.

Zopf, R., Savage, G., & Williams, M. a. (2010). Crossmodal congruency measures of lateral distance effects on the rubber hand illusion. Neuropsychologia, 48(3), 713–25.

APPENDICES

Appendix 1

Fig. S1: Experimental design



Initially the position of the participant’s hand was 13 cm away from the body midline. At the end of the adaptation procedure the left hand was 9 cm away from the body midline in all the conditions. In contrast, the shift of the right hand varied. In the Congruent condition the final position of the right hand was 9 cm from the midline (i.e. 4 cm inward; the ‘Inward’ condition) or 20 cm from the body midline (i.e. 7 cm outward; the ‘Outward’ condition). In the Incongruent condition, the right hand was 20 cm away from the midline (i.e. 7 cm rightwards from initial position), but its image was positioned at 9 cm from the midline (i.e. 4 cm leftwards from initial position). Thus, in the Incongruent condition the seen position was the same as it was in the Inward condition, but its real position was the same as it was in the Outward condition, leading to an incongruency between vision and proprioception. When the adaptation procedure was concluded, the right hand disappeared from view and the participants were either asked to keep their eyes closed for 20 sec or to keep fixating on where they felt their right hand to be. Then the localisation task started and the participants were asked to say stop when a superimposed moving red arrow was aligned with where they felt their middle fingertip to be.

Table S1: Conditions performed

Conditions	Eyes	Seen movement	Real movement	Congruency
1	Open	Inward	Inward	yes
2	Closed	Inward	Inward	yes
3	Open	Outward	Outward	yes
4	Closed	Outward	Outward	yes
5	Open	Inward	Outward	no
6	Closed	Inward	Outward	no

Training procedure: practice protocol for the localization task

Before starting the experiment, the participants underwent a training procedure in order to familiarise with the localisation task. We employed a standardised practice protocol, which consisted of three components:

(1) *Self-paced, hand seen.* The participants were able to see both of their hands, but they were asked to fixate on their right middle fingertip while the red arrow moved from the centre of the screen towards the right. The movement of the arrow across the screen was called ‘a trial’. The participants were instructed to say ‘stop’ when the arrow was aligned with their middle fingertip. The aim of this first component was to get the participants accustomed to stopping the arrow exactly when they wanted it to stop. There were no time constraints. After 5 trials, the participants were allowed more trials if either they, or the investigator, judged that they needed more practice. Once both participant and investigator were satisfied that they were accurate, we moved to the second component.

(2) *Every 15”, hand seen.* Even though the participants were still able to see their hand, they were not allowed to adjust the position of the arrow once they made their judgement. The aim of this second part was to become accustomed to the pace of the real experiment, in which a trial commenced every 15”. This also assured that the participants were sufficiently accurate in stopping the arrow exactly where they

wanted it to in a time-constrained context. This step included 7 trials (i.e. 2 trials more than the first one) in order to get the participants gradually used to the experiment full duration (as the localisation task included 13 trials). Once both the participant and the investigator were satisfied that they were accurate, then we moved to the third component.

(3) *Every 15", hand covered*. In these final practice trials, we covered the image of the right participants' hand with a black square on the screen, to mimic the experiment. The participants were told that the experimenter was going to cover their right hand, but they had to fixate on where they felt their right middle fingertip to be and stop the arrow accordingly, just as they had in the previous trials. Again, a trial commenced every 15" and the participants were not allowed to adjust its position (i.e. once they stopped, the position was recorded and the trial was complete). There were 10 trials. Once both the participant and investigator were satisfied that they were performing the task consistently, then we proceeded to the experiment.

Table S2:

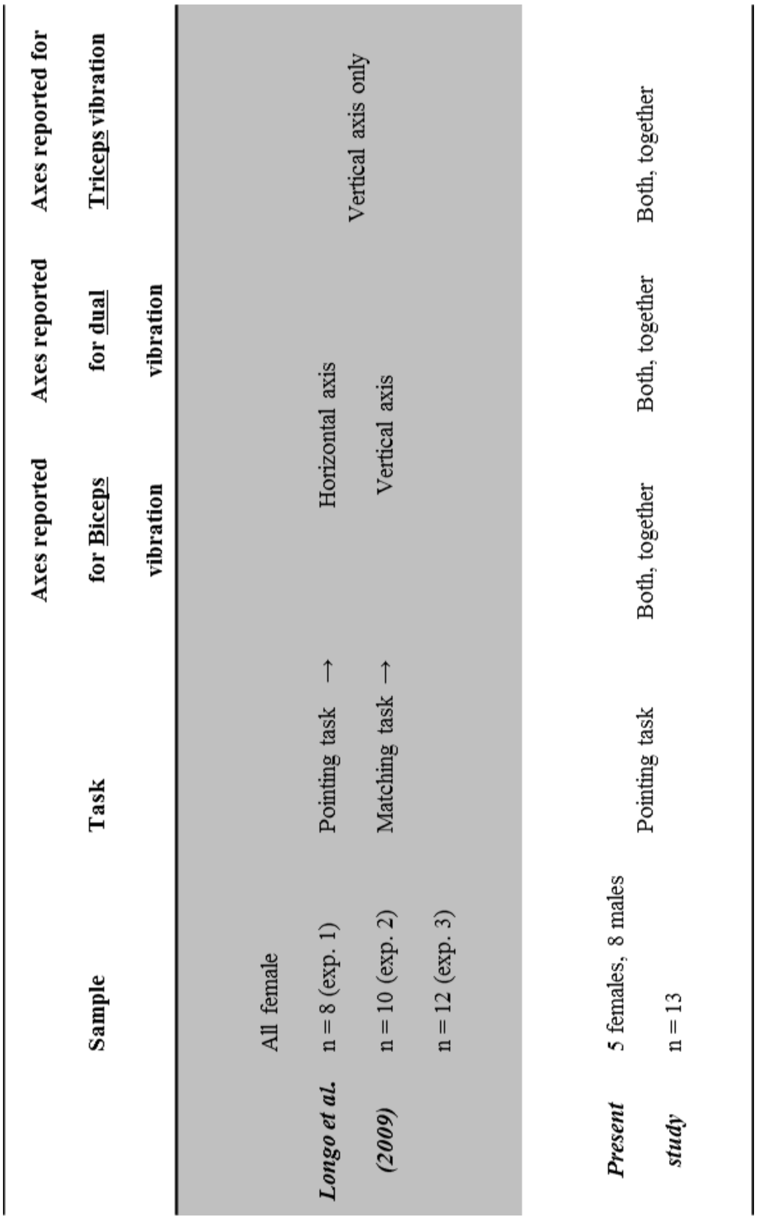
Questionnaire item	**Cond**	**mean**	**SD**	**F**	**p (α=0.0167)**
My right hand was part of my body	CI EO	9.19	1.60	1.185	0.319
	CI EC	9.37	1.09		
	CO EO	9.56	0.89		
	CO EC	9.56	0.96		
	INC EO	9.31	1.58		
	INC EC	9.12	2.03		
It seemed like I had no right hand	CI EO	1.89	2.53	0.879	0.386
	CI EC	0.75	1.34		
	CO EO	0.69	1.14		
	CO EC	1.12	2.55		
	INC EO	1.44	2.87		
	INC EC	1.25	2.69		
It seemed like my right hand was no longer there	CI EO	2.25	3.53	0.324	0.767
	CI EC	2.06	3.71		
	CO EO	2.25	3.73		
	CO EC	2.12	3.61		
	INC EO	2.06	3.60		
	INC EC	2.31	3.70		
It seemed that my right hand no longer belonged to me	CI EO	1.31	2.70	0.946	0.362
	CI EC	1.06	1.61		
	CO EO	1.19	2.66		
	CO EC	0.62	1.26		
	INC EO	1.50	2.76		
	INC EC	1.31	2.77		

I had the sensation that my hand was numb	CI EO	2.06	2.77	1.119	0.331
	CI EC	1.50	2.19		
	CO EO	1.31	1.96		
	CO EC	1.81	3.10		
	INC EO	1.37	2.30		
	INC EC	1.06	1.95		
It seemed like I had more than one right hand	CI EO	0.44	0.81	1.471	0.248
	CI EC	0.56	1.09		
	CO EO	0.50	0.97		
	CO EC	0.44	0.81		
	INC EO	0.44	0.81		
	INC EC	0.50	0.97		
I couldn’t tell where my right hand was	CI EO	4.19	3.19	0.768	0.512
	CI EC	3.87	3.54		
	CO EO	3.69	3.46		
	CO EC	4.69	3.34		
	INC EO	4.06	3.47		
	INC EC	4.75	3.36		

Mean and standard deviation (SD) responses to each statement for each condition. The participants were asked to give a number between 0 and 10 in order to describe their degree of agreement with each statement. The right-most column shows significance values for each comparison. Note that **α** was set at 0.0167, and there were no significant differences between conditions for any of the items.

Appendix 2

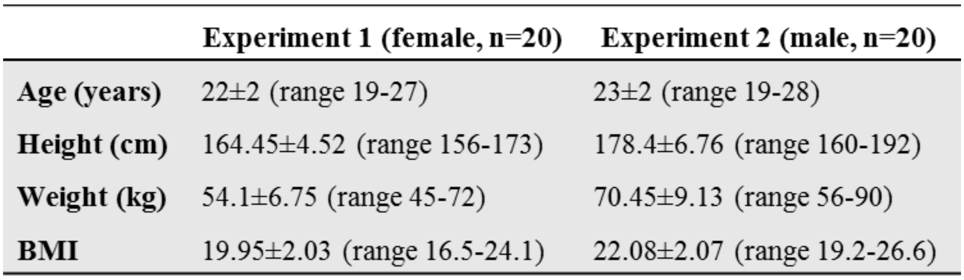
Table S1



	Sample	Task	Axes reported for **Biceps** vibration	Axes reported for **dual** vibration	Axes reported for **Triceps** vibration
Longo et al. (2009)	All female n = 8 (exp. 1) n = 10 (exp. 2) n = 12 (exp. 3)	Pointing task → Matching task →	Horizontal axis Vertical axis		Vertical axis only
Present study	5 females, 8 males n = 13	Pointing task	Both, together	Both, together	Both, together

Appendix 3

Table S1



	Experiment 1 (female, n=20)	Experiment 2 (male, n=20)
Age (years)	22±2 (range 19-27)	23±2 (range 19-28)
Height (cm)	164.45±4.52 (range 156-173)	178.4±6.76 (range 160-192)
Weight (kg)	54.1±6.75 (range 45-72)	70.45±9.13 (range 56-90)
BMI	19.95±2.03 (range 16.5-24.1)	22.08±2.07 (range 19.2-26.6)

EAT (Eating Attitude Test), Italian version (Dotti & Lazzari, 2014)

For each statement, participants were asked to report a number from 0 to 5 (0 meaning never and 5 always). The Italian version of the statements employed in both Experiment 1 and 2 follows.

1. *Ho una terribile paura di ingrassare.*
2. *Evito di mangiare quando ho fame.*
3. *Penso al cibo con preoccupazione.*
4. *Mi è capitato di mangiare con enorme voracità e di non riuscire a fermarmi.*
5. *Ho l'abitudine di sminuzzare il cibo.*
6. *Presto molta attenzione al contenuto calorico dei cibi che mangio.*
7. *Tendo ad evitare i cibi con elevato contenuto di carboidrati (pane, pasta, riso, patate, dolci).*
8. *Ho la sensazione che gli altri vorrebbero che mangiassi di più.*
9. *Dopo mangiato mi capita di vomitare.*
10. *Mi sento estremamente in colpa dopo che ho mangiato.*
11. *Sento un forte desiderio di essere più magro/a.*
12. *Quando faccio ginnastica penso a quante calorie sto bruciando.*
13. *Gli altri mi vedono troppo magro/a.*
14. *Sono preoccupato/a al pensiero di avere del grasso sul mio corpo.*
15. *Quando mangio impiego più tempo degli altri per finire il pasto.*
16. *Evito i cibi che contengono zuccheri.*
17. *Mangio cibi dietetici.*
18. *Sento che il cibo controlla la mia vita.*
19. *Mi piace mostrare auto-controllo sul cibo e dominare la fame.*
20. *Gli altri fanno pressione su di me perché io mangi di più.*
21. *Dedico al cibo troppo tempo e troppi pensieri.*
22. *Mi sento a disagio dopo aver mangiato dei dolci.*
23. *Tendo a seguire delle diete.*
24. *Mi piace quando sento che il mio stomaco è vuoto.*
25. *Provo l'impulso di vomitare dopo aver mangiato.*
26. *Mi piace provare cibi nuovi ed elaborati.*

BUT (Body Uneasiness Test), Italian version (Cuzzolaro et al., 2006)

For each statement, participants were asked to report a number from 0 to 5 (0 meaning never and 5 always). The Italian version of the statements employed in both Experiment 1 and 2 follows.

BUT-1

1. *Trascorro molto tempo davanti allo specchio.*
2. *Non mi fido del mio aspetto: temo che cambi, all'improvviso.*
3. *Mi piacciono gli abiti che nascondono le forme del mio corpo.*
4. *Passo molto tempo pensando a certi difetti della mia immagine fisica.*
5. *Quando mi spoglio evito di guardarmi.*
6. *Penso che la mia vita cambierebbe enormemente se potessi correggere alcuni miei difetti fisici.*
7. *Mangiare in presenza di altri mi provoca ansia.*
8. *Il pensiero di alcuni difetti del mio corpo mi tormenta tanto da impedirmi di stare con gli altri.*
9. *Ho il terrore di ingrassare.*
10. *Faccio lunghi confronti fra il mio aspetto e quello degli altri.*
11. *Se comincio a guardarmi mi è difficile smettere.*
12. *Farei qualsiasi cosa per modificare certe parti del mio corpo.*
13. *Resto in casa ed evito di farmi vedere dagli altri.*
14. *Mi vergogno dei bisogni fisici del mio corpo.*
15. *Mi sento deriso/a per il mio aspetto.*
16. *Il pensiero di alcuni difetti del mio corpo mi tormenta tanto da impedirmi di studiare o lavorare.*
17. *Cerco nello specchio un'immagine di me che mi soddisfi.*
18. *Mi sento più grasso/a di quello che mi dicono gli altri.*
19. *Evito gli specchi.*
20. *Ho l'impressione che la mia immagine cambi continuamente.*
21. *Vorrei avere un corpo secco e duro.*
22. *Sono insoddisfatto/a del mio aspetto.*
23. *Il mio aspetto fisico è deludente rispetto la mia immagine ideale.*
24. *Vorrei sottopormi a qualche intervento di chirurgia estetica.*
25. *Non sopporto l'idea di vivere con l'aspetto che ho.*
26. *Mi guardo allo specchio e provo un senso di inquietudine e di estraneità.*
27. *Temo che il mio corpo cambi contro la mia volontà in modi che non mi piacciono.*
28. *Mi sento scollato/a dal mio corpo.*
29. *Ho la sensazione che il mio corpo non mi appartenga.*
30. *Il pensiero di alcuni difetti del mio corpo mi tormenta tanto da impedirmi di avere una vita sessuale.*
31. *Mi osservo in quello che faccio e mi chiedo come appaio agli altri.*
32. *Vorrei decidere io che aspetto avere.*
33. *Mi sento diverso/a da come mi vedono gli altri.*
34. *Mi vergogno del mio corpo.*

BUT-2

Del mio corpo in particolare detesto:

1. *La statura*
2. *La forma della testa*
3. *La forma del viso*
4. *La pelle*
5. *I capelli*
6. *La fronte*
7. *Le sopracciglia*
8. *Gli occhi*
9. *Il naso*
10. *Le labbra*
11. *La bocca*
12. *I denti*
13. *Le orecchie*
14. *Il collo*
15. *Il mento*
16. *I baffi*
17. *La barba*
18. *I peli*
19. *Le spalle*
20. *Le braccia*
21. *Le mani*
22. *Il torace*
23. *Le mammelle*
24. *Lo stomaco*
25. *Il ventre*
26. *I genitali*
27. *Le natiche*
28. *Le anche*
29. *Le cosce*
30. *Le ginocchia*
31. *Le gambe*
32. *Le caviglie*
33. *I piedi*
34. *L'odore*
35. *I rumori*
36. *Sudare*
37. *Arrossire*